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Research paper

# Transpiration and stomatal conductance in a young secondary tropical montane forest: contrasts between native trees and invasive understorey shrubs

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**It has been suggested that vigorous secondary tropical forests can have very high transpiration rates, but sap flow and stomatal conductance dynamics of trees and shrubs in these forests are understudied. In an effort to address this knowledge gap, sap flow (thermal dissipation method, 12 trees) and stomatal conductance (porometry, six trees) were measured for young (5–7 years) *Psiadia altissima* (DC.) Drake trees, a widely occurring species dominating young regrowth following abandonment of swidden agriculture in upland eastern Madagascar. In addition, stomatal conductance ($g_s$) was determined for three individuals of two locally common invasive shrubs (*Lantana camara* L. and *Rubus moluccanus* L.) during three periods with contrasting soil moisture conditions. Values of $g_s$ for the three investigated species were significantly higher and more sensitive to climatic conditions during the wet period compared with the dry period. Further, $g_s$ of the understorey shrubs was much more sensitive to soil moisture content than that of the trees. Tree transpiration rates ($E_c$) were relatively stable during the dry season and were only affected somewhat by soil water content at the end of the dry season, suggesting the trees had continued access to soil water despite drying out of the topsoil. The $E_c$ exhibited a plateau-shaped relation with vapour pressure deficit (VPD), which was attributed to stomatal closure at high VPD. Vapour pressure deficit was the major driver of variation in $E_c$, during both the wet and the dry season. Overall water use of the trees was modest, possibly reflecting low site fertility after three swidden cultivation cycles. The observed contrast in $g_s$ response to soil water and climatic conditions for the trees and shrubs underscores the need to take root distributions into account when modelling transpiration from regenerating tropical forests.**

*Keywords*: *Lantana camara*, *Psiadia altissima*, *Rubus moluccanus*, sap flow, stomatal control, tropical forest regeneration.

## Introduction

Across the tropics, secondary forests are expanding rapidly and now constitute the dominant forest type in many regions (Chazdon 2014, FAO 2016). Despite their relative predominance, especially in areas where widespread swidden (i.e. slash-and-burn) cultivation is common (Geist and Lambin 2002, Lawrence et al. 2010), the water, carbon and nutrient dynamics of regenerating tropical forests are not well understood (Hölscher et al. 2005, Beck et al. 2013, Lacombe et al. 2016, Mukul and Herbohn 2016). Such knowledge is important to drive regional and global models for the prediction of climatic, ecological and hydrological impacts of global change (Foley et al. 2007, Bonan 2008, Nobre et al. 2009, Taylor et al. 2012, cf. Steffen et al. 2015). Globally, transpiration—the transfer of moisture from a (dry) vegetation surface to the atmosphere—is the most important component of overall evapotranspiration (Schlesinger and Jasechko 2014). Transpiration rates from forested ecosystems are controlled largely by biological factors, such as tree size and density (i.e. total conductive sapwood area; Meinzer et al. 2001) and leaf surface area, as well as by environmental factors, such as available radiation, atmospheric vapour pressure deficit (VPD), wind speed and soil moisture availability (Jarvis 1993, Tyree 1999, Roberts et al. 2005). Transpiration rates increase with increasing VPD up to a point where the stomata begin to close and transpiration is reduced (Meinzer et al. 1993, Roberts 1999). Low soil water availability also triggers stomatal closure to avoid embolism and the collapse of conductive tissue (Hernandez-Santana et al. 2008, Tognetti et al. 2009). Thus, stomatal control of water use by plants exerts an important influence on the balance between carbon gains and water losses at scales ranging from individual trees to forest stands and landscapes (Gholz and Lima 1997, Law et al. 2002, Whitehead and Beadle 2004, Jackson et al. 2005). However, knowledge in this regard for regenerating tropical vegetation is scant. Stomatal conductances ($g_s$) have been determined for several species in young successional vegetation in Amazonia (e.g. de A. Sá et al. 1999, Reich et al. 1999, Sommer et al. 2002) and Eastern Indonesia (Juhrbandt et al. 2004) while short-term diurnal patterns of transpiration for young regrowth in northern Thailand and eastern Amazonia have been derived from micrometeorological measurements (Giambelluca et al. 2000). On the other hand, concurrent estimates of seasonal or annual transpiration totals appear to be available only for 2.5- to 3.5-year-old vegetation at a single location in eastern Amazonia (Hölscher et al. 1997, Sommer et al. 2002). Moreover, these estimates were based on indirect micrometeorological rather than direct plant physiological approaches and are subject to considerable uncertainty according to the authors themselves, due to possible issues with fetch, and instrumental problems. Interestingly, both Hölscher et al. (1997) and Sommer et al. (2002) suggested that water use of the young but vigorously regenerating vegetation was at least as high as that of regional old-growth forest, a finding they attributed to a combination of rapid growth, ample soil moisture availability, as well as possibly advected heat from warmer surrounding areas (cf. Giambelluca et al. 2000). Some support for the latter argument comes from the fact that trees situated close to the edge of an 'advanced' secondary forest patch surrounded by active and recently abandoned swidden fields in Vietnam were subject to greater moisture stress than trees in the interior of the stand (Giambelluca et al. 2003). Furthermore, in their review of the literature, Juhrbandt et al. (2004) found a statistically significant 2.7-fold higher average maximum $g_s$ for early successional tropical species compared with late-successional species.

This study was conducted in montane eastern Madagascar where forests have been subject to swidden cultivation for more than a century. Due to rapid population growth in the area, the length of the fallow cycle between successive cultivation phases has decreased over the last 30 years from 8–15 years to as little as 3–5 years (Styger et al. 2007). This has resulted in numerous stands of fallow vegetation across the landscape. Growth rates of fallow stands in the area decline with the number of cultivation/fallow cycles, reflecting a progressive reduction in soil fertility (Styger et al. 2007). Many fallows are dominated by a single species of tree or shrub, mostly the endemic tree *Psiadia altissima* (DC.) Drake, which is often accompanied by two aggressive invasive shrub species: *Lantana camara* L. and *Rubus moluccanus* L. (Styger et al. 2007). Although *Lantana* has been classified as 'one of the world's ten worst weeds' (Sharma et al. 2005) because of its strong allelopathic effect (Sharma et al. 1988) and high phenotypic plasticity (Carrion-Tacuri et al. 2011), *Rubus* is considered more aggressive and capable of out-competing and suppressing both *Lantana* and *Psiadia* (Styger et al. 2007). Invasive woody plants are often (but not always, e.g. Pratt and Black 2006) superior to (even congeneric) native species in terms of their water relations and water transport, as well as in their photosynthetic characteristics and nutrient-use efficiency (McDowell 2002, Funk and Vitousek 2007, Caplan and Yeakley 2010, Shen et al. 2011, Cavaleri et al. 2014, Zeballos et al. 2014), allowing them a competitive advantage over native species with respect to growth and reproductive rates. In a global analysis, Cavaleri and Sack (2010) concluded that the greater water use by invasive species compared with native species tends to be enhanced in hotter, wetter climates. However, despite the ubiquitous occurrence of *Psiadia*, *Rubus* and *Lantana* in the study area (cf. Schatz 2001) and of *Lantana* across the tropics where it causes reductions in native species diversity and soil fertility (Day et al. 2003, Taylor et al. 2012), little is known about the physiological behaviour of these species in the field, or of their combined effect on local soil water conditions and water availability (cf. Le Maitre et al. 2015). Such knowledge is critically important in view of the seasonal climate of the study region, where water is a precious commodity during the dry season (Portela et al. 2012). Here, we present the results of in situ measurements of transpiration (sap flow) and $g_s$ for *Psiadia* trees dominating a 5- to 7-year-old regenerating stand under a wide range of VPD, radiation and soil water conditions. Furthermore, the response of $g_s$ to changes in VPD and soil water content for *Lantana* and *Rubus* in the understorey are compared with that of the *Psiadia* trees. Specifically, we address the following research questions: (i) how does $g_s$ of over- and understorey species respond to changes in VPD, radiation and soil water content, and (ii) what are the main drivers and regulators of transpiration by *P. altissima*? In addition, we test the following hypotheses: (i) $g_s$ of the *P. altissima* trees is less sensitive to variations in soil water content than $g_s$ of the two understorey shrubs; (ii) stomatal conductance of the reputedly more aggressive *R. moluccanus* is higher than that for *L. camara* throughout the year; and (iii) water use by *P. altissima* is not sensitive to changes in soil water content despite the seasonal climate of the study site.

## Materials and methods

### Study site

Our 50 m × 50 m study site (18.94722° S; 48.39527° E) is located at an elevation of 990 m above sea level (a.s.l.) on a 16° hillslope of northwesterly orientation near Andasibe in the central part of the Ankeniheny-Zhamena rain forest Corridor (CAZ) in eastern Madagascar. The CAZ is a newly protected area that encompasses one of the largest remaining blocks of rain forest in Madagascar and experiences a tropical monsoon climate (Köppen-type Am). Mean (± standard deviation (SD)) annual rainfall at Andasibe for the period 1983–2013 was 1625 (±260) mm (Météo Madagascar, unpublished data). The climate is characterized by two seasons: a hot, rainy season from November to April; and a cooler, dry season from May to October. The rainy season brings ~75% of the total annual rainfall. In general, September is the driest month with an average monthly precipitation of 35 mm (2% of the annual total), while the wettest months are January and February (average monthly precipitation of 303 and 290 mm, respectively), which together account for ~36% of the annual rainfall (Météo Madagascar, unpublished data). Average monthly temperatures at Andasibe range from 15 °C in July to 22 °C in December. Average monthly relative humidity measured between October 2014 and November 2015 varied from 85% in October to 94% in July. Average monthly wind speeds are $<2$ m $s^{-1}$.

