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Tree stomata conductance estimates of a wax myrtle-tree heath (*fayal-brezal*) cloud forest as affected by fog

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ABSTRACT

Direct transpiration measurements of tree species obtained with Granier's heat dissipation probes, combined with micrometeorological data were used to derive tree conductance estimates in a cloud-immersed wax myrtle-tree heath forest located in the Garajonay National Park (La Gomera, Canary Islands, Spain). The one-year period time series were analysed distinguishing between foggy and fog-free conditions in order to evaluate the vegetation response to fog. The presence of fog was found to reduce transpiration (*T*) in both species investigated (*E. arborea* and *M. faya*), such that the yearly medians of the hourly *T* values were 6–15.6 times higher when no fog was present as compared to cloud immersed periods. By contrast the g_c estimates exhibit larger values in the afternoon during foggy conditions when compared in terms of the hourly g_c medians at each time of the day, and were clearly greater on a daily basis. During foggy conditions, g_c followed a monotonically increasing trend. Large variability of conductance estimates was observed across the ranges of micrometeorological conditions explored. The largest conductance values were associated with low solar radiations, air temperatures between 8 and 15 °C, low *VPD* (< 0.5 kPa), and wind velocities of 2–4 m s^{-1}. Laurel forest trees, previously referred as following a profligate water use strategy, may thus profit from the foggy environment by maintaining the stomata opened during the day without significant water losses, while benefiting with the associated carbon gain.

1. Introduction

Cloud forests have received increased attention from a hydrological point of view (Bruijnzeel, 2001; Bruijnzeel et al., 2011). However long-term physiological studies of cloud-immersed (e.g. fog and mist) forests are limited. In this respect, some estimates of whole tree transpiration measured with sap flow gauges in cloud forests have been reported previously (Hafkenscheid 1994; Jiménez et al., 1996, 1999; Hutley et al., 1997; Santiago et al., 2000; Burgess and Dawson 2004; Motzer et al., 2005; McJannet et al., 2007; Ritter et al., 2009a; Carbone et al., 2013; Chu et al., 2014). At the leaf level, Johnson and Smith (2008) reported an 83–95% reduction in leaf transpiration during cloud immersion, as compared to clear skies, of seedling of both, an evergreen conifer (*Abies fraseri* (Pursh) Poiret.) and a broadleaf (*Rhododendron catawbiense* Minchx.) in the southern Appalachian Mountains. Also porometric and gas exchange measurements of leaf stomata conductance were carried out in different tree species of a laurel cloud forest ('laurisilva') in Tenerife, Canary Islands (Zöhlen et al., 1995; González-Rodríguez et al., 2001, 2002a, 2002b; Tausz et al., 2004). The wax myrtle-tree heath ('fayal-brezal') forest, relegated to exposed crests within the relict 'laurisilva' ecosystem, is particularly relevant with respect to the cloud water interception phenomena. Although it shares some tree species with the typical valley and hillside laurel forests, it is characterized by the abundance of *Myrica faya* Ait. (wax myrtle) trees and *Erica arborea* L. (tree heath) arboreal shrubs (Pérez de Paz et al., 1990). *M. faya* has glossy broad leaves. By contrast *Erica* leaves are short and closely acicular (Gratani and Varone 2004; Güvenç and Kendir, 2012), such that its needle-like morphology has been suggested to be favourable for fog water interception in those regions where cloud immersion phenomena are manifest (Ritter et al., 2008). *E. arborea* is not only present in the Macaronesian intertropical region, but it is also extended throughout the Mediterranean basin and at high elevations in Eastern African (Désamoré et al., 2010). However, it is in the Macaronesian forests where fog is highly relevant due to the presence of a quasi-permanent cloud belt at 900–1500 m a.s.l. This originates from the vertical structure of the troposphere at these latitudes, characterized in its lowest part by the existence of a thermal inversion (Guerra et al., 2007; Carrillo et al., 2015). The persistent north-east trade winds saturated with water vapour stop their ascension up the steep slopes of the Macaronesian islands due to such temperature inversion, thus

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leading to a stable windward bank cloud formed by orographic adiabatic cooling. Consequently the laurel forests are subject to frequent fog events and cloud immersion, adopting the appearance of a cloud forest, with abundance of epiphytic lichens and mosses as a clear sign of such an exposition to fog and low clouds (Hernández Padrón et al., 1990; Losada Lima et al., 1990).

Indirect estimates of stomata conductance in *E. arborea* were provided by Mereu et al. (2009), but for a short period (15th May–31st July) and analysing mainly nighttime trends. In addition, their study, carried out under Mediterranean weather conditions, clearly differs from the above-described humid atmospheric regime prevailing in the cloud forests of the Macaronesia. The same would apply for the leaf stomata conductance measurements carried out in *E. arborea* by Tognetti et al. (2000) at a natural CO_2 spring in Pisa and by Gratani and Varone (2004) in the Mediterranean maquis shrublands at the Castelporziano Estate (Italy). Estimates of tree stomata conductance of *E. arborea* under the fog-affected environment of the Macaronesian cloud forests are thus needed. Leaf stomata conductance of broad-leaf trees in a laurel forest of the Agua García Mountain in Tenerife (Canary Islands) showed weak stomata control, and thus a prodigal water use strategy, characteristic of plants subject to mild or short duration droughts, despite the moderate precipitation (~700 mm year^{-1}) and dry summer conditions prevailing in the area (González-Rodríguez et al., 2002a, 2002b). Although fog was present at the Agua García Mountain, clouds were presumably stagnant since fog water precipitation was found to be negligible at the site (Aboal Viñas, 1998). Cloud immersion may explain the current distribution of the relic evergreen laurel forests, a paleoecosystem representative of the lauroid-leaved trees present during the Neogene Era along the edges of the Tethys Sea (currently the Mediterranean basin and northwestern Africa), and that seek refugee in the Macaronesia during the Quaternary glaciations (Nogué et al., 2013). The Neogene was characterized by rains concentrated during the warm season, which contrasts with the contemporary dry summers of the Canary Islands. Thus fog may compensate for such a prodigal water use, given also the shade tolerance of laurel species (Morales et al., 1996). Noticeably such non-conservative use of water has been also observed in the redwood forests of the cloud-immersed coastline of California and Oregon (Burgess and Dawson, 2004), and the yellow cypress montane cloud forests of Taiwan (Chu et al., 2014).

