

Fog reduces transpiration in tree species of the Canary relict heath-laurel cloud forest (Garajonay National Park, Spain)

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Summary The ecophysiological role of fog in the evergreen heath-laurel ‘laurisilva’ cloud forests of the Canary Islands has not been unequivocally demonstrated, although it is generally assumed that fog water is important for the survival and the distribution of this relict paleoecosystem of the North Atlantic Macaronesian archipelagos. To determine the role of fog in this ecosystem, we combined direct transpiration measurements of heath-laurel tree species, obtained with Granier’s heat dissipation probes, with micrometeorological and artificial fog collection measurements carried out in a 43.7-ha watershed located in the Garajonay National Park (La Gomera, Canary Islands, Spain) over a 10-month period. Median ambient temperature spanned from 7 to 15 °C under foggy conditions whereas higher values, ranging from 9 to 21 °C, were registered during fog-free periods. Additionally, during the periods when fog water was collected, global solar radiation values were linearly related ($r^2 = 0.831$) to those under fog-free conditions, such that there was a $75 \pm 1\%$ reduction in median radiation in response to fog. Fog events greatly reduced median diurnal tree transpiration, with rates about 30 times lower than that during fog-free conditions and approximating the nighttime rates in both species studied (the needle-like leaf *Erica arborea* L. and the broadleaf *Myrica faya* Ait.). This large decrease in transpiration in response to fog was independent of the time of the day, tree size and species and micrometeorological status, both when expressed on a median basis and in cumulative terms for the entire 10-month measuring period. We conclude that, in contrast to the turbulent deposition of fog water droplets on the heath-laurel species, which may be regarded as a localized hydrological phenomenon that is important for high-altitude wind-exposed *E. arborea* trees, the cooler, wetter and shaded microenvironment provided by the cloud immersion belt represents a large-scale effect that is crucial for reducing the transpirational water loss of trees that have profligate water use, such as those of the ‘laurisilva’.

Keywords: climate change, cloud immersion, Granier probes, sap flow, solar radiation reduction, transpiration monitoring.

Introduction

During the climate changes associated with the Quaternary Ice Age, laurel forests present in the Mediterranean basin and northwestern Africa were able to survive in the more favorable climatic conditions of the North Atlantic Macaronesian archipelagos in the Canary Islands, Madeira and Azores (Axelrod 1975, Gioda et al. 1995, Rodríguez-Sánchez and Arroyo 2008). The climatic oscillations during the Pleistocene were buffered in Macaronesia partly because of the oceanic influence, enabling the laurel species in this area to survive (Höllermann 1981). Nowadays the subtropical relic laurel forests growing in the Canary Islands (27–29° N) at northern elevations between 500 and 1400 m asl are dominated by endemic evergreen tree species adapted to a humid Mediterranean-type microclimate (Pérez de Paz 1990). The persistent northeast trade winds in the area are forced to ascend by the steep slopes of the most occidental islands, leading to a resident windward belt of clouds formed by orographic adiabatic cooling, < 900–1500 m asl temperature inversion (Höllermann 1981, Sperling et al. 2004). Consequently, the laurel forests are immersed in fogs almost the entire year, adopting the appearance of a cloud forest, where nonvascular epiphytic species are abundant (Pérez de Paz 1990). It is generally assumed that turbulent deposition of fog water droplets on vegetation is a key mechanism for the survival of the Macaronesian laurel stand. However, the role of fog in the laurel forests has not been demonstrated, because none of the previous studies has confirmed the role of the cloud immersion phenomenon in the Macaronesian elfin cloud forests (Kämmer 1974, Höllermann 1981, Santana 1986, Pérez de Paz 1990, Aboal Viñas 1998). Recently, micrometeorological measurements in a laurel forest watershed of the Garajonay National Park (La Gomera,

Canary Islands) showed that fog collection was only significant ($> 100\%$ rainfall) in localized windward areas of the Park, exposed to the predominant trade winds and supporting a high density of *Erica arborea* L. heath trees (Ritter et al. 2007). Based on a 2-year study, Ritter et al. (2008) suggested that the key role of fog in limiting tree evapotranspiration of laurel cloud forests is through reductions in mean global radiation and mean ambient temperature, with foggy conditions resulting in reductions of up to 58% in mean global radiation and concomitant decreases of 3–6 °C in mean ambient temperature compared with fog-free periods.

Fog is recognized as an important ecological factor in mountain cloud forests around the world (Azevedo and Morgan 1974, Stadtmüller 1987, Cavelier and Goldstein 1989, Schemenauer and Cereceda 1994, Walmsley et al. 1996, Bruijnzeel 2001). However, the ecophysiological consequences of fog may be manifold and in some instances with opposite effects. Dripping water resulting from the turbulent deposition of fog water droplets on vegetation may serve as an additional water source supplementing that of precipitation (Kämmer 1974, Zadroga 1981, Ingraham and Matthews 1988, Bruijnzeel and Proctor 1995, Hutley et al. 1997, Chang et al. 2002, Gutiérrez et al. 2008), although its relative contribution to total soil water may be limited (Beiderwieden et al. 2007, Eugster 2007, Ritter et al. 2008). Additionally, cloud immersion may contribute to sustaining epiphytic mosses and lichens (Jarvis 2000, Chang et al. 2002, Hölscher et al. 2004), rather than vascular plants. Microelements dispersed in fog may provide an additional source of dissolved nutrients, mainly nitrogen, to the forest vegetation (Weathers et al. 1988, 2000, Hafkenscheid 2000, Beiderwieden et al. 2007, Eugster 2007). However, if the magnitude of fog water contribution is small compared with rain, the fog-related soil fertilization gain may be negligible (Beiderwieden et al. 2007). Additionally, the fog may reduce incoming solar radiation (Baynton 1968, Aylett 1985, Cavelier and Mejia 1990) concomitantly with a reduced vapor pressure deficit (VPD) and reduced ambient temperatures, resulting in cooler leaves and thereby lowering the amount of energy available for evapotranspiration and photosynthesis (Gu et al. 2002, Johnson and Smith 2008). Giambelluca and Nullet (1991) reported a 36% attenuation of global radiation by fog in a Hawaiian forest. Eugster et al. (2006) observed a 53% reduction in photosynthetic photon flux (PPF) in dense fog (visibility < 200 m) and a 35% decrease in light fog (visibility = 200–1000 m) in a Puerto Rican elfin cloud forest. In contrast, based on indirect methods such as the eddy covariance techniques and the Bowen ratio method, Beiderwieden et al. (2008) concluded that significant evapotranspiration could occur even during the fog events in a subtropical montane cypress forest. This finding emphasizes the need for more direct measurements of transpiration such as those obtained from sap flow probes or from stable isotope experiments (Burgess and Dawson 2004). Several previous studies measured whole-tree transpiration in the cloud forests with sap flow gauges (Hafkenscheid 1994, Jiménez et al. 1996,

Santiago et al. 2000, Motzer et al. 2005, see also McJannet et al. 2007 for a review). However, only a few studies have simultaneously measured sap flow and fog water. Hutley et al. (1997), working in the Australian subtropical rainforest of southeast Queensland, reported a 40% reduction in tree transpiration rate in response to foggy conditions (1.5 mm on a fog-free day versus 0.9 mm on a foggy day) based on heat pulse measurements carried out in a single emergent tree in a small forest plot. More recently, based on the heat ratio method, Burgess and Dawson (2004) showed that transpiration was suppressed and xylem sap flow reversed in *Sequoia sempervirens* (D. Don) when fog was applied under the greenhouse conditions. Complementing these whole-tree transpiration studies, Johnson and Smith (2008) recently reported a 83–95% reduction in estimated leaf transpiration in *Rhododendron catawbiense* Michx. and *Abies fraseri* (Pursh) Poiret seedlings during cloud immersion compared with clear days, in a 6-day study in the southern Appalachian Mountains.

The objective of this study was to demonstrate, by direct transpiration measurements at the tree level, the effect of fog as a potential contributor of transpiration suppression in *E. arborea* and *Myrica faya* Ait. heath-laurel forest species. We combined data from artificial fog collectors, the micrometeorological instruments and the sap flow gauges to explore the connections between fog and climatic and physiological variables. This study was carried out in the Garajonay National Park, the most extensive and the best conserved laurel ecosystem of the Canary Islands, and which was included in UNESCO's World Heritage List in 1986 (Pérez de Paz 1990).