The study site was covered by primary lower montane rain forest (sensu Grubb 1977) before it was cut and burned for rice cultivation in 1990, after which it underwent three slash-and-burn cycles over a period of ~10 years. No slash-and-burn activities have occurred at the site since 2000 when a forest restoration programme was initiated in the area. Several indigenous tree species were planted as part of the reforestation programme but these were rapidly out-competed by *Psiadia.* The *Psiadia* stand extended beyond the 50 m × 50 m plot boundary for another 20–50 m (depending on direction) before being surrounded by mixed trees and shrubs or tree plantations of similar age as the study site. As such, edge effects were considered small to negligible (cf. Giambelluca et al. 2003). At the start of the measurements (October 2014) the young secondary forest (henceforth referred to as YSF) consisted mostly of ~6-year-old *Psiadia* trees (representing 95% of the overall stem density of 2133 trees $ha^{-1}$ with a diameter at breast height (DBH) ≥5 cm) with the native species *Cassinopsis madagascariensis* Baill. and *Harungana madagascariensis* Lam. Ex Poir. together making up nearly 5%. The vast majority of trees with DBH ≥5 cm were similarly sized, with 85% belonging to the 5–7 cm diameter class, 14% to the 7–9 cm class and the remaining 1% to the 9–11 cm class. The average height of the dominant trees was 5.0 ± 0.3 m. The average DBH was 6.1 ± 1.3 cm and tree basal area was 6.3 $m^2$ $ha^{-1}$. Leaf area index (LAI) of the tree stratum varied slightly through the year with *Psiadia trees* shedding a small proportion of its leaves towards the end of the dry season (September), while new leaves emerged rapidly after the return of the rains in November/December. Tree LAI (measured using a Licor LAI 2000 Plant Canopy Analyzer, Lincoln, Nebraska, USA) was 1.75 ± 0.18 in September 2014, increasing to 1.83 ± 0.18 in January 2015 and 2.15 ± 0.26 in May 2015, with an overall mean value of 1.91 ± 0.21. Based on throughfall measurements for small rainfall events a canopy gap fraction of 45% was derived using the method of Jackson (1975), implying a canopy cover fraction of 55% (see Ghimire et al. (2017) for details). The understorey was dominated by *R. moluccanus*, *L. camara* and *Clidemia hirta* (L.) D. Don. Understorey LAI in January 2017 (wet season) (determined by destructive sampling of *Rubus* and *Lantana* in five 1 m × 2 m plots) was 0.25 ± 0.10 for *Lantana* and 0.26 ± 0.22 *Rubus*. Above-ground biomass for eight similarly aged tree fallows around Andasibe was estimated at 21.8 t $ha^{-1}$ (Andriamananjara et al. 2016). The geological substrate consists of Precambrian gneisses (Du Puy and Moat 1996), in which a Tropudult have developed. Soil texture varied little with depth, apart from an increase in clay content at 60–70 cm (Andriamananjara et al. 2016). Soil bulk density was 1.0 ± 0.1 g $cm^{-3}$ at 2.5–7.5 cm depth, increasing to 1.2 ± 0.2 g $cm^{-3}$ at 12.5–17.5 cm depth and 1.3 g $cm^{-3}$ at 22.5–27.5 cm. The median field-saturated hydraulic conductivity of the soil was high (1033 mm $h^{-1}$ at the surface and 136 mm $h^{-1}$ at 10–20 cm depth; cf. Zwartendijk et al. 2017). Average soil organic carbon stored in the top 30 cm for eight similar tree fallows around Andasibe was estimated at 98 t $ha^{-1}$, implying a corresponding average carbon concentration of 3.3% (Andriamananjara et al. 2016). Roots were concentrated in the top 30 cm of the soil profile and consisted of 40% fine roots (2–10 mm diameter) vs 60% coarser roots (>10 mm diameter; Andriamananjara et al. 2016).

### Climatic conditions and soil moisture dynamics

Climatic conditions were monitored at 2 m above the forest canopy using a 7 m mast. Air temperature ($T$, °C) and relative humidity (RH, percentage of saturation) were measured using Skye sensors (Skye Instruments Ltd, Llandrindod Wells, UK) that were protected against direct sunlight and precipitation by a radiation shield. Wind speed (m $s^{-1}$) was measured using an A100R digital anemometer (Vector Instruments, Rhyl, UK). Measurements were taken every 30 s, and 10-min averages were recorded by DataHog2 data-loggers (Skye Instruments Ltd). Volumetric soil moisture content ($\theta$) was measured at depths of 5, 15, 40, 75, 110 and 160 cm using Time Domain Reflectometry sensors (CS616, Campbell Scientific Ltd, Logan, UT, USA) and recorded at 5-min intervals (CR1000 data-logger, Campbell Scientific Ltd). To facilitate the interpretation of the influence of soil moisture content on tree transpiration rates, soil moisture content at permanent wilting point ($\theta_{\mathrm{PWP}}$) was estimated from soil texture, bulk density and moisture content at field capacity for the site (Zwartendijk et al. 2017) using the ROSETTA model (Schaap et al. 2001). It is acknowledged that the value of $\theta_{PWP}$ obtained in this way represents an approximation and that any comparisons with actual moisture contents will require some caution.

Weather data were also acquired by an automatic weather station located in a fire-climax grassland located 1.5 km from the YSF site at an elevation of 965 m a.s.l. Incoming short-wave radiation ($R_s$) was measured with a CM6B-pyranometer (Kipp and Zonen, Delft, The Netherlands), while $T$, RH, wind speed and wind direction were measured using a Vaisala WXT520 Weather Transmitter (Vaisala Oyj, Helsinki, Finland). Measurements were taken every 30 s, and 5-min averages were recorded by a Campbell Scientific Ltd CR1000 data-logger. Because of the proximity to the YSF plot and the very similar elevations of the two sites, $R_s$ measured at the fire-climax grassland was considered to be the same as that for the YSF.

### *Stomatal conductance*

Stomatal conductance ($g_s$) was measured with a steady-state leaf porometer (SC-1 Leaf Porometer, Decagon Devices, Pullman, WA, USA). Measurements were always made on the same six *Psiadia* trees, representing different tree sizes and crown positions (see Table 1 below), as well as on three *Lantana* and three *Rubus* shrubs. Tree crowns were accessed using a 3 m high ladder. Intensive measurement campaigns were held during three periods with contrasting soil moisture conditions, viz. in August 2015 (dry), December 2015 (moist) and February 2016 (wet), to allow analysis of the dependence of $g_s$ on climatic conditions and soil moisture content. During each of these campaigns, $g_s$ was measured on 8–10 consecutive days. Measurements were restricted between 09:00 and 16:00 h local time to avoid wet canopy conditions caused by morning dew or late afternoon rainfall (leading to high values of $g_s$). Typically, three to four cycles of measurements were made per day. During each measurement cycle, $g_s$ was measured on five mature leaves on each selected canopy tree and understorey shrub. The ratio of abaxial to adaxial conductance for the investigated species was ~20. Therefore, measurements were made on the abaxial leaf surface only. The entire porometer dataset comprised ~2000 measurements for *Psiadia* trees and ~1000 measurements for the two shrubs.

The sensitivity of stomatal conductance to changes in VPD and $R_s$ during the three intensive campaigns was examined using the multiplicative Jarvis (1976) function:

$$g_s = (aR_s + b)(1 - m\ln(\text{VPD})) \tag{1}$$

where $a$, $b$ and $m$ are parameters that are estimated through non-linear regression analysis for each specific period. The first part of the equation ($aR_s + b$) represents the reference value of $g_s$ (at VPD = 1 kPa), whereas $m(aR_s + b)$ represents the sensitivity of $g_s$ to changes in VPD ($-\partial g_s/\partial\ln(\text{VPD})$). The sensitivity of $g_s$ to changes in VPD as a function of $R_s$ was analysed by plotting $m(aR_s + b)$ against $R_s$.

### *Estimation of tree- and stand-scale transpiration from sap flow measurements*

The quantification of individual tree transpiration rates was accomplished by in situ xylem sap flow rate ($Q_t$) measurements involving the measurement of xylem sap flux density ($J_p$) and sapwood area ($A_x$). The $J_p$ was measured using the thermal dissipation method (TDP; Granier 1985), whereas $A_x$ was estimated at the end of the measurement campaign from wood cores extracted at different azimuthal positions at breast height using an increment borer (Grissino-Mayor 2003). Radial sapwood depth was estimated visually and verified using a staining method (Holz 1959). The TDP method deploys a pair of 20 mm long and 2 mm diameter probes (UP GmbH, Munich, Germany), which were inserted above each other at a vertical distance of 100 mm.

Table 1. Characteristics of the canopy trees (*Psiadia altissima*) used for sap flow and stomatal conductance measurements and mean (±SD) daily sap flow rates (kg day$^{-1}$) for the investigated trees.

| Tree ID | DBH (cm) | Sapwood depth (cm) | Sapwood area (cm$^2$) | Crown projection area (m$^2$) | Average sap flow (kg day$^{-1}$) |
|---|---|---|---|---|---|
| 1* | 5.5 | 2.5 | 22.0 | 4.34 | 1.4 (±0.6) |
| 2* | 7.4 | 3.5 | 40.7 | 4.52 | 3.5 (±1.3) |
| 3 | 5.7 | 2.6 | 23.7 | 0.95 | 1.3 (±0.7) |
| 4* | 7.6 | 3.6 | 43.0 | 1.65 | 3.1 (±1.3) |
| 5* | 6.6 | 3.1 | 32.1 | 1.33 | 1.8 (±1.1) |
| 6 | 7.0 | 3.3 | 36.3 | 2.69 | 4.1 (±1.3) |
| 7 | 5.0 | 2.3 | 18.1 | 0.64 | 0.5 (±0.3) |
| 8 | 6.1 | 2.8 | 27.3 | 1.65 | 1.3 (±0.8) |
| 9* | 6.0 | 2.8 | 26.4 | 0.95 | 1.5 (±0.6) |
| 10* | 5.0 | 2.3 | 18.1 | 1.33 | 1.1 (±0.4) |
| 11 | 5.6 | 2.6 | 22.9 | 1.43 | 1.1 (±0.7) |
| 12 | 5.6 | 2.6 | 22.9 | 2.14 | 1.4 (±0.5) |

*Trees used for stomatal conductance measurements.

The upper (downstream) probe was heated continuously, creating a temperature difference with respect to the lower (upstream) non-heated probe. The sensors were always placed on the south side of the trunks to minimize sun-exposure, and were insulated using a locally made radiation shield to minimize any externally induced heat influence. The natural thermal gradients between the two sensors (Do and Rocheteau 2002) measured in three *Psiadia* trees were <0.2 °C. Therefore, its effect on measured sap flow rates was considered negligible. The temperature difference between the upper and the lower probe was measured every 30 s, and 5-min averages were recorded by a CR1000 data-logger (Campbell Scientific Ltd). Recorded temperature differences were converted to sap flux densities ($J_p$, cm$^3$ cm$^{-2}$ h$^{-1}$) as described by Granier (1985, 1987) and subsequently revalidated by Clearwater et al. (1999) and presented in Lubczynski et al. (2012) as follows:

$$J_p = 42.84\left(\frac{\Delta T_{\max} - \Delta T}{\Delta T}\right)^{1.231} \qquad (2)$$

where $\Delta T$ is the temperature difference (°C) between the two probes and $\Delta T_{\max}$ (°C) is the maximum value of $\Delta T$ recorded in the absence of transpiration, i.e., when $J_p$ is zero or near zero. The probes were repositioned once every 2 months to avoid possible drift in $\Delta T$ due to deterioration of the contact between the probe and the surrounding wood (Lu et al. 2004). The $J_p$ was monitored on 12 *Psiadia* trees of different sizes between October 2014 and November 2015 (see Table 1 for tree characteristics), using one TDP sensor per tree. A stratified sampling approach based on the frequency of occurrence of different tree sizes (DBH) was used to select the trees for the sap flow measurement. Given that the vast majority of the stand's trees were comparably small (5–7 cm DBH), the effect of any circumferential variation in sap flux density on the estimated sap flow rates was assumed to be minimal. Further, the ratio of the area of the outermost 2 cm of sapwood to the entire sapwood area for the investigated trees was always greater than 0.78. Thus, the effect of radial variation in $J_p$ on sap flow rate was also assumed to be minimal, as also reported for a lower montane forest in Costa Rica (Aparecido et al. 2016) and young native tree plantations in seasonally dry Panamá (N. Kunert, personal communication). Sap flow was therefore estimated assuming that $J_p$ was constant throughout the sapwood profile and similar to that measured by the TDP sensors in the outer 2 cm of sapwood:

$$Q_t = J_p \times A_x \qquad (3)$$

where $J_p$ is conventionally expressed in cm$^3$ cm$^{-2}$ h$^{-1}$ and $A_x$ in cm$^2$. It is acknowledged that this assumption may have produced a slight overestimation of $Q_t$.