The low temperature and moist conditions provided by fog may reduce leaf temperature and vapour pressure deficit thus enhancing stomata conductance (Smith and Mcclean, 1989). However leaf moistening by intercepted fog water droplets may also reduce carbon assimilation because of the reduced diffusivity of CO_2, four orders of magnitude lower in water than in air (Letts and Mulligan, 2005; Asbjornsen et al., 2011). By contrast, the hydrophobic textured surface of leaves may counteract leaf wetting reducing the contact angle of intercepted water droplets and thus favouring sliding and consequently droplet removal (Holder 2007; Mildenberger et al., 2009). This magnifies as well, incident sunlight due to the presumable lensing effect of such beading droplets (Brewer et al., 1991). Cloud immersion may also modify the quality of light and thus favour photosynthesis (Letts and Mulligan 2005; Johnson and Smith 2006; Dengel and Grace, 2010). These opposite physiological effects of the intercepted fog water thus deserve further investigation, especially in forests subjected to prolonged drought periods (Simonin et al., 2009). In this respect several studies accumulated over the past pointing towards the benefits of leaf wetting and foliar water uptake in alleviating plant water stress (Munné-Bosh et al., 1999; Burguess and Dawson, 2004; Simonin et al., 2009; Eller et al., 2013).

For the current study we selected a watershed within the Garajonay National Park (La Gomera, Canary Islands) where we have previously documented the existence of fog and associated water dripping below the canopy (Ritter et al., 2008; 2009a; Ritter and Regalado, 2010). The orientation of the study plot selected within the watershed makes this an ideal site for investigating the physiological response of vascular plants to fog interception, and in particular the wax myrtle-tree heath ecosystem or 'fayal-brezal', which is abundant in trade wind exposed areas. We aim at investigating to what extent low clouds and the associated fog phenomena affect the vapour exchange characteristics of this relict forest. Since long-term direct measurements of gas exchange parameters across the leaf surface under these circumstances are difficult, we derived these indirectly from an inverse method based on the Penman-Monteith model and sap-flow measurements carried out during a one year period in two tree species with different leaf morphologies: *E. arborea* and *M. faya*.

2. Materials and methods

2.1. Study site

The study was carried out in the upper part (1270 m a.s.l.) of a 43.7 ha watershed X: 278 088 m Y: 3 113 496 m, (28N R zone; WGS84) within the Garajonay National Park (Canary Islands, Spain). Temperatures in the area are mild (13 °C) and precipitation is moderate (< 1100 mm year^{-1}) (Ritter et al., 2008). The Park is immersed in clouds almost throughout the whole year rendering frequent high relative humidity episodes. Canopy fog water interception has been reported at this site (Ritter et al., 2008; Ritter and Regalado, 2010), representing about 10–20% of the total forest water input (Katata et al., 2009). Soils of the Park developed under an udic water regime are of volcanic origin (Andosols), acidic, over two meters deep and with a highly organic dark top horizon (Jiménez-Mendoza et al., 1990). Abundant decayed vegetative material conforms a 2–3 cm thick O horizon of biomass mulching. The vegetation is classified as wax myrtle-tree heath, typical of exposed upper altitudes and crests in laurisilva forests, mainly composed by 3–17 m tall *M. faya* (wax myrtle) trees and *E. arborea* (tree heath) arboreal shrubs (Regalado and Ritter, 2013).

2.2. Micrometeorological instrumentation

Micrometeorological variables were monitored over the canopy at 3-min intervals (and stored as 15-min averages or cumulative totals) during the period February 8th 2003–February 7th 2004. The following variables were measured approximately 3 m above the top of the canopy with the indicated equipment: global radiation (SKS 1110 pyranometer, Skye Instruments Ltd., Powys, UK), temperature and relative humidity (HMP45C thermo-hygrometer, Campbell Scientific Ltd., Lougborough, UK), wind speed (A100R anemometer, Campbell Scientific Ltd.) and direction (W200P wind vane, Campbell Scientific Ltd.), and rainfall (Rain-O-Matic Professional 0.2 mm resolution spoon tipping raingauge from Pronamic Bekhøi International Trading Engineering Co. Ltd., Denmark). The presence of fog was quantified from the water collected by a fog catcher (QFC) northeastern oriented. The QFC consists of a 0.5 m by 0.5 m framed vertical screen built with a single layer of polypropylene Raschel-type mesh, with a 65% shading coefficient, and which drains below into a gutter connected to a spoon tipping Rain-O-Matic raingauge. The fog water thus registered (F) is referred in terms of volume over the QFC screen area, i.e. it has units of l m^{-2} of mesh. In order to avoid spurious counts on the QFC raingauge, only those fog events when no rain was registered were considered in the fog water records. Based on these measurements, fog conditions were defined here as those when relative humidity, $RH \geq 95\%$ or fog water was collected by the fog gauge, while fog-free conditions where those with $RH < 95\%$ and no tips being detected in the QFC's raingauge.

2.3. Sap velocity measurements

Sap flow was measured with Granier type thermal dissipation probes (SFS-2 system from Up GmbH, Germany) in four *E. arborea* tree