Materials and methods

Experimental site and micrometeorological measurements

This study was carried out in a 43.7-ha watershed (113°87' N and 278°17' E; 28R zone) within the Garajonay National Park (Canary Islands, Spain) (Figure 1). At high elevations (1200–1300 m asl), the area is exposed to the wind-driven fogs prevailing in the area. Variations in mean annual temperature are small (13 ± 5 °C standard deviation) and precipitation is moderate (< 1100 mm year⁻¹) (Ritter et al. 2008). These conditions have resulted in udic soil water and in a mesic soil temperature regime. Soils are derived from volcanic ash and may be classified as Aluandic Andosols (Fulvudands) (Soil Survey Staff 1999). The vegetation mainly comprises wax myrtle-tree heath ('fayal-brezal') dominated by *E. arborea* coniferous trees of 7–12 m height with abundant epiphytic mosses and lichens. Broad-leaf tree species, such as *Laurus azorica* (Seub.) Franco and *M. faya*, are also present (Golubic 2001). A plot was selected in the area (Figure 1), and is hereafter referred as P1270 after its location at an altitude of 1270 m asl. At P1270, a 15-m scaffolding tower was instrumented to measure micrometeorological variables:

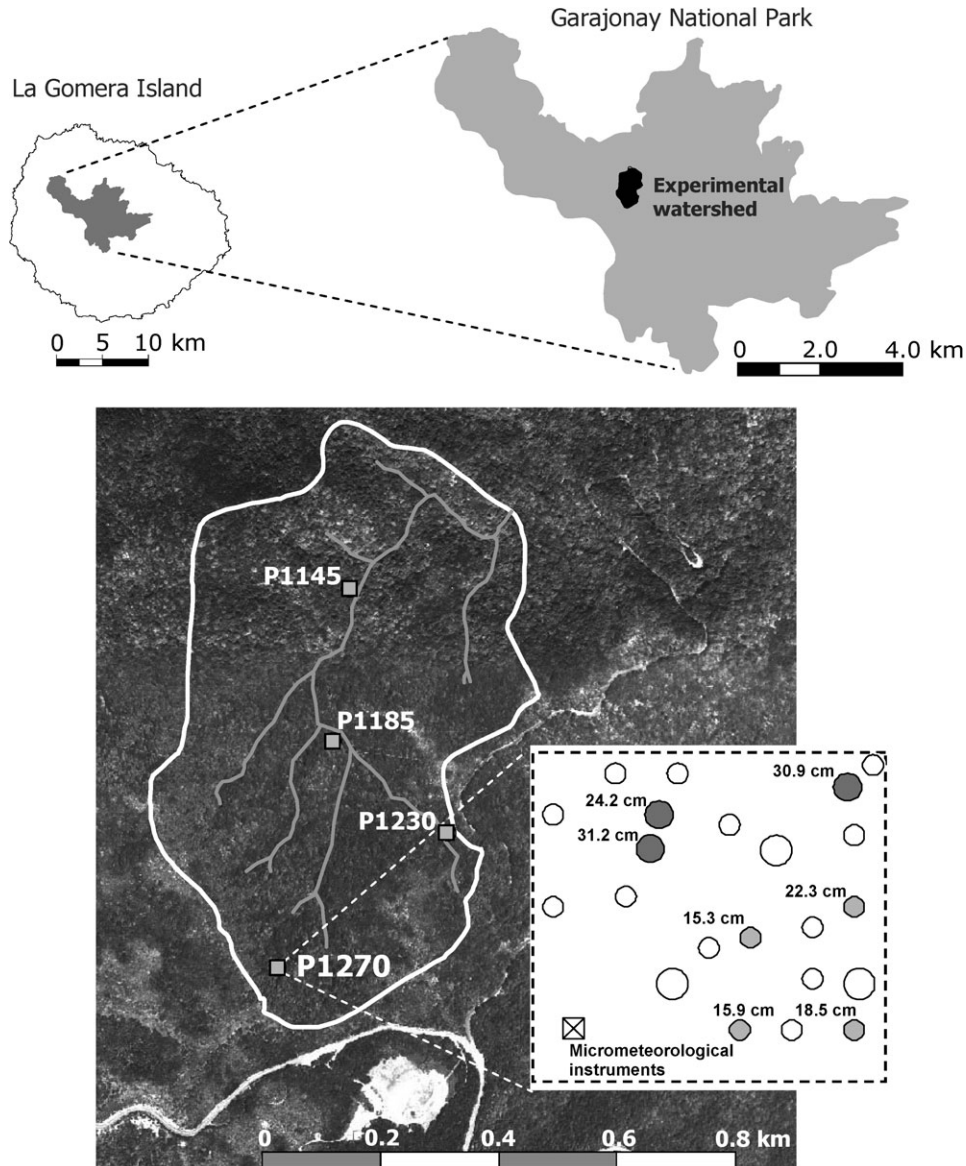


Figure 1. Location of the experimental watershed and the monitoring plots. Numbers in P1270 inset correspond to DBH of trees monitored for sap flow. Light and dark-gray circles represent *E. arborea* and *M. faya* tree individuals, respectively. Open circles denote tree stems that were not measured.

temperature and relative humidity (HMP45C thermohygrometer, Campbell Scientific, Loughborough, UK), global radiation (SKS 1110 pyranometer, Skye Instruments Ltd., Powys, UK), wind velocity (A100R anemometer, Campbell Scientific), wind direction (W200P wind vane, Campbell Scientific), rainfall (Rain-O-Matic Professional 0.2-mm resolution spoon-tipping rain-gauge from Pronamic Bekhøi International Trading Engineering Co., Denmark) and fog water collection above the stand. The fog catcher (QFC) consisted of a 0.5 by 0.5 m screen with a single layer of polypropylene, Raschel-type mesh with 65% shade coefficient and oriented in the NE direction. The QFC was connected to a spoon-tipping Rain-O-Matic rain-gauge to measure frequency and intensity of the collected fog water. In combination with micrometeorological measurements, QFC fog data, when rain was not registered, were used as an indicator of potential fog occurrence.

Quantification of the actual fog water collected by vegetation requires more elaborate methods (Ritter et al. 2008). Fog-free periods at time t were taken as those when the rain-gauge associated with the QFC did not register any pulse during the preceding $t - 30$ min. Additionally, and constrained by the number of available channels of the Combilog data logger (Up GmbH, Cottbus, Germany) used and the limitations of the solar power supply, tree transpiration was continuously monitored with a Granier's sap flow system at P1270 in seven trees (Figure 1) from two of the most common species at the site which exhibit different leaf morphology: needle-like leaf (*E. arborea*) and broad-leaf (*M. faya*). Diameters at breast height (DBH) of the tree species monitored were: 15.3, 15.9, 18.5 and 22.3 cm for *E. arborea* and 24.2, 30.9 and 31.2 cm for *M. faya*.

Three additional plots, denoted as P1145, P1185 and P1230 based on their altitude (m) above sea level, were

selected (Figure 1) for measurements of the same micrometeorological variables as at P1270; i.e., global radiation, wind direction and velocity, relative humidity, air temperature, rainfall and QFC fog water above the stand. Sap flow was not measured at these plots. The objective behind the use of these supplementary micrometeorological data was to verify whether the relations obtained between fog events, transpiration and micrometeorological variables measured at P1270 could be extrapolated to the whole watershed. Data were stored at 15-min intervals as mean values (temperature, relative humidity, radiation, wind direction and velocity) or cumulative totals (rain and fog water) of 3-min periods monitored from March to December 2003.

Sap flow system

Xylem sap flow was estimated by the heat dissipation method of Granier (1985, 1987) with an Up GmbH SFS-2 system. Each SFS-2 setup consisted of two cylindrical needle-like probes (length = 20 mm and diameter = 2 mm). The temperature difference, ΔT ($^{\circ}\text{C}$), between probes was related to sap flux density, (v ; $\text{kg m}^{-2} \text{s}^{-1}$) as (Granier 1985):

$$v = 0.199 \left(\frac{\Delta T_{\max}}{\Delta T} - 1 \right)^{1.231}, \quad (1)$$

where $\Delta T_{\max} \geq \Delta T$ is the temperature difference for zero sap flow, and is approximated by the maximum ΔT at nighttime. Uncertainty may arise in computing ΔT_{\max} from predawn ΔT values, because sap may continue to flow during the nighttime (Goldstein et al. 1998, Sakuratani et al. 1999, Burgess et al. 2000, Regalado and Ritter 2007). However, the nighttime sap flow is expected to be small (Snyder et al. 2003, Ludwig et al. 2006), especially under low VPD foggy conditions (Dawson et al. 2007). Another drawback of the heat dissipation method is the error introduced by natural temperature gradients (Do and Rocheteau 2002). These are expected to have little influence in our case because the trunk measuring area was protected with aluminum deflectors, and the high leaf area index of the laurel forest provides natural shelter from incident solar radiation (Aschan et al. 1994).