Tree transpiration per unit ground-projection of canopy area ($E_c$, mm h$^{-1}$), also known as normalized sap flow, was computed by dividing sap flow rate ($Q_t$) by crown projection area. The crown projection area was quantified through the measurement of the crown radius of the individual trees in four cardinal (N, S, E and W) and four intermediate directions (NE, SE, SW and NW). The average radius was then used to calculate the crown projection area.

The transpiration rates for the measured trees were also scaled to the plot level to estimate tree transpiration per unit area of land ($E_t$). This was done in three steps. First, the cross-sectional area of all tree stems within the plot was measured and a simple least-square regression between cross-sectional stem area ($A_s$) and sapwood area ($A_x$) ($A_x = 0.94 \times A_s - 1.8$, $R^2 = 1.0$) was used to estimate stand-level sapwood area. Second, the sap flow rate ($Q_t$, cm$^3$ h$^{-1}$) for the stand was calculated by multiplying the average sap flux density ($J_p$) from the 12 measured trees by the total sapwood area. Finally, the daily sap flow at the plot level was divided by the plot area corrected for slope gradient ($A$, m$^2$) to determine the daily stand transpiration ($E_t$, mm day$^{-1}$). Any gaps in the $E_t$ data (4 rainy season days and 31 dry season days) were filled using a regression equation linking $E_t$ to VPD and $R_s$.

### *Statistical analysis*

The significance of the differences in stomatal conductance among species and for a given species between periods was determined using analysis of variance (ANOVA, followed by a post-hoc Tukey HSD test). Differences in tree water use between seasons or periods were tested for statistical significance using a paired Student's *t*-test. Regression models were evaluated based on the goodness of fit. For all statistical analyses, except the stepwise multi-linear analyses described below, the language and environment of R, version 3.4.1 9 (R Development Core Team 2011) was used.

Stepwise multi-linear regression was used to evaluate the relationship between canopy transpiration ($E_c$), micrometeorological variables and soil moisture content $\theta$. This was done in Matlab using the *stepwise* function for both hourly and daily data, applying an entrance tolerance value of 0.05, and an exit tolerance of 0.10. The $E_c$ values obtained before 07:00 h and after 17:00 h were excluded to avoid bias towards extremely low values of $E_c$. Because the relations between canopy transpiration and $R_s$ and VPD were non-linear (see Results), the stepwise multi-linear analyses were also performed using log-transformed data (i.e., $\log E_c = c_1 \log(\mathrm{VPD}) + c_2 \log(R_s) + c_3\,\theta + c_4$), where $c_1$–$c_4$ are fitting parameters.

## Results

### *Climatic conditions and soil moisture dynamics*

Seasonal variations in average daily temperature $T$, incoming short-wave radiation $R_s$ and vapour pressure deficit VPD during the study period are shown in Figure 1. Average (±SD) daytime $T$ was 22 (±3.3) °C with a maximum of 28 °C in December and a minimum of 13 °C in August (Figure 1a). Overall average daytime $R_s$ was 459 ± 157 W $m^{-2}$. Incoming short-wave radiation was intermediate during the rainy season (November–April), while higher values were observed during the transition to the dry season (April–May), after which $R_s$ declined to a minimum in June–July (northern summer) before increasing again during the latter part of the dry season (Figure 1b). Vapour pressure deficit decreased gradually as the rainy season progressed (December–March), with the highest values being observed during the transitions between seasons (April–May and late October/early November; Figure 1c). Mean daytime VPD in the rainy season was 0.79 (±0.36) kPa vs 0.61 ± 0.38 kPa in the dry season. The highest daytime VPD (~2 kPa) was recorded in October and the lowest (0.02 kPa) in July.

As expected, volumetric soil moisture contents were higher during episodes with heavy rains, with values measured at 5 and 15 cm depth responding much more sharply to rainfall than those at 40 cm depth and below (Figure 2). Changes in $\theta$ were most pronounced in the top layer, with soil moisture at 5 cm and 15 cm depth declining frequently to values around the inferred wilting point (19%) during the dry season. Conversely, there was little seasonal change in $\theta$ below 40 cm depth (Figure 2), suggesting limited water uptake from deeper layers and limited drainage below this depth.

### Stomatal conductance

There were significant differences in stomatal conductance ($g_s$) between the dry, moist and wet periods for each species ($P < 0.016$), with the highest average values being observed for all species during the wet period (Table 2). Average $g_s$ for all three species increased significantly with increases in soil moisture content ($P < 0.016$). However, the absolute difference between average values of $g_s$ during dry (August 2015) and wet (February 2016) periods was much lower for the *Psiadia* trees (~125 mmol $m^{-2}$ $s^{-1}$) than for the two understorey species

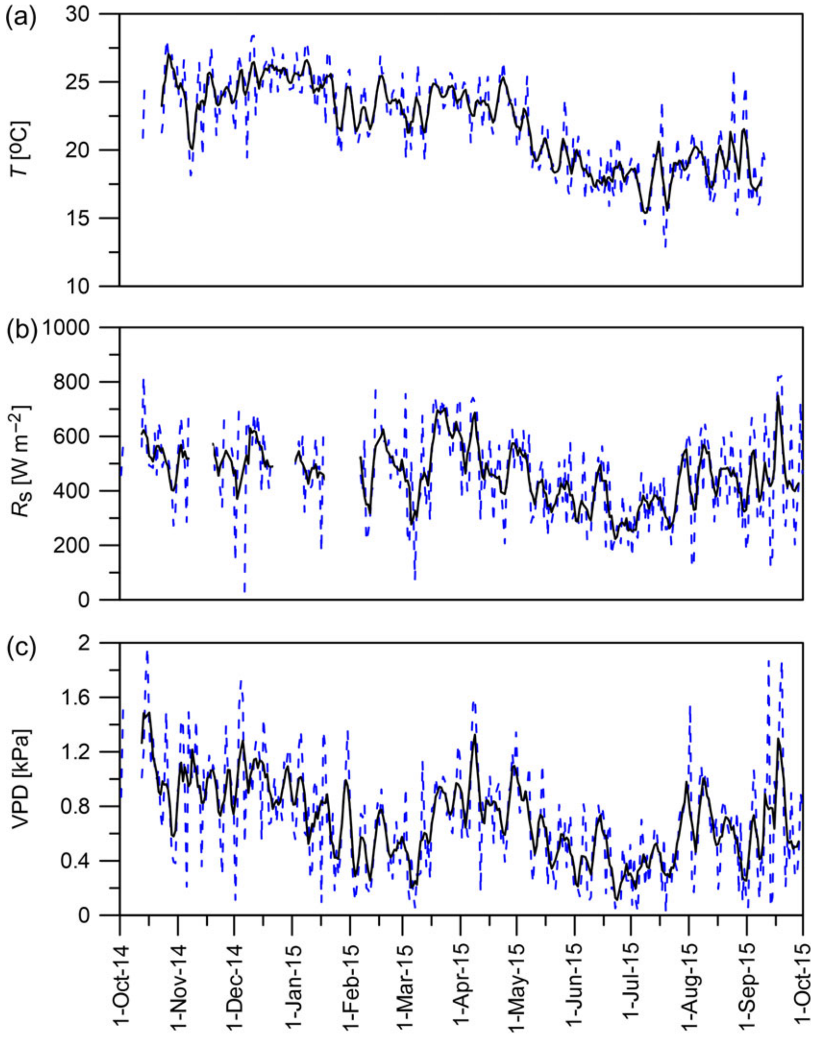

Figure 1. Daily averages (dashed lines) and 5-day moving averages (solid lines) of (a) above-canopy air temperature ($T$, °C), (b) incoming short-wave radiation ($R_s$, W $m^{-2}$) and (c) vapour pressure deficit (VPD, kPa) for the investigated young secondary forest site near Andasibe between 1 October 2014 and 30 September 2015.

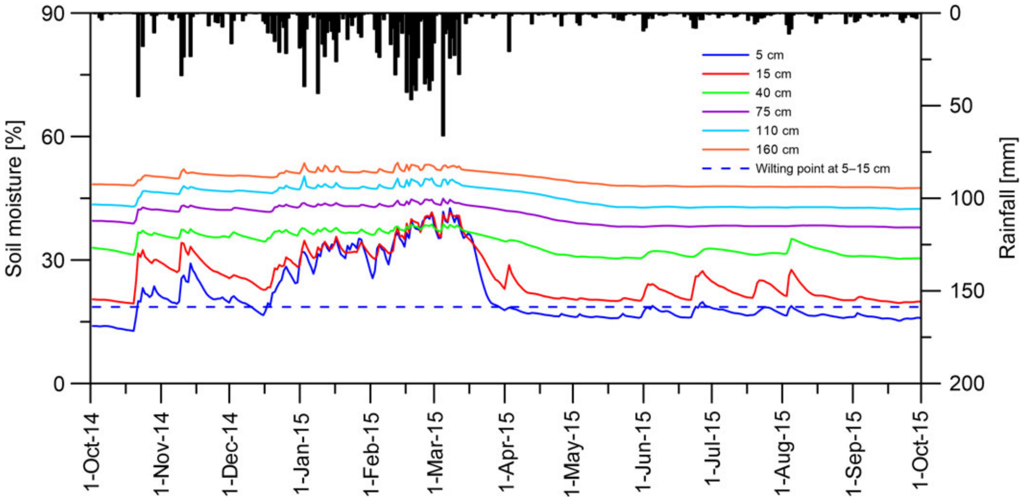

Figure 2. Daily rainfall (mm) and volumetric soil moisture content (%) at six different depths at the Andasibe young secondary forest site for the period between 1 October 2014 and 30 September 2015. The dashed horizontal line represents the approximate soil moisture content at wilting point at 5–15 cm depth as derived with the ROSETTA model (Schaap et al. 2001).

Table 2. Average stomatal conductance (±SD) ($g_s$, mmol m$^{-2}$ s$^{-1}$) for the three investigated species during the three periods with different soil moisture conditions. Values differ significantly between the three periods for each species ($P < 0.016$). Values sharing the same superscript for a given soil moisture condition do not differ significantly from each other and vice versa.

| Date | Soil moisture condition | Mean $g_s$ (mmol m$^{-2}$ s$^{-1}$) | | |
|---|---|---|---|---|
| | | *Psiadia altissima* | *Lantana camara* | *Rubus moluccanus* |
| August 2015 | Dry | 301 (±55)$^a$ | 271 (±43)$^a$ | 162 (±34)$^b$ |
| December 2015 | Moist | 360 (±62)$^c$ | 540 (±96)$^d$ | 468 (±58)$^d$ |
| February 2016 | Wet | 423 (±81)$^e$ | 673 (±111)$^f$ | 570 (±167)$^{e,f}$ |

(~400 mmol m$^{-2}$ s$^{-1}$; Table 2). There were no significant differences ($P > 0.016$) in $g_s$ for *Lantana* and *Rubus* in the moist and dry periods, but the difference was statistically significant for the wet period (higher for *Lantana*; Table 2). Also, there was no significant difference ($P > 0.016$) in $g_s$ between *Psiadia* and *Lantana* in the dry period, but conductances for *Psiadia* were significantly smaller than those for *Lantana* during the wet and moist periods. Conductances of *Psiadia* trees did not differ from those of *Rubus* during wet conditions but differences were significant during the moist period (lower for *Psiadia*) and the dry period (lower for *Rubus*; Table 2).

Variations in $g_s$ for *Psiadia trees* were explained mostly by VPD (Figure 3) and less by incoming short-wave radiation $R_s$ (Figure 4). Stomatal conductance of the *Psiadia* trees was related more closely to VPD for increasing soil moisture content, although there was considerable variation, during dry and wet conditions (Figure 3a and c). On the other hand, the response of $g_s$ of *Lantana* to increased VPD varied from almost no decline (wet period) to a very sharp decline (dry period) (Figure 3f and d), while the response of *Rubus* to VPD was much less pronounced throughout the three campaigns (Figure 3g–i). Relationships between $g_s$ and $R_s$ for the two shrubs were positive during the moist and wet periods but negative in the dry period (Figure 4d–i), while no clear trends were observed in this regard for *Psiadia* (Figure 4a–c).

The parameter values for the multiplicative (Jarvis-type) function to predict $g_s$ from $R_s$ and VPD (Eq. 1) for the three species and periods are listed in Table 3, whereas the sensitivity of $g_s$ to changes in VPD as a function of $R_s$ is presented in Figure 5. The values of the parameters $a$ and $b$ (which represent a measure of $g_s$ at VPD = 1 kPa) were lowest during the dry period for all three species, while *Psiadia* and *Rubus* showed the highest values for the parameter $a$ during the wet period and the highest values for the parameter $b$ during the moist period. The parameter $m$ (which represents a measure of the sensitivity of $g_s$ to changes in VPD) attained its maximum value in different seasons depending on the species, i.e. in the dry period for *Lantana*, in the moist period for *Psiadia* and in the wet period for *Rubus*. Consequently, the sensitivity of $g_s$ to increases in VPD as a function of $R_s$ was greatest for *Lantana* during the dry period, for *P. altissima* during the moist period and for *Rubus* under wet conditions (Figure 5).

### *Sap flux density and transpiration rates*

Figure 6 shows the diurnal variation in sap flux density ($J_p$) for the 12 measured *Psiadia* trees during a 5-day period towards the end of the dry season (18–23 October 2014) and during a

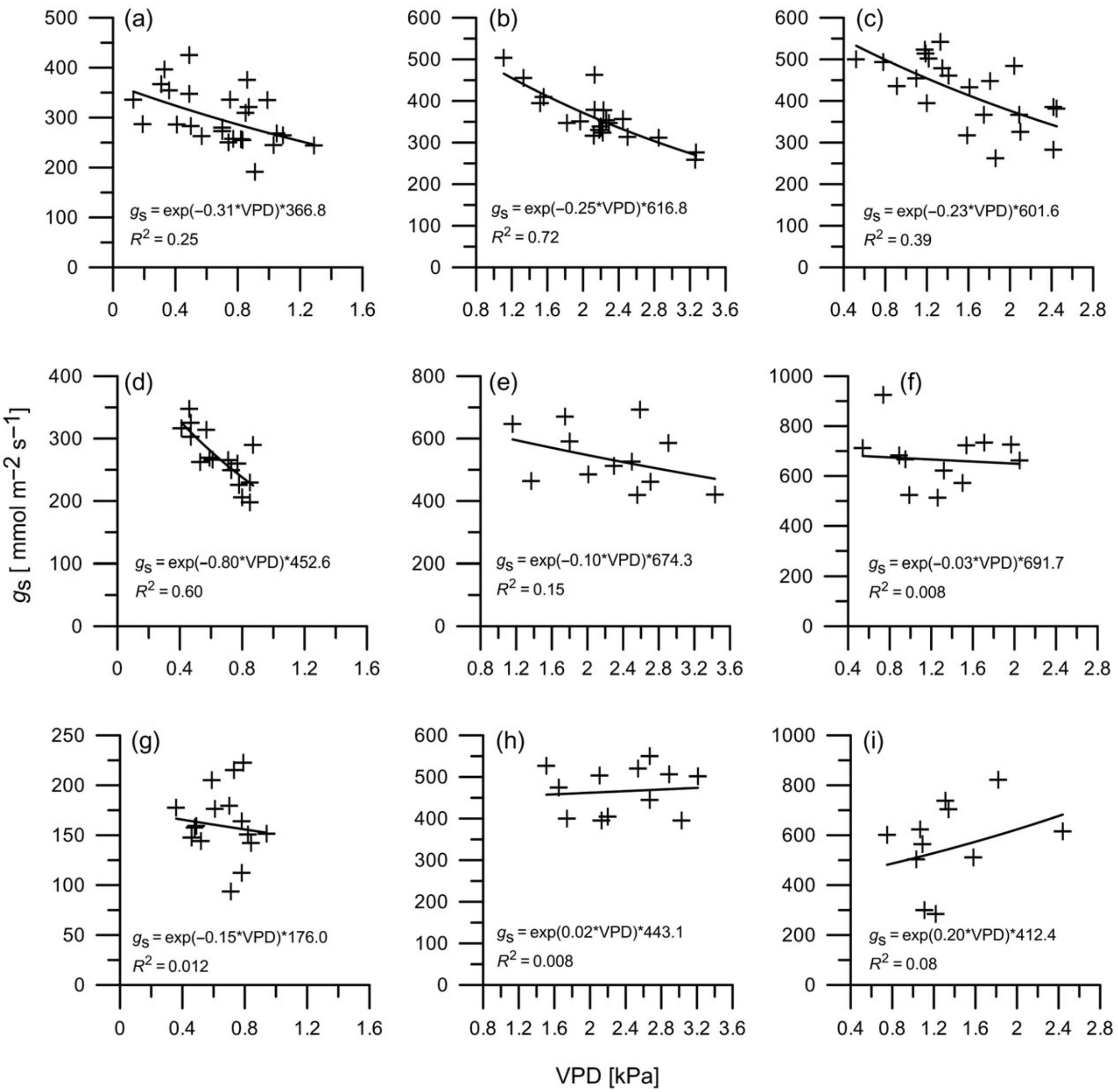

Figure 3. Relationships between stomatal conductance ($g_s$, mmol m$^{-2}$ s$^{-1}$) and VPD (kPa) during: (i) dry (left-hand panels a, d and g), (ii) moist (central panels b, e and h) and (iii) wet conditions (right-hand panels c, f and i), for *Psiadia altissima* (top row; a, b, c), *Lantana camara* (middle row; d, e, f) and *Rubus moluccanus* (bottom row; g, h, i). Each data point represents the average of 30 measurements on leaves of *P. altissima* and 15 leaves from each understorey shrub (taken during a single measurement run).

period with ample rain (26–31 January 2015), along with corresponding fluctuations in above-canopy VPD and $R_s$. Diurnal variation in $J_p$ appears to be closely tied to fluctuations in $R_s$ and VPD (Figure 6a). Typically, $J_p$ increased rapidly in the morning as both VPD and solar radiation increased, and generally reached a maximum around mid-day, declining again in the afternoon. Mid-day peaks in $J_p$ were around 15 cm$^3$ cm$^{-2}$ h$^{-1}$ in October (end of dry season) vs around 7–9 cm$^3$ cm$^{-2}$ h$^{-1}$ during the wet season (January). Interestingly, no increase in mid-day maximum $J_p$ was observed after ~40 mm of rainfall occurred on 20 October 2014 (Figure 6a), suggesting soil moisture availability was not limiting tree transpiration even at the end of the dry season. Positive relationships were observed between sap flux density and sapwood area for both seasons, as well as between $J_p$ and crown projected area (Figure 7c and d), suggesting a tendency for larger or more exposed trees to transpire at faster rates, although the range in values of $J_p$ was fairly narrow at 6–14 cm$^3$ cm$^{-2}$ h$^{-1}$. Similarly, daily sap flow totals for individual trees generally increased with tree size and ranged from 1 to 5 kg day$^{-1}$ (Table 1).