Volumetric flux, Q_{SF} , or tree transpiration (g s^{-1}) was obtained by integrating Eq. (1) in the trunk radial direction, r , within the conducting sapwood radial interval (r_{h} and r_{x}) such that:

$$Q_{\text{SF}} = 2\pi \int_{r_{\text{h}}}^{r_{\text{x}}} r v_I dr, \quad (2)$$

where v_I is sap flux density at trunk radial depth I . Polynomial functions are usually fitted to $v_I(r)$ measurements carried out at different I trunk depths, such that the integral in Eq. (2) renders Q_{SF} as v times a multiplication factor, which is a combination of the coefficients in the fitted polynomial and the radii (m) at the heartwood, r_{h} and the

cambium, r_{x} (Čermák et al. 2004). We derived the required polynomials to estimate tree transpiration from Eq. (2) in different individuals of *E. arborea* and *M. faya* after Jiménez et al. (2000).

Statistics

Temperature, global radiation, transpiration and collected fog water were characterized by their median values because, unlike mean values, median values are unaffected by outliers. Accordingly, variability was quantified through the median absolute deviation (MAD), a robust estimator of variability. Given the dataset $X \equiv X_1, X_2, \dots, X_n$, MAD is defined as the median of the absolute values of the residuals from the median of the data:

$$\text{MAD} = \text{median}|X_i - \text{median}(X)|. \quad (3)$$

Data spread around the median were quantified by the standard error of the median (SE_{M}). Because of the non-normal data distributions, SE_{M} was estimated with a nonparametric bootstrapping method (Efron 1981), implemented in Matlab[®] R2007a (The Mathworks, Inc.).

Results

Micrometeorological conditions during the monitoring period

During the monitoring period (March 1, 2003 to December 31, 2003), micrometeorology within the watershed exhibited median \pm MAD air temperature and relative humidity values of 13.2 ± 3.3 $^{\circ}\text{C}$ and $87.8 \pm 12.2\%$, respectively. Precipitation at P1270 was 464 mm with rainfall intensities < 2 mm h^{-1} in 73% of the events. Storm durations of 15 and 30 min represented 74% of the events that were recorded. Fog collection by the QFCs was observed in the four plots throughout the observation period; however, the amounts measured at P1270 were significantly higher (one order of magnitude) than those at lower elevations. Total QFC fog water collected at P1270 was 375 l m^{-2} horizontal area. The distribution of fog water collected by the QFC at each time of the day indicated that QFC fog water occurred mostly during the night until early morning and in late afternoon. Rainfall exhibited seasonality with a rainy period and a dry summer, whereas the QFC fog water was distributed more evenly over the year. The presence of fog (i.e., when the QFC pluviometer stored events) was associated with high relative humidity ($\text{RH} > 93\%$) and lower median ambient temperature compared with fog-free conditions (8 versus 12 $^{\circ}\text{C}$). Although wind speeds < 2 m s^{-1} were frequent at all plots, higher wind speeds values (up to 12 m s^{-1}) were recorded at P1270, with wind blowing mainly from the north and the northeast as a consequence of the predominant direction of the trade winds.

Some examples of fog occurrence and transpiration effects

Qualitative evidence supporting our main hypothesis that fog affects tree transpiration in the Garajonay National Park cloud forest is summarized in Figures 2–4, corresponding to different 10-day periods throughout the measuring campaign. Although the periods shown were not the only times when fog was observed to affect tree transpiration, these snapshots were selected either because they are representative examples of transpiration being affected by the fog conditions at different times of the year or because they illustrate different micrometeorological scenarios. Figures 2–4 each comprise seven panels corresponding to (A) QFC collected fog water, F (l m^{-2}), (B) *M. faya* and (C) *E. arborea* tree transpiration, Q_{SF} (g s^{-1}), (D) global radiation, R_g (kW m^{-2}), (E) VPD (kPa), (F) air temperature, T ($^{\circ}\text{C}$) and (G) wind

velocity, u (m s^{-1}) at P1270. In general, the transpiration trend in all trees was similar in both species investigated independently of tree diameter (cf. panels (B) and (C)). In Figure 2 (March 5–14, 2003), a fairly regular pattern of tree transpiration during a week when no fog was detected was interrupted by a 3-day period of almost constant fog during which sap flow nearly ceased. Figure 3 (May 9–19, 2003) provides an example where fog greatly affected tree transpiration for several days resulting in almost no sap flow, followed by three non-foggy days during which tree gas exchange recovered, and then the foggy conditions resumed again, but because most of these fog events occurred at nighttime, their effect on Q_{SF} was less prominent. Figure 4 (October 6–16, 2003) shows that although only low quantities of QFC fog water were collected (Figure 4A), probably because of the lower wind velocity registered during this period

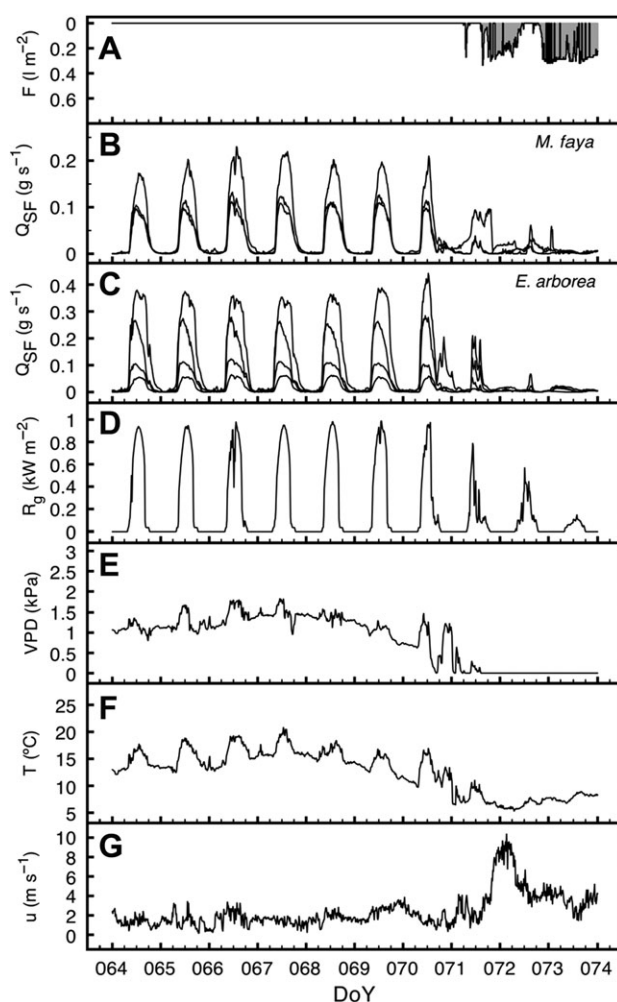


Figure 2. The 10-day period (March 5–14, 2003) illustrating the effects of fog on tree transpiration and concomitant micrometeorological conditions measured at P1270. (A) QFC collected fog water (F , l m^{-2}), (B) *M. faya* and (C) *E. arborea* tree transpiration (Q_{SF} , g s^{-1}), (D) global radiation (R_g , kW m^{-2}), (E) VPD (kPa), (F) air temperature (T , $^{\circ}\text{C}$) and (G) wind velocity (u , m s^{-1}).