Over the 1-year study period, the highest average daily tree transpiration $E_c$ was obtained for October 2014 (1.72 mm day$^{-1}$) and the lowest for September 2015 (0.63 mm day$^{-1}$). Average daily $E_c$ was relatively high between October and mid-December and

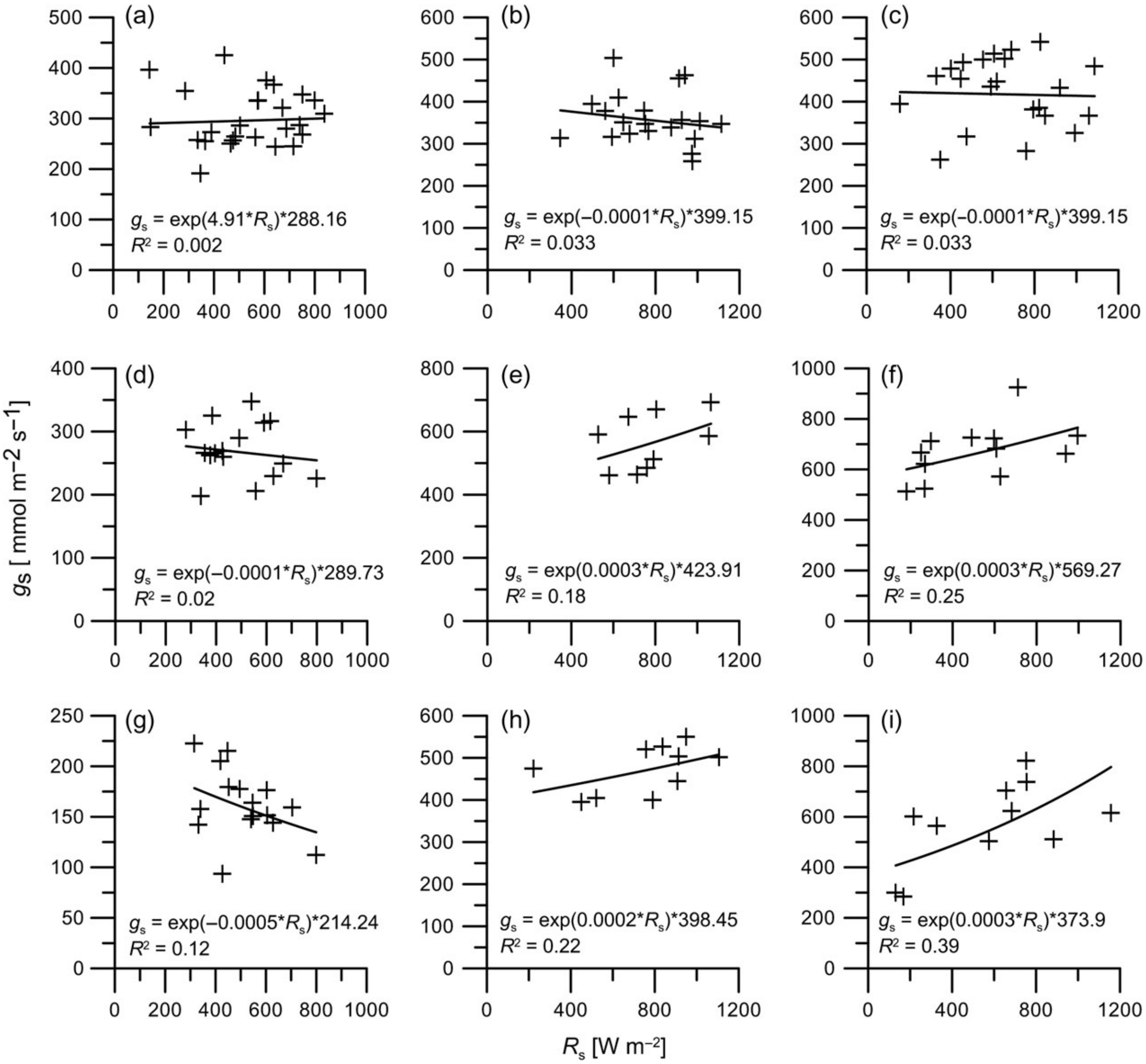

Figure 4. Relationships between stomatal conductance ($g_s$, mmol $m^{-2}s^{-1}$) and incoming short-wave radiation ($R_s$, W $m^{-2}$) during: (i) dry (left-hand panels a, d and g), (ii) moist (middle panels b, e and h) and (iii) wet conditions (right-hand panels c, f and i), for *Psiadia altissima* (top row; a, b, c), *Lantana camara* (middle row; d, e, f) and *Rubus moluccanus* (bottom row; g, h, i). Each data point represents the average of 30 measurements on leaves of *P. altissima* and 15 leaves from each understorey shrub taken during a single measurement run.

Table 3. Parameter values for the multiplicative function ($g_s = (aR_s + b) \cdot (1 - m\ln(\mathrm{VPD}))$; Eq. 3) for predicting stomatal conductance $g_s$ (mmol $m^{-2}$ $s^{-1}$) from incoming short-wave radiation $R_s$ (W $m^{-2}$) and above-canopy vapour pressure deficit VPD (kPa) for the three-investigated species during the three periods with different soil moisture conditions.

| Soil moisture condition | Species | *a* | *b* | *m* |
|---|---|---|---|---|
| Dry<br>August 2015 | *Psiadia altissima* | −0.010 | 282.27 | 0.16 |
| | *Lantana camara* | 0.013 | 201.60 | 0.66 |
| | *Rubus moluccanus* | −0.098 | 208.48 | 0.06 |
| Moist<br>December 2015 | *Psiadia altissima* | 0.09 | 446.43 | 0.40 |
| | *Lantana camara* | 0.34 | 378.85 | 0.16 |
| | *Rubus moluccanus* | 0.11 | 401.03 | 0.03 |
| Wet<br>February 2016 | *Psiadia altissima* | 0.13 | 404.62 | 0.32 |
| | *Lantana camara* | 0.33 | 532.35 | 0.22 |
| | *Rubus moluccanus* | 0.51 | 336.38 | 0.31 |

lower but comparatively stable thereafter (Figure 8). However, there was no significant difference in average daily tree transpiration rates between the two seasons ($P > 0.05$). Overall daily average $E_c$ was 0.97 ± 0.41 mm $day^{-1}$. There was little (September 2015) or no decline in tree water use during periods in which soil moisture content in the uppermost layers was low (i.e. around wilting point at 5–15 cm depth from April 2015 onwards; cf. Figure 2), suggesting continued uptake from deeper layers. Similarly, average daily tree transpiration at the stand level ($E_t$) was highest in October 2014 (1.2 mm $day^{-1}$) and lowest in September 2015 (0.52 mm $day^{-1}$), with an overall average of 1.0 mm $day^{-1}$. Both absolute and relative $E_t$ (i.e. normalized by net radiation inputs $R_n$) gradually decreased as the wet season progressed in response to lower VPD. Absolute values of $E_t$ remained

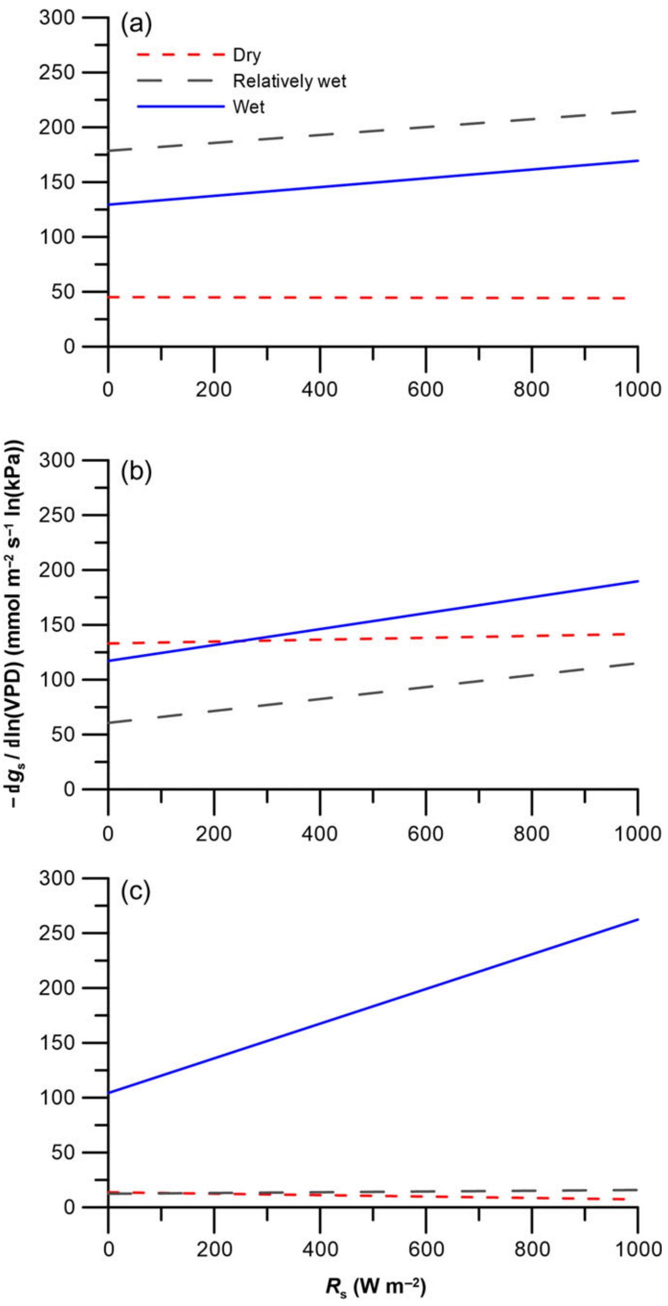

Figure 5. The sensitivity of the stomatal conductance ($g_s$, mmol m$^{-2}$ s$^{-1}$) to increasing VPD ($-\partial g_s/\partial \ln(\text{VPD})$) as a function of incoming short-wave radiation ($R_s$, W m$^{-2}$) for three different moisture conditions for: (a) *Psiadia altissima*, (b) *Lantana camara* and (c) *Rubus moluccanus*.

more or less constant during the dry season between May and August but dropped by ~19% in September. Annual $E_t$ was estimated at 265 mm, of which 135 mm occurred during the wet season (November–April) and 130 mm during the dry season.

Hourly transpiration rates for *Psiadia* increased with VPD for VPD <1 kPa but tended to level off at higher VPD values (Figure 9a and b). Likewise, an increase in $R_s$ was initially matched by a concurrent increase in $E_c$, after which transpiration tended to level off somewhat at $R_s$ values above 700 W m$^{-2}$ (Figure 9c and d). Separating the data into morning (07:00–12:00 h) and afternoon (13:00–17:00 h) data did not reveal any systematic difference in the relationships between $E_c$ and VPD or $R_S$ (Figure 9a–d). Tree transpiration was not related to average soil moisture content within the top 40 cm (Figure 9e and f).

The non-linear relation between VPD and hourly tree transpiration explained 64% and 77% of the variation in $E_c$ during the dry and the wet season, respectively (see Table S1 available as Supplementary Data at *Tree Physiology* Online). Corresponding values for the daily data were 61% (dry season) and 67% (wet season; see Table S1 available as Supplementary Data at *Tree Physiology* Online). Similarly, incoming short-wave radiation alone explained 31% and 53% of the variation in hourly $E_c$, and 53% and 66% of the variation in daily $E_c$ for dry- and wet-season data, respectively (see Table S1 available as Supplementary Data at *Tree Physiology* Online). Soil water content proved to be the least influential variable, explaining only 3% and 9% of the variation in hourly $E_c$ and 12% and 26% for daily data during dry and wet conditions, respectively (see Table S1 available as Supplementary Data at *Tree Physiology* Online). Vapour pressure deficit was chosen as the first explanatory variable in the all stepwise multiple linear regression analyses for the log-transformed data, except for the hourly dataset for the entire study period, for which $R_s$ was chosen as the first explanatory variable (Table 4). Soil moisture content was included as the third explanatory variable only when analysing the data for dry and wet periods separately (Table 4). The multi-linear models of the log-transformed data explained 68% and 73% of the variation in daily transpiration, and 67 and 81% of the variation in hourly transpiration for dry- and wet-season conditions, respectively (Table 4). Thus, the mutli-linear models of the log-transformed data did not explain much more of the variation in $E_c$ than the individual non-linear relations with VPD (or $R_s$).

## Discussion

### *Stomatal conductance*

Comparative information on the magnitude of stomatal conductance for secondary or even old-growth vegetation within the tropical lower montane rain forest (LMRF) zone is very limited. Average $g_s$ for the 6-year-old *Psiadia* trees of the study site (301–425 mmol m$^{-2}$ s$^{-1}$, depending on soil moisture conditions; Table 2) compared favourably to both average (83–289 mmol m$^{-2}$ s$^{-1}$) and maximum (233 ± 93 mmol m$^{-2}$ s$^{-1}$) $g_s$ for a range of upper canopy trees in a mature Ecuadorian LMRF, although the latter values may have been suppressed somewhat by fog incidence and high atmospheric humidity (Motzer et al. 2005, Küppers et al. 2008). At 590 mmol m$^{-2}$ s$^{-1}$, the overall average maximum $g_s$ determined for eight early successional trees (3–4 years old) at a comparable elevation (1100 m a.s.l.) within

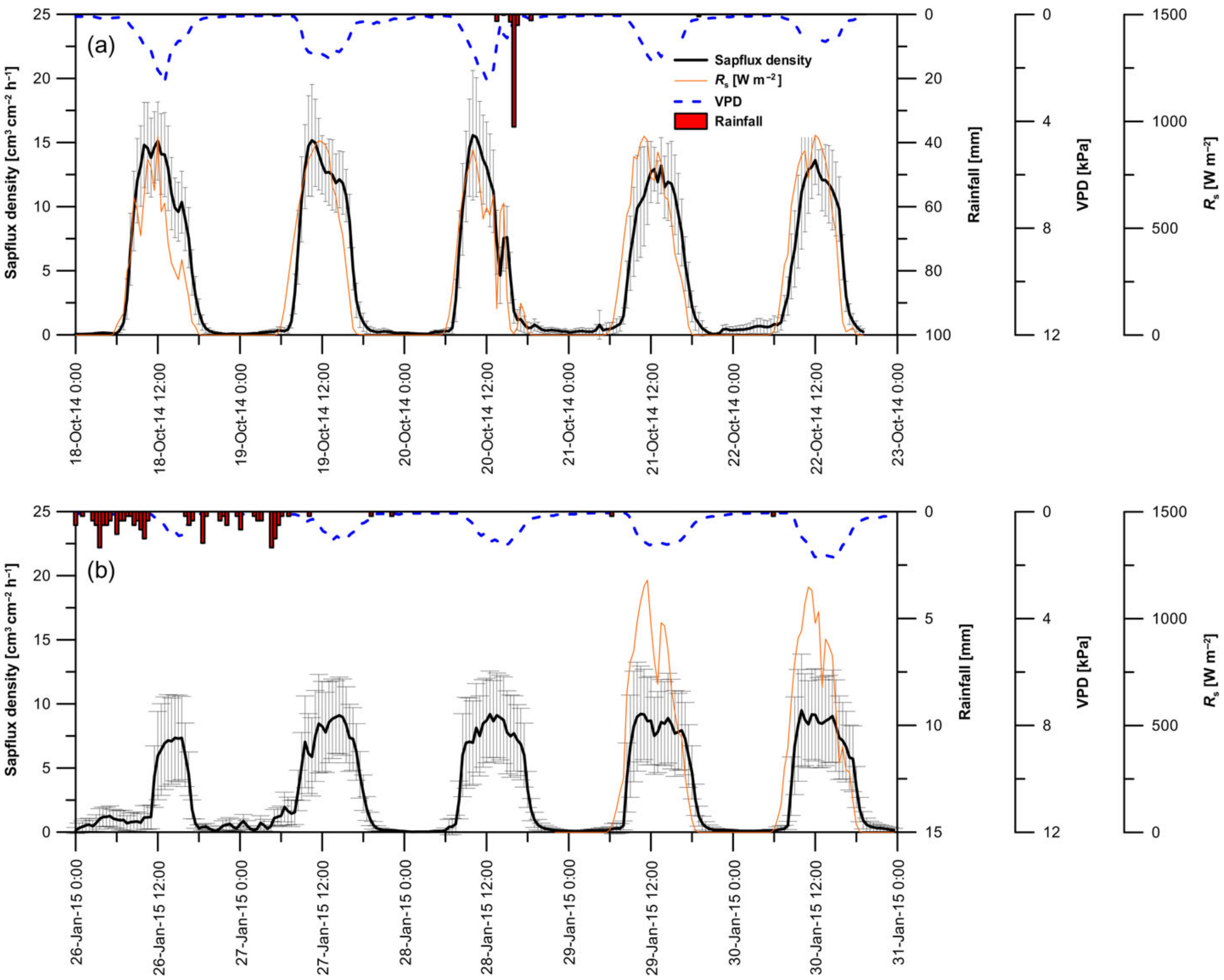

Figure 6. Diurnal variations in average sap flux density ($J_p$, cm$^3$ cm$^{-2}$ h$^{-1}$) for the 12 measured *Psiadia altissima* trees along with incoming short-wave radiation ($R_s$, W m$^{-2}$), vapour pressure deficit (VPD, kPa) and rainfall: (a) between 18 and 23 October 2014 (dry) and (b) between 26 and 31 January 2015 (wet). Data are 30-min averages and error bars indicate ±SD.

the LMRF zone of Eastern Indonesia (Juhrbandt et al. 2004) was distinctly higher than $g_s$ for the *Psiadia* trees but closer to $g_s$ for the two understorey shrubs *Lantana* (540–672 mmol m$^{-2}$ s$^{-1}$) and *Rubus* (468–570 mmol m$^{-2}$ s$^{-1}$) during times of ample soil moisture (Table 2). Nevertheless, $g_s$ for *Psiadia* trees was similar to the range established for 6-year-old fallow vegetation in lowland Amazonia (158–334 mmol m$^{-2}$ s$^{-1}$, de A. Sá et al. 1999). Sommer et al. (2002) drew attention to the fact that $g_s$ of young regrowth in eastern Amazonia tends to decrease with age, with high initial $g_s$ (~400 mmol m$^{-2}$ s$^{-1}$) in 2- to 3-year-old fallows and values approaching those of upper canopy trees in old-growth forests after ~10 years (cf. Roberts et al. 1990, de A. Sá et al. 1999, Reich et al. 1999). It is thus possible that $g_s$ of the *Psiadia* trees will decrease as the trees grow older.

Like the three species examined in this study (Figure 3), the (maximum) $g_s$ of all successional trees investigated by Juhrbandt et al. (2004) in eastern Indonesia showed a negative relationship with VPD, although there was considerable variation between species. Overall, *Rubus* was less sensitive in this regard than either *Lantana* or *Psiadia* (Figure 3). Although $g_s$ for all three species was highest during times of ample soil moisture, the observed range in values was much greater for the two shrubs than for the *Psiadia* trees (Table 2), suggesting a greater effect of soil moisture on the degree of stomatal opening in the case of the possibly less deeply rooted shrubs. This further suggests that the shrubs are more isohydric than the trees. Similar relationships between $g_s$ and soil moisture have been observed in Amazonian (Roberts et al. 1990, Harris et al. 2004) and Bornean rain forests (Kumagai et al. 2004*a*) and may reflect a strategy to cope with short-term water stress induced by partial root zone drying during dry periods (Figure 2). Trees in perennially wet tropical rain forests tend to have their roots concentrated

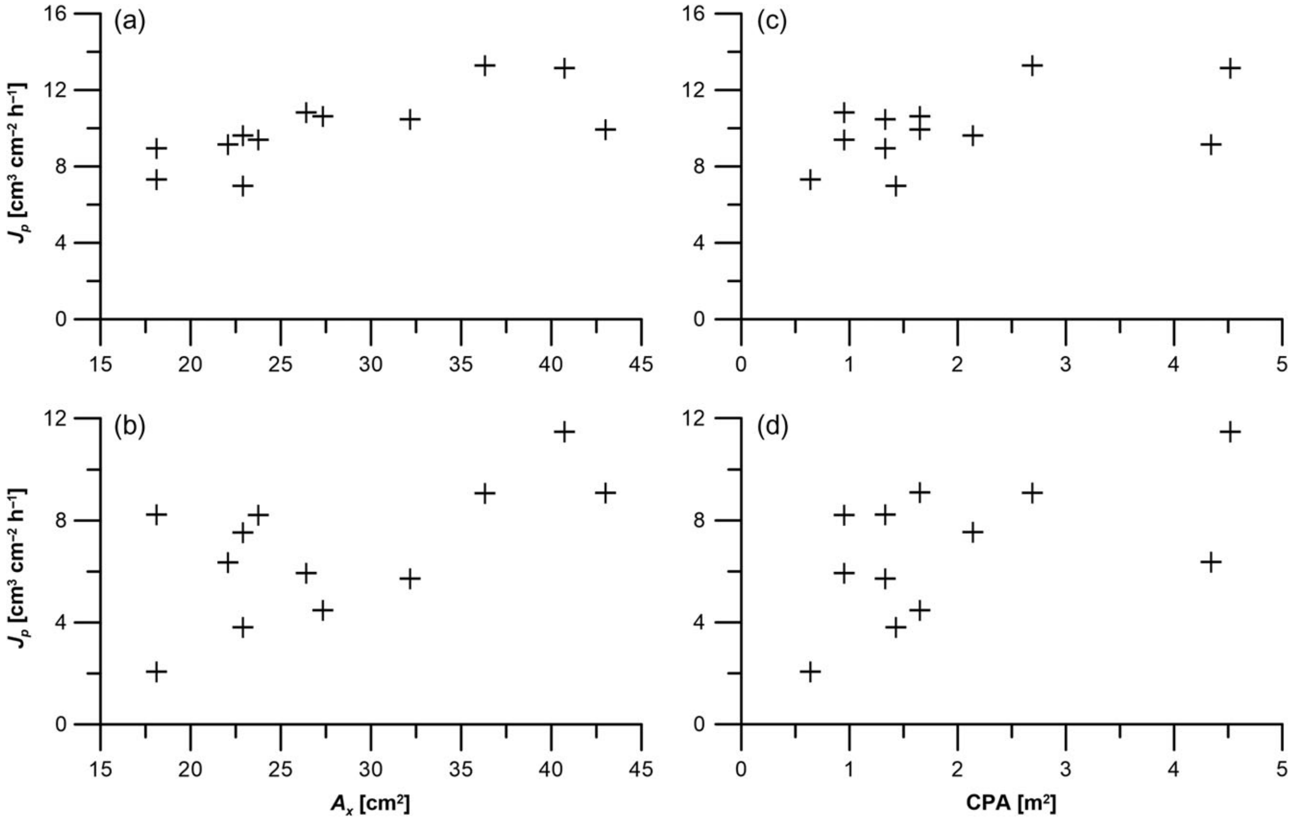

Figure 7. Relationships between daytime-averaged sap flux density ($J_p$, cm$^3$ cm$^{-2}$ h$^{-1}$) for 12 *Psiadia altissima* trees and conductive sapwood area ($A_x$, cm$^2$) for (a) clear-sky (19 October 2014) and (b) rainy (29 January 2015) conditions. Idem between $J_p$ and crown projection area (CPA, m$^2$) for (c) clear-sky and (d) rainy conditions.