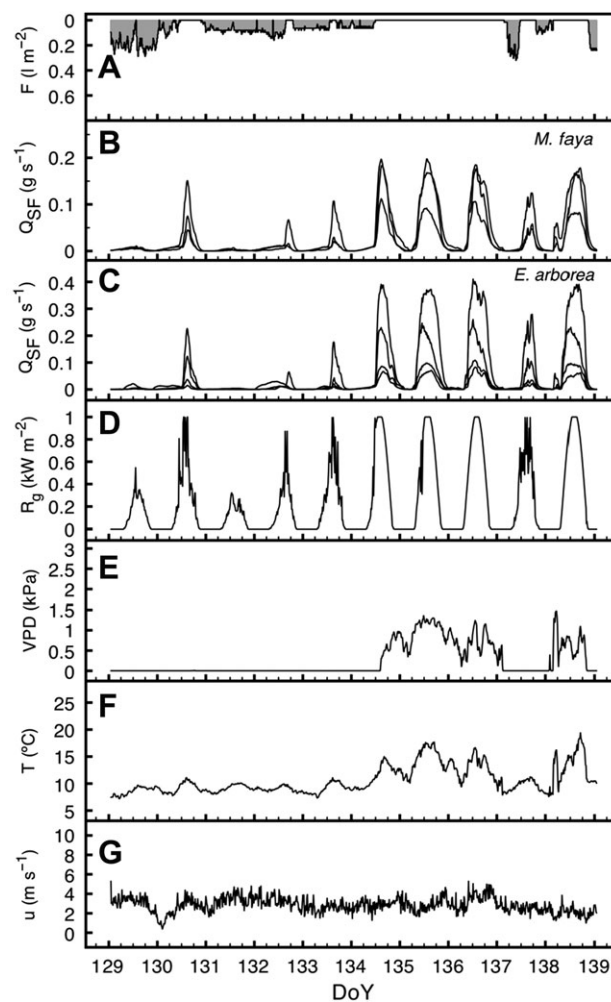


Figure 3. The 10-day period (May 9–June 19, 2003) illustrating the effects of fog on tree transpiration and concomitant micrometeorological conditions measured at P1270. (A) QFC collected fog water (F , l m^{-2}), (B) *M. faya* and (C) *E. arborea* tree transpiration (Q_{SF} , g s^{-1}), (D) global radiation (R_g , kW m^{-2}), (E) VPD (kPa), (F) air temperature (T , $^{\circ}\text{C}$) and (G) wind velocity (u , m s^{-1}).

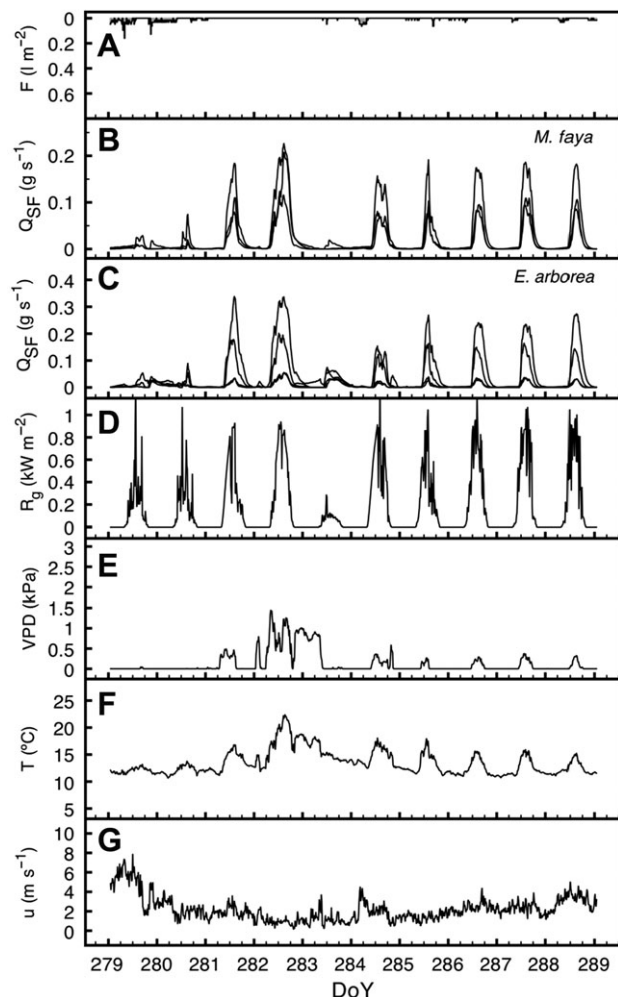


Figure 4. The 10-day period (October 6–16, 2003) illustrating the effects of fog on tree transpiration and concomitant micrometeorological conditions measured at P1270. (A) QFC collected fog water (F , l m^{-2}), (B) *M. faya* and (C) *E. arborea* tree transpiration (Q_{SF} , g s^{-1}), (D) global radiation (R_g , kW m^{-2}), (E) VPD (kPa), (F) air temperature (T , $^{\circ}\text{C}$) and (G) wind velocity (u , m s^{-1}).

(Figure 4G), these conditions were sufficient to affect tree transpiration (Figure 4B). The main result that can be derived from Figures 2–4 is that, during fog episodes, transpiration was greatly reduced in both tree species. When the QFC fog water was not detected, tree volumetric flux exhibited the usual bell-shaped Q_{SF} pattern, rising from low morning values to a maximum plateau around midday and then decreasing to near zero at nighttime. As expected, this pattern was also observed for solar radiation (panel D) in Figures 2–4). However, this trend was modified when fog appeared. Generally, relative humidity rose close to 100% saturation, i.e., $\text{VPD} \approx 0$ (Figures 2E–4E) and air temperature decreased during periods of QFC collected fog (Figures 2F–4F). Wind velocity was also higher when fog was captured, although panels (G) appear noisier, probably because the 3-min sampling period was insufficient for this variable.

Fog-free and foggy conditions

The examples discussed in the previous section illustrate the effects of fog in qualitative terms. We also conducted a more thorough analysis to verify whether the effect of fog on tree transpiration was consistent throughout the entire measuring period from March to December 2003. The approach we adopted was as follows. Because fog may be more frequent at certain times of the day and also because some meteorological variables that may affect transpiration (e.g., radiation and temperature) vary during the day, comparing foggy and fog-free conditions without taking into account the time of the day could lead to bias or even erroneous conclusions. Therefore, we compared data for the foggy versus the fog-free conditions on an hourly basis. Figure 5 shows the cumulative hourly transpiration from March to December 2003, for both study species at P1270. We observed a large reduction in total tree transpiration in response to fog (note the different y -axes in Figure 5) for both *E. arborea* and *M. faya*. When transpiration is compared as median values instead of cumulative totals, for every time of the day when fog is present median Q_{SF} is reduced about 30-fold in both *M. faya* and *E. arborea* and for trees differing in DBH (Figure 6). This finding implies a linear trend ($r^2 = 0.665$), such that the median diurnal transpiration rate under foggy conditions is proportional to Q_{SF} when QFC fog was not collected. Hence, the reduction in tree transpiration associated with fog was independent of the time of the day (i.e., radiation), tree species studied (either *M. faya* or *E. arborea*) and the tree size investigated. Furthermore, the enveloping curve of daily median values of Q_{SF} versus F showed that transpiration is drastically reduced as the amount of QFC collected fog water increases (Figure 7), probably because, under similar wind exposure and speed conditions, a higher F implies a higher fog liquid water content and therefore a greater reduction in radiation (Eugster et al. 2006, Ritter et al. 2008).

In an attempt to identify the mechanisms underlying the large reduction in stand transpiration in response to fog, we analyzed the variations in the hourly micrometeorological variables by comparing foggy and fog-free conditions for the four plots, because it is widely known that stomatal conductance is mainly affected by temperature, radiation and VPD. The strongest interrelations were found with radiation and air temperature, because air was almost fully saturated ($\text{RH} > 93\%$) under foggy conditions, and wind velocity (both mean and maximum) did not span a wide range. Hence, global radiation and air temperature are the only micrometeorological variables considered here. We already illustrated in Figures 2–4 some examples showing the attenuation in radiation and the concomitant ambient temperature decrease associated with fog at P1270. Figure 8A shows the hourly accumulated fog at the four plots from March until December 2003. The QFC collected fog at P1270 was significantly greater than that at the other stations, because of its higher altitude and greater exposure

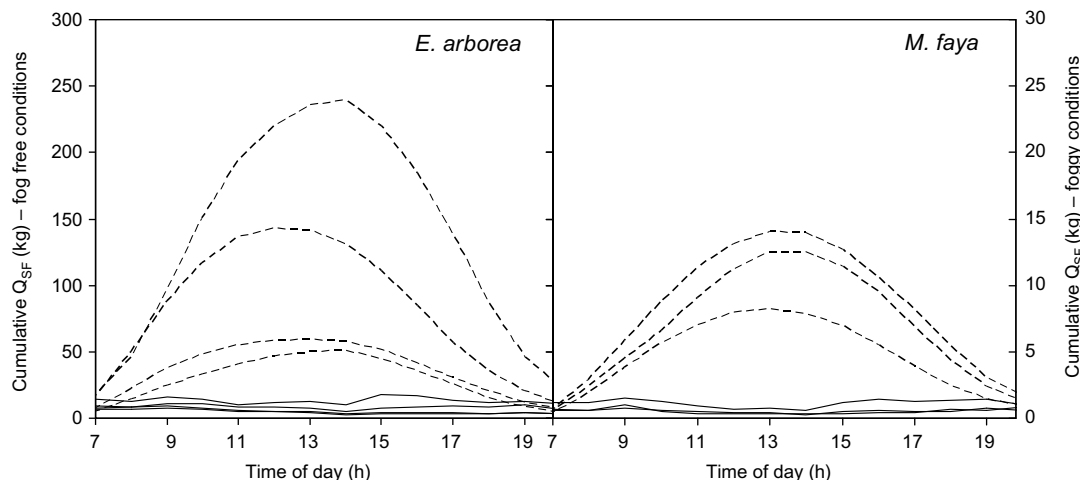


Figure 5. Diurnal trends in cumulative tree transpiration (Q_{SF} , kg) under foggy (solid line and secondary right axis) and fog-free (dashed-line and main left axis) conditions during the period March 1, 2003 to December 31, 2003 at P1270 in heath-laurel tree species differing in DBH.