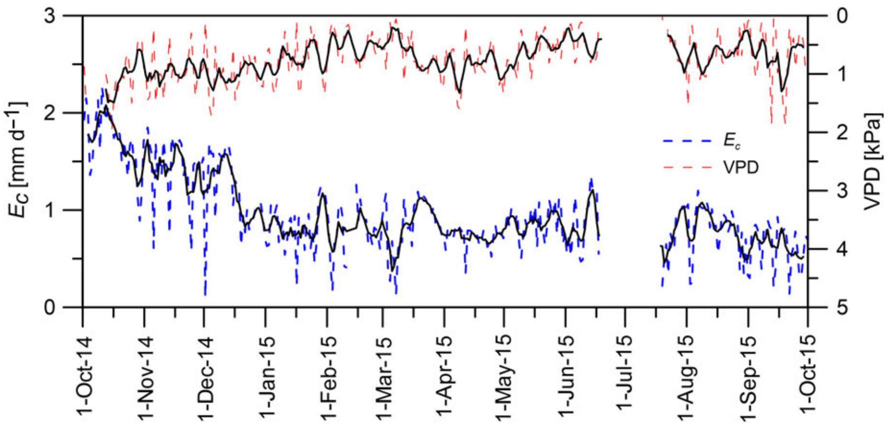

Figure 8. Seasonal variation in daily tree transpiration $E_c$ (averaged for 12 trees; in mm d$^{-1}$) and atmospheric vapour pressure deficit VPD (kPa) at the Andasibe young secondary forest site between 1 October 2014 and 30 September 2015. The solid black lines represent 5-day moving averages.

in the uppermost soil layers (Vogt et al. 1996, Yamashita et al. 2003), which is adequate as long as the soil profile remains wet for most of the year (Doley 1981) and nutrients are readily available due to rapid decomposition of leaf litter and fine roots (Vitousek and Sanford 1986). Instead, in areas experiencing a more extended dry season like the study area (Figure 2), maintaining modest rates of water uptake over longer periods (Figure 8) may well be the most effective strategy (Doley 1981). Despite the similarity in total fine root biomass (2–10 mm diameter) in the first 100 cm for shrub and tree fallows in the Andasibe study area (Andriamananjara et al. 2016), the possibly more shallow rooted understorey shrubs exhibited a much stronger response to declining soil water contents than the *Psiadia* trees, which kept having access to soil moisture in

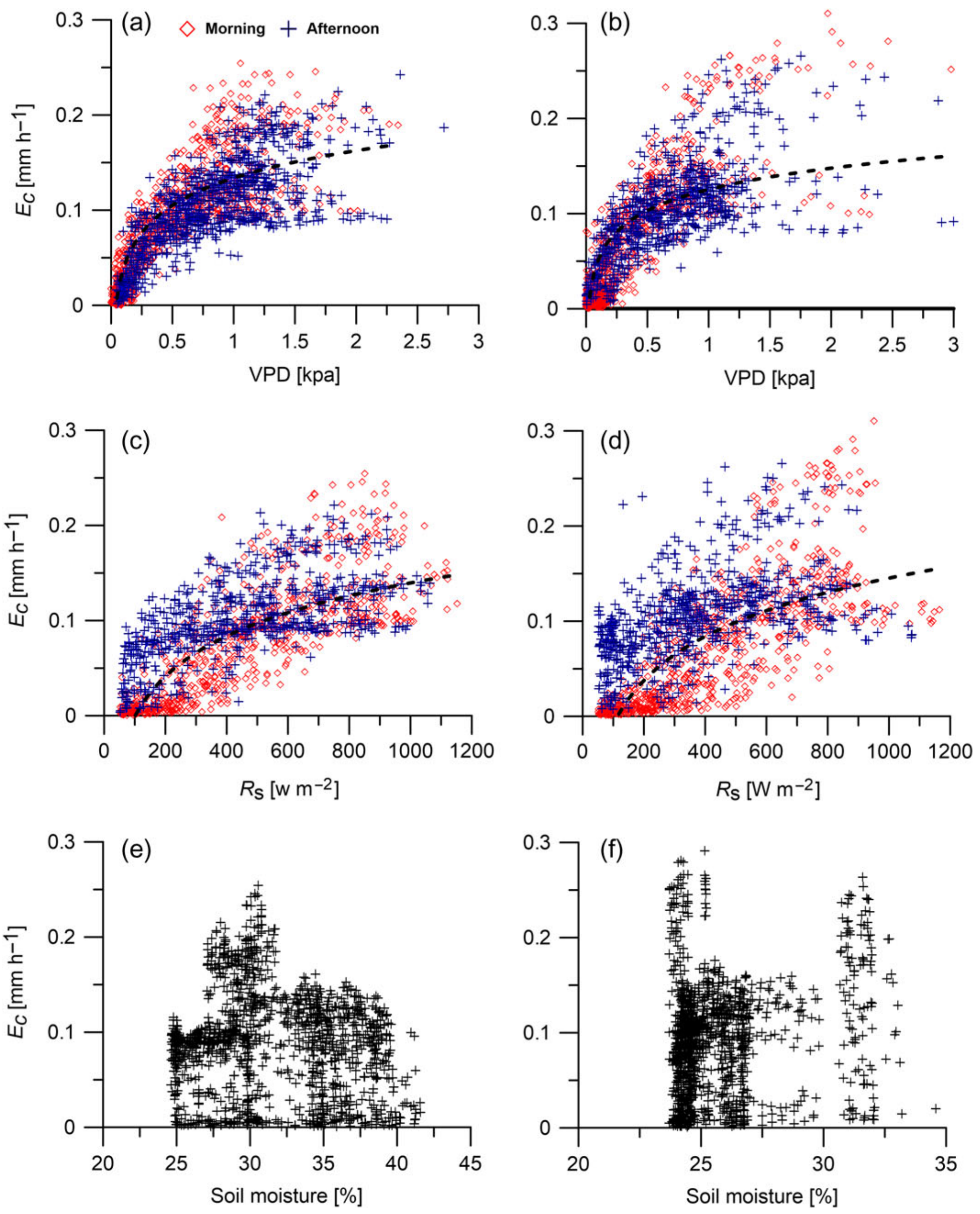

Figure 9. Relationships between hourly tree transpiration per unit crown area ($E_c$, mm h$^{-1}$) and atmospheric vapour deficit (VPD, kPa), short-wave radiation ($R_s$, W m$^{-2}$) or average soil moisture (%) in the top 40 cm during the wet (a, c, e) and the dry season (b, d, f) at the Andasibe young secondary forest site. Red diamonds denote morning observations (07:00–12:00 h) and blue crosses afternoon observations (13:00–17:00 h).

Table 4. Stepwise multi-linear model to predict tree transpiration ($E_c$) from vapour pressure deficit (VPD, kPa), incoming short-wave radiation ($R_s$, W m$^{-2}$) and average soil moisture content in the top 40 cm ($\theta$, %) using the equation $\log(E_c) = c_1 \log(\text{VPD}) + c_2 \log(R_s) + c_3\theta + c_4$. RMSE, root mean square error; –, not included in the multi-linear model. For the non-log-transformed stepwise multi-linear model results, see Table S2 available as Supplementary Data at *Tree Physiology* Online.

| | | Rank VPD | Rank $R_s$ | Rank $\theta$ | $c_1$ | $c_2$ | $c_3$ | $c_4$ | $R^2$ | RMSE |
|---|---|---|---|---|---|---|---|---|---|---|
| Hourly data | All | 2 | 1 | – | 0.10 | 0.74 | – | −3.03 | 0.54 | 0.346 |
| | Wet | 1 | 2 | 3 | 0.73 | 0.30 | 0.013 | −2.03 | 0.81 | 0.208 |
| | Dry | 1 | 2 | 3 | 0.63 | 0.25 | 0.017 | −1.98 | 0.67 | 0.248 |
| Daily data | All | 1 | 2 | – | 0.35 | 0.40 | – | −1.02 | 0.65 | 0.122 |
| | Wet | 1 | 2 | 3 | 0.45 | 0.43 | 0.006 | −1.32 | 0.73 | 0.105 |
| | Dry | 1 | 3 | 2 | 0.35 | 0.345 | 0.024 | −1.48 | 0.68 | 0.120 |

deeper layers to maintain transpiration (Figures 2 and 8). With regard to the relative competing ability of the two invasive shrub species, values of $g_s$ of *Rubus* were always smaller than those for *Lantana*, although the difference was only significant during the dry season (Table 2). As such, the hypothesis that the reputedly more vigorous *Rubus* (Styger et al. 2007) would exhibit higher stomatal conductances throughout the year was rejected.

The response of $g_s$ to changes in VPD for *Psiadia* trees was more pronounced when $R_s$ was high, especially under conditions of ample soil moisture, while no such tendency was found during low soil moisture conditions (Figure 5). Similar findings have been reported by Roberts et al. (1990) for lowland rain forest in Amazonia and by Kumagai et al. (2004*a*) in Bornean forest. *Lantana* behaved in a similar way to the canopy trees but *Rubus* reacted most strongly in this regard but only when soil moisture was plentiful (Figure 5). Such contrasting behaviour highlights the need to take differences in root distribution and responses in $g_s$ to soil moisture conditions into account when modelling transpiration from regenerating vegetation.