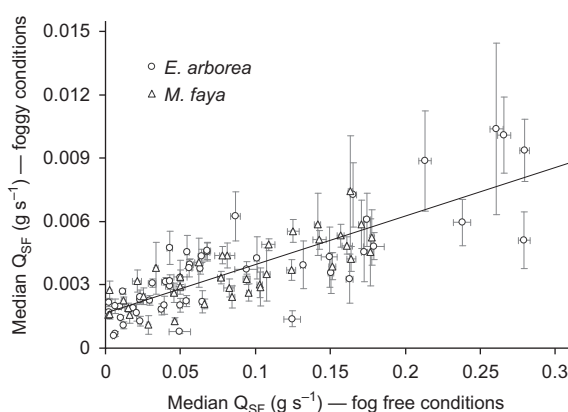


Figure 6. Diurnal hourly median tree transpiration (Q_{SF} , $g\ s^{-1}$) under foggy versus fog-free conditions during the period March 1, 2003 to December 31, 2003 at P1270 for heath-laurel tree species differing in DBH: *E. arborea* (circles) and *M. faya* (triangles). Bars represent the median standard error, SE_M . The best fitting (solid) line for the whole dataset is shown ($r^2 = 0.665$).

to the predominant trade winds. Fog water collection occurred mostly at nighttime, during early morning and in late afternoon (Figure 8A). The higher ambient temperature at midday (Figure 8B) has been proposed as an explanation for the evaporation of droplets leading to the disappearance of fog at this time of the day (Eugster et al. 2006). Although most fog was collected at the highest altitude ($375\ l\ m^{-2}$ at P1270 versus $36\ l\ m^{-2}$, $13\ l\ m^{-2}$ and $12\ l\ m^{-2}$ at P1230, P1185 and P1145, respectively), the effects of fog on related micrometeorological variables was similar at the lower sites (Figures 8B–D). Figure 8B shows the hourly temperature reduction associated with the presence of fog. The MAD of air temperature spanned from 9 to 15 °C under foggy conditions, with a higher MAD range registered during

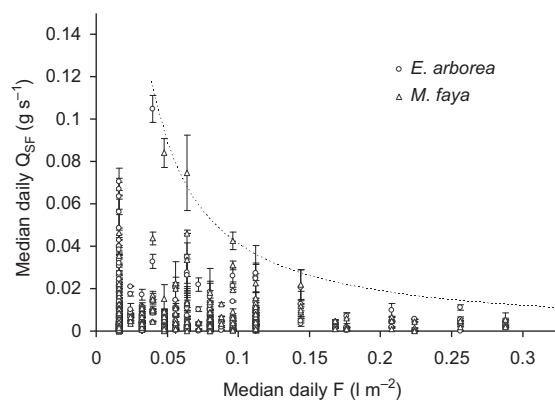


Figure 7. Diurnal daily medians of tree transpiration (Q_{SF} , $g\ s^{-1}$) and QFC collected fog water, F , during foggy conditions at P1270 for heath-laurel tree species differing in DBH: *E. arborea* (circles) and *M. faya* (triangles). Bars represent the median standard error, SE_M , of daily Q_{SF} values. The dotted line corresponds to the enveloping curve.

fog-free periods (14 to 21 °C). Figure 8C illustrates the attenuation of median radiation by fog at the four plots. Figure 8D shows that the median hourly global radiation when fog was collected was linearly related to solar radiation under fog-free conditions. A decrease of $75 \pm 1\%$ ($r^2 = 0.831$) in median radiation in response to fog occurred at the four plots independently of the measuring altitude, indicating that most short-wave radiation is already reflected above 1270 m asl.

Discussion

Heath-laurel forests are frequently immersed in clouds, which provide a moist microenvironment suitable for water

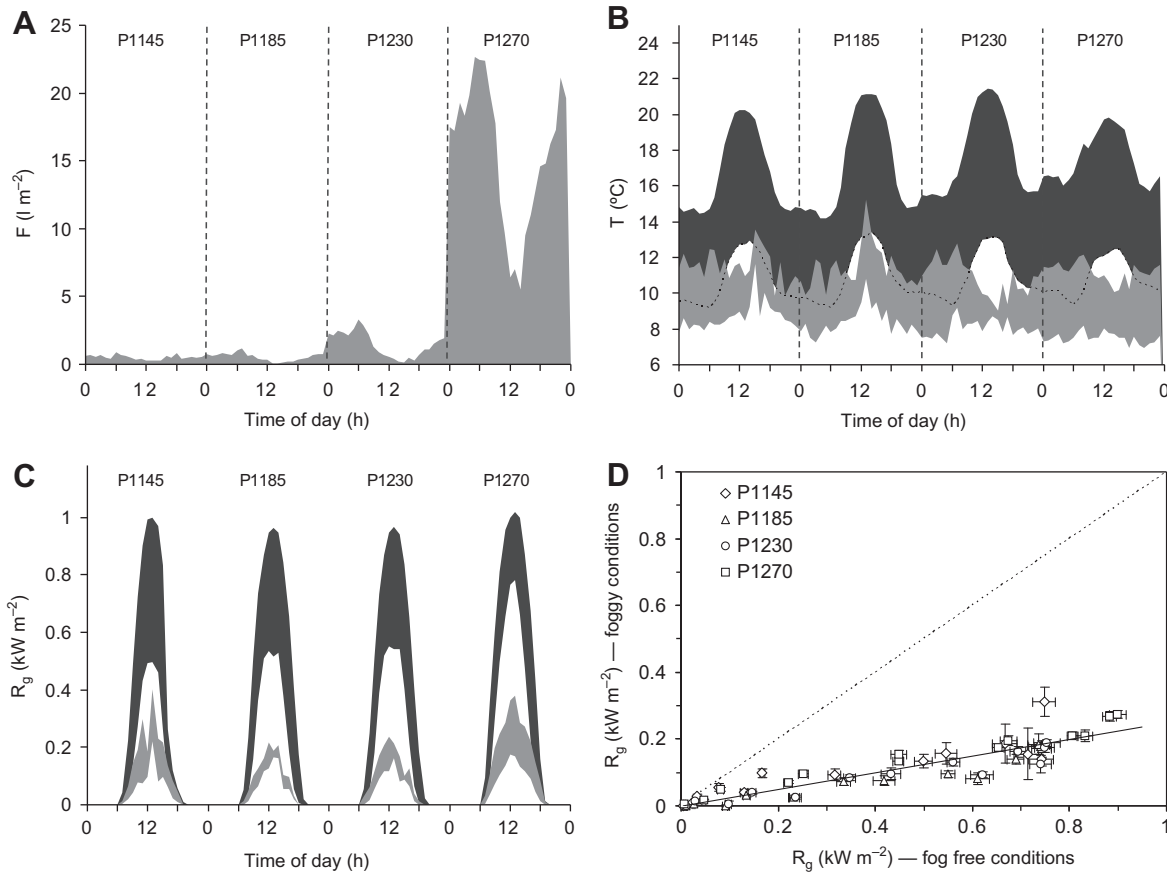


Figure 8. Concomitant micrometeorological conditions for foggy and fog-free QFC periods at the four plots during the period March 1, 2003 to December 31, 2003. (A) daily trend of cumulative fog collected by the QFCs; MAD ranges of (B) temperature and (C) global radiation daily evolution under foggy (gray band) and fog-free (black band) conditions, (D) hourly median \pm SE_M values of global solar radiation during foggy versus fog-free conditions (the dotted line indicates the 1:1 bisection, and the solid line is the best fit ($r^2 = 0.831$) for the whole four-plot dataset.

collection by the turbulent deposition of fog water droplets on tree leaves. This supplementary water source has previously been shown to be restricted to localized wind-exposed areas of the Garajonay National Park. We have now identified another larger-scale effect of the cloud immersion phenomenon and demonstrated that tree transpiration is reduced as a consequence of the environmental conditions prevailing during the cloud immersion. We arrived at this conclusion after monitoring transpiration in individual trees by direct sap flow measurements. Alternative indirect methods, such as the Penman–Monteith equation, require assumptions and determination of ad hoc parameters not readily available for all species that are investigated, and thus in most cases provide only the potential transpiration estimates. Additionally, under humid conditions, the Penman–Monteith model may be rather sensitive to the VPD and the net irradiance calculation methods used (Yoder et al. 2005). Equally, water budget techniques suffer from important drawbacks because they rely on accurate measurements of all components of the hydrological balance to provide a consistent transpiration estimate (Bruijnzeel 2001), requiring heavy instrumentation because of the large spatial heteroge-

neity within the forest stand (Lloyd et al. 1988, Holwerda et al. 2006) and the many components (throughfall, stem flow, rainfall, occult precipitation, canopy storage, evaporation, etc.) that may need to be measured. Additionally, when several tree species cohabit within the same ecosystem the water balance approach does not easily permit distinction of the contribution of each species to the total forest transpiration. Estimates derived from water budget calculations suggest a reduced transpiration in tropical montane cloud forests ($250\text{--}300\text{ mm year}^{-1}$) compared with lowland forests (Bruijnzeel and Proctor 1995), although much higher values ($500\text{--}850\text{ mm year}^{-1}$) for the former forest type have recently been reported (Bruijnzeel 2001).

Hourly median transpiration was reduced about 30-fold in response to the foggy conditions in both study species, independently of their leaf morphology (broadleaf or needle-like). In contrast, the broad leaves of *M. faya* are not well suited for fog collection, whereas the needle-like leaves of *E. arborea*, which are cylindrical in form, are highly efficient in capturing fog. Thus, fog droplet formation is unlikely to occur on the leaves of *M. faya*, whereas fog droplets form readily on the needle-like leaves of *E. arborea* (Ritter

et al. 2008). This suggests that the effect of fog in reducing transpiration is more likely related to the concomitant meteorological conditions (lower radiation, temperature and VPD) than to a saturation of the boundary layer by merged water droplets sitting on the leaf surface. Nevertheless, fog moistening of leaf surfaces may reduce photosynthetic carbon gain (Letts and Mulligan 2005) because of the low diffusivity of carbon dioxide in water ($< 10^4$ times in air), such that trees may have developed hydrophobic epicuticular structures that reduce wetness favoring water dripping to the soil (Holder 2007), thus increasing incident sunlight by the lensing effect of the water droplets beading on the leaf surface (Brewer et al. 1991). Merged water droplets sitting on repellent leaf surfaces may reduce transpiration and increase carbon gain (Smith and McClean 1989).

We obtained evidence that the effect of fog on tree transpiration is related to an associated 75% reduction in median global radiation that is accompanied by decreases in both the median ambient temperature range (from 9–21 to 7–15 °C) and the VPD, across an altitudinal gradient from 1270 to 1145 m asl. The attenuation of incident photon flux above the canopy may be further reinforced in the understory (Johnson and Smith 2006) because of the high leaf area index of the laurel forest. Previous studies have reported that only 2% of photosynthetically active radiation reaches the laurel forest ground (Aschan et al. 1994). Laurel species are highly shade tolerant (Morales et al. 1996), and may thus benefit from cool, moist foggy conditions to offset the higher rates of water loss that occur when fog is absent. As fog is less frequent at midday and global solar radiation during the dry summer season may be considerable ($> 1 \text{ kW m}^{-2}$) at the latitudes where the Canary Islands are situated (27–29° N), early morning and late noon foggy periods may compensate for the high transpiration demand at midday. Equally, fog may be important in suppressing tree water loss both in the dark and during daytime (Burgess and Dawson 2004). Burgess and Dawson (2004) observed that transpiration was suppressed in response to artificial fog application in redwood (*S. sempervirens*), a tree species restricted to fog-immersed regions of the Californian and the Oregon coastlines and which exhibits poor stomatal control – a characteristic of plant species that are subject to mild or short-duration drought periods, including most laurel species (Zohlen et al. 1995, González-Rodríguez et al. 2001, 2002a, 2002b). Thus, cloud immersion may be crucial in compensating for the prodigal water use of tree species with poor stomatal control.

The laurel forest is a paleoecosystem relict of the ancient laurel communities existing in the Neogene period (Höller-mann 1981). The Neogene period was characterized by precipitation events that were concentrated in the warm season, which sharply contrasts with the contemporary dry summer conditions presently experienced by the laurel forests of the Canary Islands, and also by the coastal Californian redwood forests. The cloud belt of the Canary Islands is most

persistent during the dry summer months, when the temperature inversion is more stable than in winter because of the dominating effect of the Azores anticyclone (Fernandopulle 1976). In summer, the cloud immersion layer descends and is at its shallowest, whereas in autumn and in winter both the upper limit and the thickness of the humid cloud belt increases (Kämmer 1974). Thus, the current cloud immersion pattern prevailing at northern mid elevations in the Canary Islands may have supplemented such low summer pluviometry, permitting the establishment of stands with high demands for water. Additionally, light quality under cloud immersion may be more photosynthetically appropriate (i.e., more homogeneously distributed, with greater penetrability into the understory, reduced irradiance during sunlight flecks and more photosynthetically optimal for carbon capture) than direct-beam sunlight (Johnson and Smith 2006), and laurel species may take advantage of this light environment to maximize carbon capture during the foggy periods. González-Rodríguez et al. (2002b) reported that, in *Persea indica* (L.) K. Spreng laurel trees, overall transpiration was lower and carbon assimilation rate highest during a cloudy day with PPF mostly $< 1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ than during the two cloudless days with diurnal PPF $> 1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Similar behavior was observed in *L. azorica* and *M. faya* (González-Rodríguez 1998). Although González-Rodríguez et al. (2002b) did not monitor fog capture, the low VPD, diurnal course of attenuated light and lower leaf temperature during the cloudy day may be comparable with the cloud immersion conditions.

These effects of fog on transpiration that we observed do not preclude the possibility of other associated phenomena not investigated in our study such as water uptake by foliar absorption, for e.g. repair of cavitated conduits in *E. arborea* (Tognetti et al. 2001) and other laurel species (Čermák et al. 2002). For example, Breazeale et al. (1950) observed cuticular absorption of water from a saturated atmosphere by leaves of tomato plants and Burgess and Dawson (2004) reported that fog droplets deposited on leaves of *S. sempervirens* trees may be incorporated by the foliar absorption.

Climate change simulations predict a downward shift of the cloud base in the North Atlantic area by 2100 (Sperling et al. 2004), thus exposing the upper part of the heath-laurel forest stand to higher radiation and drier and warmer conditions. A downward altitudinal shift of the heath-laurel stand (Rodríguez-Sánchez and Arroyo 2008) may not necessarily follow, however, because of competing land-use practices and population pressure at lower altitudes (Fernández-Palacios and Martín Esquivel 2001, Sperling et al. 2004). In the tropical counterpart of the subtropical heath-laurel forests, changes in the cloud base height (upper-shift) have been previously related to population declines in the montane cloud forests (Still et al. 1999, Pounds et al. 1999). We found that median tree transpiration was increased about 30-fold under fog-free conditions compared with foggy periods, suggesting that a climatic change would pose a significant threat to the biodiversity

of the heath-laurel stand, by imposing a higher transpirational demand on the tree species and thus potentially affecting the forest hydrological cycle.

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References

- Aboal Viñas, J.R. 1998. Los flujos netos hidrológicos y químicos asociados de un bosque de laurisilva en Tenerife. Ph.D. Thesis. University of La Laguna, La Laguna, Spain, 184 p. Available at <http://dialnet.unirioja.es/servlet/tesis?codigo=637> (last accessed June 27, 2008) (in Spanish).
- Aschan, G., M.S. Jiménez, D. Morales and R. Lösch. 1994. Aspectos microclimáticos de un bosque de laurisilva en Tenerife. *Vieraea* 23:125–141 (in Spanish).
- Axelrod, D.I. 1975. Evolution and biogeography of Madrean-Tethyan sclerophyll vegetation. *Ann. Mo. Bot. Gard.* 62: 280–334.
- Aylett, G.P. 1985. Irradiance interception, leaf conductance and photosynthesis in Jamaican upper montane rain forest trees. *Photosynthetica* 19:323–337.
- Azevedo, J. and D.L. Morgan. 1974. Fog precipitation in coastal California forests. *Ecology* 55:1135–1141.
- Baynton, H.W. 1968. The ecology of an elfin cloud forest in Puerto Rico, 2: the microclimate of Pico del Oeste. *J. Arnold Arboret.* 49:419–430.
- Beiderwieden, E., A. Schmidt, Y.-J. Hsia, S.-C. Chang, T. Wrzesinsky and O. Klemm. 2007. Nutrient input through occult and wet deposition into a subtropical montane cloud forest. *Water Air Soil Pollut.* 186:273–288.
- Beiderwieden, E., V. Wolff, Y.-J. Hsia and O. Klemm. 2008. It goes both ways: measurements of simultaneous evapotranspiration and fog droplet deposition at a montane cloud forest. *Hydrol. Process* 22:4181–4189.
- Breazeale, E.L., W.T. McGeorge and J.F. Breazeale. 1950. Moisture absorption by plants from an atmosphere of high humidity. *Plant Physiol.* 25:413–419.
- Brewer, C.A., W.K. Smith and T.C. Vogelmann. 1991. Functional interaction between leaf trichomes, leaf wettability and the optical properties of water droplets. *Plant Cell Environ.* 14:955–962.
- Bruijnzeel, L.A. 2001. Hydrology of tropical montane cloud forests: a reassessment. *Land Use Water Res.* 1:1.1–1.18.
- Bruijnzeel, L.A. and J. Proctor. 1995. Hydrology and biochemistry of tropical montane cloud forests: What do we really know? *In* Tropical Montane Cloud Forests. Eds. L.S. Hamilton, J.O. Juvik and F.N. Scatena. Ecological Studies, Vol. 110. Springer-Verlag, New York, pp 38–78.
- Burgess, S.S.O. and T.E. Dawson. 2004. The contribution of fog to the water relations of *Sequoia sempervirens* (D. Don): foliar uptake and prevention of dehydration. *Plant Cell Environ.* 27:1023–1034.
- Burgess, S.S.O., M.A. Adams and T.M. Bleby. 2000. Measurements of sap flow in roots of woody plants: a commentary. *Tree Physiol.* 20:909–913.
- Cavelier, J. and G. Goldstein. 1989. Mist and fog interception in elfin cloud forests in Colombia and Venezuela. *J. Trop. Ecol.* 5:309–322.
- Cavelier, J. and C.A. Mejia. 1990. Climatic factors and tree stature in the elfin cloud forest of Serrania-de-Macuire, Colombia. *Agric. Forest Meteorol.* 53:105–123.
- Čermák, J., M.S. Jiménez, A.M. González-Rodríguez and D. Morales. 2002. Laurel forests in Tenerife, Canary Islands. II. Efficiency of the water conducting system in *Laurus azorica* trees. *Trees* 16:538–546.
- Čermák, J., J. Kučera and N. Nadezhdina. 2004. Sap flow measurements with some thermodynamic methods, flow integration within trees and scaling up from sample trees to entire forest stands. *Trees* 18:529–546.
- Chang, S.-C., I.-L. Lai and J.-T. Wu. 2002. Estimation of fog deposition on epiphytic bryophytes in a subtropical montane forest ecosystem in northeastern Taiwan. *Atmos. Res.* 64: 159–167.
- Dawson, T.E., S.S.O. Burgess, K.P. Tu, R.S. Oliveira, L.S. Santiago, J.B. Fisher, K.A. Simonin and A.R. Ambrose. 2007. Nighttime transpiration in woody plants from contrasting ecosystems. *Tree Physiol.* 27:561–575.
- Do, F. and A. Rocheteau. 2002. Influence of natural temperature gradients on measurements of xylem sap flow with thermal dissipation probes. 1. Field observations and possible remedies. *Tree Physiol.* 22:641–648.
- Efron, B. 1981. Nonparametric estimates of standard error: The jackknife, the bootstrap and other methods. *Biometrika* 68:589–599.
- Eugster, W. 2007. The relevance of fog for the vegetation: is it the water or the nutrients that matter? *In* Proc. Fourth International Conference on Fog, Fog Collection and Dew. Eds. A. Biggs and P. Cereceda. La Serena, Chile, pp 359–362.
- Eugster, W., R. Burkard, F. Holwerda, F.N. Scatena and L.A. Bruijnzeel. 2006. Characteristics of fog and fogwater fluxes in a Puerto Rican elfin cloud forest. *Agric. Forest Meteorol.* 139:288–306.
- Fernández-Palacios, J.M. and J.L. Martín Esquivel. 2001. Naturaleza de las Islas Canarias: Ecología y Conservación. Publicaciones Turquesa S.L, Santa Cruz de Tenerife.
- Fernandopulle, D. 1976. Climatic characteristics of the Canary Islands. *In* Biogeography and Ecology of the Canary Islands. Ed. G. Kunkel. Junk Publisher, The Hague, pp 185–207.
- Giambelluca, T.W. and D. Nullet. 1991. Influence of the trade-wind inversion on the climate of a leeward mountain slope in Hawaii. *Clim. Res.* 1:207–216.
- Gioda, A., J. Maley, R.E. Guasp and A.A. Baladón. 1995. Some low elevation fog forests of dry environments: applications to African paleoenvironments. *In* Tropical Montane Cloud Forests. Eds. L.S. Hamilton, J.O. Juvik and F.N. Scatena. Ecological Studies, Vol. 110. Springer-Verlag, New York, pp 156–164.
- Goldstein, G.G., J.L. Andrade, F.C. Meinzer, N.M. Holbrook, J. Cavelier, P. Jackson and A. Celis. 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant Cell Environ.* 21:397–406.
- Golubic, I. 2001. Vegetationskundliche Analyse von Lorbeerwald-und ähnlichen Beständen im Rahmen einer Untersuchung des Landschaftswasserhaushalts im Garajonay National

- Park La Gomera (Kanarische Inseln). Diploma Thesis. Essen University GH, Germany (in German).
- González-Rodríguez, A.M. 1998. Caracterización fotosintética de árboles de la Laurisilva canaria (*Laurus azorica*, *Persea indica* y *Myrica faya*). Ph.D. Thesis. University of La Laguna, Spain, 268 p. (in Spanish). Available at <http://dialnet.unirioja.es/servlet/oaiites?codigo=811> (last accessed June 27, 2008).
- González-Rodríguez, A.M., D. Morales and M.S. Jiménez. 2001. Gas exchange characteristics of a Canarian laurel forest tree species (*Laurus azorica*) in relation to environmental conditions and leaf canopy position. *Tree Physiol.* 21:1039–1045.
- González-Rodríguez, A.M., D. Morales and M.S. Jiménez. 2002a. Leaf gas exchange characteristics in relation to canopy position of *Myrica faya* in its native environment (Tenerife, Canary Islands). *Plant Biol.* 4:576–583.
- González-Rodríguez, A.M., D. Morales and M.S. Jiménez. 2002b. Leaf gas exchange characteristics of a Canarian laurel forest tree species [*Persea indica* (L.) K. Spreng.] under natural conditions. *J. Plant Physiol.* 159:695–704.
- Granier, A. 1985. Une nouvelle méthode pour la mesure des flux de sève dans le tronc des arbres. *Ann. Sci. For.* 42:193–200.
- Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol.* 3:309–319.
- Gu, L.H., D. Baldocchi, S.D. Verma, T.A. Black, T. Vesala, E.M. Falge and P.R. Dwyer. 2002. Advantages of diffuse radiation for terrestrial ecosystem productivity. *J. Geophys. Res.* 107: doi:10.1029/2001JD001242.
- Gutiérrez, A.G., O. Barbosa, D.A. Christie, E.K. Del-Val, H.A. Ewing, C.G. Jones, P.A. Marquet, K.C. Weathers and J.J. Armesto. 2008. Regeneration patterns and persistence of the fog dependent Fray Jorge forest in semiarid Chile during the past two centuries. *Global Change Biol.* 14:161–176.
- Hafkenscheid, R.L. 1994. Hydrological observations in rain forests of contrasting stature on Gunung Rakata (Krakatau), Indonesia, with special reference to the 'Massenerhebung' effect. M.Sc. Thesis. Vrije Universiteit, Amsterdam, The Netherlands.
- Hafkenscheid, R.L.L.J. 2000. Hydrology and biogeochemistry of montane rain forests of contrasting stature in the Blue Mountains of Jamaica. Ph.D. Thesis. Vrije Universiteit, Amsterdam, The Netherlands, 302 p.
- Holder, C.D. 2007. Leaf water repellency of species in Guatemala and Colorado (USA) and its significance to forest hydrology studies. *J. Hydrol.* 336:147–154.
- Höllermann, P. 1981. Microenvironmental studies in the laurel forest of the Canary Islands. *Mt. Res. Dev.* 3(4):193–207.
- Hölscher, D., L. Köhler, A.I.J.M. van Dijk and L.A. Bruinjeel. 2004. The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. *J. Hydrol.* 292:308–322.
- Holwerda, F., F.N. Scatena and L.A. Bruinjeel. 2006. Throughfall in a Puerto Rican lower montane rain forest: a comparison of sampling strategies. *J. Hydrol.* 327:592–602.
- Hutley, L.B., D. Doley, D.J. Yates and A. Boonsaner. 1997. Water balance of an Australian subtropical rainforest at altitude: the ecological and physiological significance of intercepted cloud and fog. *Aust. J. Bot.* 45:311–329.
- Ingraham, N.L. and R.A. Matthews. 1988. Fog drip as a source of groundwater recharge in northern Kenya. *Water Resour. Res.* 24:1406–1410.
- Jarvis, A. 2000. Measuring and modelling the impact of land-use change in tropical hillsides: the role of cloud interception to epiphytes. *Adv. Environ. Monit. Model.* 1:118–148.
- Jiménez, M.S., J. Čermák, J. Kucera and D. Morales. 1996. Laurel forests in Tenerife, Canary Islands: the annual course of sap flow in *Laurus* trees and stand. *J. Hydrol.* 183:307–321.
- Jiménez, M.S., N. Nadezhdina, J. Čermák and D. Morales. 2000. Radial variation in sap flow in five laurel forest tree species in Tenerife, Canary Islands. *Tree Physiol.* 20: 1149–1156.
- Johnson, D.M. and W.K. Smith. 2006. Low clouds and cloud immersion enhance photosynthesis in understory species of a southern Appalachian spruce-fir forest (USA). *Am. J. Bot.* 93:1625–1632.
- Johnson, D.M. and W.K. Smith. 2008. Cloud immersion alters microclimate, photosynthesis and water relations in *Rhododendron catawbiense* and *Abies fraseri* seedlings in the southern Appalachian Mountains, USA. *Tree Physiol.* 28:385–392.
- Kämmer, F. 1974. Klima und Vegetation auf Tenerife, besonders in Hinblick auf den Nebelniederschlag. *Scripta Geobot.* 7:1–78.
- Letts, M.G. and M. Mulligan. 2005. The impact of light quality and leaf wetness on photosynthesis in north-west Andean tropical montane cloud forest. *J. Trop. Ecol.* 21:549–557.
- Lloyd, C.R., J.H.C. Gash, W.J.U. Shuttleworth, F. Marques and F. De O. 1988. The measurement and modeling of rainfall interception by Amazonian rain forest. *Agric. Forest Meteorol.* 43:277–294.
- Ludwig, F., R.A. Jewitt and L.A. Donovan. 2006. Nutrient and water addition effects on day- and nighttime conductance and transpiration in a C3 desert annual. *Oecologia* doi:10.1007/s00442-006-0367-6.
- McJannet, D., P. Fitch, M. Disher and J. Wallace. 2007. Measurements of transpiration in four tropical rainforest types of north Queensland, Australia. *Hydrol. Process.* 21:3549–3564.
- Morales, D., A.M. González-Rodríguez, J. Čermák and M.S. Jiménez. 1996. Laurel forest in Tenerife, Canary Islands: the vertical profiles of leaf characteristics. *Phyton* 36:251–263.
- Motzer, T., N. Munz, M. Küppers, D. Schmitt and D. Anhufo. 2005. Stomatal conductance, transpiration and sap flow of tropical montane rain forest trees in the southern Ecuadorian Andes. *Tree Physiol.* 25:1283–1293.
- Pérez de Paz, P.L. 1990. Parque Nacional de Garajonay, Patrimonio Mundial. Excmo. Cabildo Insular de La Gomera Instituto Nacional para la Conservación de la Naturaleza, Spain (In Spanish).
- Pounds, J.A., M.P.L. Fodgen and J.H. Campbell. 1999. Biological response to climatic change on a tropical mountain. *Nature* 398:411–415.
- Regalado, C.M. and A. Ritter. 2007. An alternative method to estimate zero flow temperature differences for Granier's thermal dissipation technique. *Tree Physiol.* 27:1093–1102.
- Ritter, A., C.M. Regalado and G. Aschan. 2007. An impactation model for estimating fog water collection in a subtropical laurel cloud forest of the Garajonay National Park. *In Proc. Fourth International Conference on Fog, Fog Collection and Dew.* Eds. A. Biggs and P. Cereceda. La Serena, Chile, pp 355–358. Available at <http://www.icia.es/icia/download/suelosyriegos/355-358.pdf> (last accessed June 27, 2008).
- Ritter, A., C.M. Regalado and G. Aschan. 2008. Fog water collection in a subtropical elfin laurel forest of the Garajonay National Park (Canary Islands): a combined approach using

- artificial fog catchers and a physically based model. *J. Hydrometeorol.* 9:920–935.
- Rodríguez-Sánchez, F. and J. Arroyo. 2008. Reconstructing the demise of Tethyan plants: climate-driven range dynamics of *Laurus* since the Pliocene. *Glob. Ecol. Biogeogr.* 17:685–695.
- Sakuratani, T., T. Aoe and H. Higuchi. 1999. Reverse flow in roots of *Sesbania rostrata* measured using the constant power heat method. *Plant Cell Environ.* 22:1153–1160.
- Santana, L. 1986. Estudio de la precipitación de niebla en Tenerife. Instituto Nacional para la Conservación de la Naturaleza, 97 p.
- Santiago, L.S., G. Goldstein, F.C. Meinzer, J.H. Fownes and D. Mueller-Dombois. 2000. Transpiration and forest structure in relation to soil waterlogging in a Hawaiian montane cloud forest. *Tree Physiol.* 20:673–681.
- Schemenauer, R.S. and P. Cereceda. 1994. The role of wind in rainwater catchment and fog collection. *Water Intl.* 19:70–76.
- Smith, W.K. and T.M. McClean. 1989. Adaptive relationship between leaf water repellency, stomatal distribution and gas exchange. *Am. J. Bot.* 76:465–469.
- Snyder, K.A., J.H. Richards and L.A. Donovan. 2003. Night-time conductance in C₃ and C₄ species: do plants lose water at night? *J. Exp. Bot.* 54:861–865.
- Soil Survey Staff. 1999. Soil taxonomy. A basic system of soil classification for making and interpreting soil surveys. 2nd Edn. USDA-NRCS-US Government Printing Office, Washington, DC.
- Sperling, F.G., R. Washington and R.J. Whittaker. 2004. Future climate change of the subtropical north Atlantic: implications for the cloud forests of Tenerife. *Clim. Change* 65:103–123.
- Stadtmüller, T. 1987. Cloud forests in the humid tropics. The United Nations University, Costa Rica.
- Still, C.J., P.N. Foster and S.H. Schneider. 1999. Simulating the effects of climate change on tropical montane cloud forests. *Nature* 398:608–610.
- Tognetti, R., A. Longobucco, A. Raschi and M.B. Jones. 2001. Stem hydraulic properties and xylem vulnerability to embolism in three co-occurring Mediterranean shrubs at a natural CO₂ spring. *Aust. J. Plant Physiol.* 28:257–268.
- Walmsley, J.L., R. Schemenauer and H.A. Bridgman. 1996. A method for estimating the hydrologic input from fog in mountainous terrain. *J. Appl. Meteorol.* 35:2237–2249.
- Weathers, K.C., G. E. Likens, F.H. Bormann et al. 1988. Cloudwater chemistry from ten sites in North America. *Environ. Sci. Technol.* 22:1018–1026.
- Weathers, K.C., G.M. Lovett, G.E. Likens and N.F.M. Caraco. 2000. Cloudwater inputs of nitrogen to forest ecosystems in southern Chile: Forms, fluxes and sources. *Ecosystems* 3: 590–595.
- Yoder, R.E., L.O. Odhiambo and W.C. Wright. 2005. Effects of vapor-pressure deficit and net-irradiance calculation methods on accuracy of standardized Penman–Monteith equation in a humid climate. *J. Irrig. Drain. Engineer* 131:228–237.
- Zadroga, F. 1981. The hydrological importance of a montane cloud forest area of Costa Rica. *In* Tropical Agricultural Hydrology. Eds. R. Lal and E.W. Russel. John Wiley, New York, pp 59–73.
- Zohlen, A., A.M. González-Rodríguez, R. Lösch, M.S. Jiménez and D. Morales. 1995. Transpiración y regulación estomática en árboles de la laurisilva canaria medidos en primavera. *Vieraea* 24:91–104 (in Spanish with English abstract).