### *Tree sap flux density, daily sap flow and transpiration*

To our knowledge, the data on sap flux densities ($J_p$) and daily sap flow rates ($Q$) for *Psiadia* trees presented here provide some of the first quantitative observations for young (as opposed to more mature; Giambelluca et al. 2003) secondary tropical forest. Daytime-averaged values of $J_p$ appeared to increase with the increasing sapwood cross-sectional area $A_x$ during either season, indicating higher sap flux densities in larger trees throughout the year. However, variability amongst similarly sized trees was considerable (Figure 7a and b). Although such variability suggests that crown position (i.e. degree of shading) is an important factor determining $J_p$ (and thus $Q$), the relationships between projected crown area and sap flux density were not particularly strong, also because of the uncertainty with regards to radial changes in $J_p$ (Figure 7c and d). Average daily sap flow increased with tree size (crown projected area) but stabilized for crowns $\geq 3\ \mathrm{m}^2$ (Table 1). Similar positive relationships between tree size (DBH, $A_x$) and $Q$ have been reported for various species-rich old-growth tropical lowland (Granier et al. 1996, Andrade et al. 1998, Meinzer et al. 2001) and lower montane rain forests (Motzer et al. 2005, McJannet et al. 2007, Aparecido et al. 2016). However, sap flow studies conducted in tall old-growth forests typically include a much wider range of sample tree diameters than encountered in young secondary stands or tree plantations, which would tend to enhance a tree-size effect. Also, despite the demonstrated dependence on tree size, important (two- to fourfold) inter-species differences in (daily maximum) $J_p$ have been reported for similarly tall trees in the upper canopies of several old-growth lowland and montane rain forests (e.g. Granier et al. 1996, Horna et al. 2011, Aparecido et al. 2016). Likewise, comparative investigations involving multiple tropical broad-leaved plantation species exhibiting contrasting growth rates under equal site conditions have shown average maximum $J_p$ and average annual $Q$ to typically vary about twofold between species (Dierick and Hölscher 2009, Kunert et al. 2010, 2012). As such, both in young, even-aged, vertically less structured forest stands, and in tall, species-rich old-growth forests, plant traits other than stem diameter (e.g. phenology) appear to affect the magnitude of sap flux density and tree water use (Motzer et al. 2005, Dierick and Hölscher 2009, Kunert et al. 2010).

At ~15 $\mathrm{cm^3\ cm^{-2}\ h^{-1}}$ during the dry season and 7.5–9 $\mathrm{cm^3\ cm^{-2}\ h^{-1}}$ during the rainy season (Figure 6), values of maximum sap flux density for the *Psiadia* trees of the study forest were intermediate between those observed for upper canopy trees in mature LMRF in Pacific Costa Rica (3–6.2 $\mathrm{cm^3\ cm^{-2}\ h^{-1}}$; Aparecido et al. 2016) and Ecuador (18–36 $\mathrm{cm^3\ cm^{-2}\ h^{-1}}$; Motzer et al. 2005), but similar to those for an old-growth LMRF in eastern Indonesia (10–13 $\mathrm{cm^3\ cm^{-2}\ h^{-1}}$; Horna et al. 2011). The main climatic contrast between these LMRF sites appears to be the amount of precipitation, suggesting lower maximum $J_p$-values for sites experiencing more prolonged wet canopy conditions (Horna et al. 2011, Aparecido et al. 2016). Because the comparatively low annual rainfall at our study sites (1625 mm), as well as a relatively long dry season (Figure 2), the stand's low maximum $J_p$ and low DBH (6.1 ± 1.3 cm after 6 years of regrowth) likely reflect a combination of adaptation to limited topsoil water availability during a major part of the year during which moisture must be supplied by deeper layers (cf. Ghimire et al. 2014) and reduced soil fertility following several slash and burn cycles (Styger et al. 2007) as also evidenced by the low above-ground biomass of the stand (Andriamananjara et al. 2016). However, relatively low values of maximum $J_p$ (5–12 $\mathrm{cm^3\ cm^{-2}\ h^{-1}}$; C.P. Ghimire, unpublished data) were also observed for *Eugenia* and *Erythroxylum* trees in the upper canopy (DBH 16–17 cm) of a nearby semi-mature forest at Andasibe that had been manually logged some 22 years ago but had never experienced the serious nutrient losses typically associated with burning and swidden cultivation (Hölscher et al. 2005, cf. Styger et al. 2007). Therefore, low $J_p$ values may indeed be characteristic of the forests of the study area and possibly represent an adaptation to the prevailing conditions (cf. Ghimire et al. 2014).

Average daily sap flow totals for the 12 measured *Psiadia* trees were mostly below 5 kg $\mathrm{day^{-1}}$, with an overall average of only 1.8 ± 1.1 kg $\mathrm{day^{-1}}$ (Table 1). As stated, comparative data for secondary tropical forests of any age class are lacking but average values of $Q$ for similarly aged native trees grown in plantations in (lowland) Panamá (but roughly two to three times larger in terms of their DBH than the *Psiadia* trees of the study forest) ranged between ~6 and 12.5 kg $\mathrm{day^{-1}}$ (Kunert et al. 2012), while average daily sap flow rates observed for 12-year-old native plantation trees in the (lowland) Philippines (DBH range: 6.6–22 cm) varied between 4 and 62 kg $\mathrm{day^{-1}}$ (Dierick and Hölscher 2009). Likewise, the few existing data on $Q$ for old-growth LMRF sites at comparable elevations to the Malagasy study site (990 m a.s.l.) indicate much higher values for upper canopy trees (25–132 kg day$^{-1}$; Motzer et al. 2005, McJannet et al. 2007, Horna et al. 2011) vs 1–10 kg day$^{-1}$ for suppressed or sub-canopy trees (Motzer et al. 2005, Horna et al. 2011). Note that the trees sampled in these studies had much larger DBH (range for upper canopy trees 20–220 cm and for suppressed trees generally >10 cm), while $Q$ was strongly related to sapwood area $A_x$. As such, the low sap flow rates derived for the *Psiadia* trees mostly reflect their small sapwood area (<50 cm$^2$; cf. Eq. (3) and Table 1). However, expressed in terms of mean daily tree transpiration rate per unit crown area ($E_c$), the 0.97 mm day$^{-1}$ derived on average for the *Psiadia* trees was similar to values reported for four similarly aged native tree plantations in seasonally dry Panamá (0.57–1.07 mm day$^{-1}$; Kunert et al. 2010). Likewise, expressed per unit ground surface area, the average daily transpiration rate for the 6- to 7-year-old *Psiadia* stand ($E_t$, 0.73 mm day$^{-1}$ or 265 mm year$^{-1}$) was very similar to stand-scale values obtained for similarly sized *Anacardium excelsum* and *Hura crepitans* plantations in Panamá (0.56–0.82 mm day$^{-1}$ or 204–298 mm year$^{-1}$; Kunert et al. 2012) and at the low end of the range for tall old-growth LMRF at comparable elevations (0.7–1.7 mm day$^{-1}$ or 253–590 mm year$^{-1}$; Motzer et al. 2005, McJannet et al. 2007, Horna et al. 2011, Aparecido et al. 2016). Naturally, 'direct' comparisons of transpiration rates for different sites require some caution because of potential differences in site radiation and rainfall seasonality. Normalizing transpiration from the *Psiadia* trees by net radiation $R_n$ showed $E_t/R_n$ to be remarkably low (0.13 for rainy months, 0.19 during the dry season), especially compared with values derived by micrometeorological means for young regrowth in Amazonia (0.73–0.79; Hölscher et al. 1997, Sommer et al. 2002), vigorous 6-year-old pines in Fiji (0.80; Waterloo et al. 1999) and old-growth lowland rain forest in Borneo (0.55; Kumagai et al. 2004*b*), but also compared with values for old-growth montane rain forests at comparable elevations elsewhere in the tropics (0.33–0.62; Küppers et al. 2008, McJannet et al. 2007). Whilst transpiration rates obtained by micrometeorological methods will be higher than those based on sap flow measurements made in the tree stratum alone because of the incorporation of (the comparatively minor) evaporative contributions by sub-canopy trees, the understorey and the forest floor (Motzer 2003, Aparecido et al. 2016), it cannot be excluded that the cited high values of $E_t/R_n$ that were derived by micrometeorological means also include evaporation from a partially wetted canopy during and after rainfall events, apart from any evaporation-enhancing effects of advected energy (Hölscher et al. 1997, Giambelluca et al. 2000). Nevertheless, at 265 mm year$^{-1}$, transpiration from the *Psiadia* trees in the young regenerating forest at Andasibe cannot be considered particularly high and is certainly lower than values inferred for the tree stratum of the nearby semi-mature forest (460 mm year$^{-1}$; C.P. Ghimire, unpublished data) and old-growth montane rain forest (~725 mm year$^{-1}$; based on catchment water budget data in Bailly et al. (1974) and rainfall interception data in Ghimire et al. (2017), hence this estimate includes evaporative contributions from all forest strata). More work is needed to ascertain the magnitude of transpiration in differently aged regenerating tropical forests in different settings (lowlands vs montane, regrowth on abandoned pasture land vs swidden cultivation cycles; cf. Hölscher et al. 2005, Styger et al. 2007).

### Response of tree transpiration to environmental drivers

Our results showed that VPD and to a lesser extent $R_s$ were the main drivers and regulators of tree transpiration, during both the wet and the dry season (Figure 9a–d and see Table S1 available as Supplementary Data at *Tree Physiology* Online), while soil water availability played a comparatively minor role (Figures 2 and 9e, f; see Tables S1 and S2 available as Supplementary Data at *Tree Physiology* Online). Similar relationships have been reported for rain forests (Meinzer et al. 1993, Granier et al. 1996, Motzer et al. 2005, Roberts et al. 2005, McJannet et al. 2007, Horna et al. 2011) and plantations (Cienciala et al. 2000, Kunert et al. 2010, 2012) across the humid tropics. The plateau-shaped relationship between hourly VPD and canopy transpiration is usually attributed to gradual stomatal closure at higher VPD levels (Figure 6; Meinzer et al. 1993, Granier et al. 1996, Motzer et al. 2005, Horna et al. 2011). Our results further support the finding of Jarvis (1993) that in aerodynamically rough forests that are well coupled to the atmosphere and not limited by overall soil water availability (as in this study), transpiration will continue at the rate imposed by VPD.

## Conclusions

Tree transpiration and stomatal conductance ($g_s$) of the dominant tree species (*P. altissima*), as well as the stomatal response of two invasive understorey shrubs (*L. camara* and *R. moluccanus*) were studied in a 6- to 7-year-old regenerating forest in upland eastern Madagascar. Atmospheric vapour pressure deficit (VPD) and to a lesser extent incoming solar radiation ($R_s$) were the main drivers and regulators of tree transpiration, during both the wet and the dry season, while soil moisture availability played a very minor role. Stand-level transpiration from the *Psiadia* trees was comparable to values reported for similarly aged native tree plantations elsewhere in the seasonal tropics but lower than for various old-growth tropical montane rain forests, both in absolute terms and after normalizing by net radiation. Vapour pressure deficit, $R_s$ and soil moisture had varying influences on $g_s$. Vapour pressure deficit strongly influenced $g_s$ of the trees while $R_s$ had a larger influence on $g_s$ of the understory shrubs. The presumably more shallow-rooted shrubs exhibited a much stronger response to declining soil water contents than the *Psiadia* trees, indicating the more isohydric nature of the shrubs compared with the trees. Despite its reputedly more vigorous growth, $g_s$ of *Rubus* was not higher than that of *Lantana*. The contrasting behaviour in $g_s$ response to changes in soil moisture and environmental variables for the trees and shrubs highlights the need to take differences in root distribution into account when modelling transpiration from regenerating vegetation.

## Supplementary Data

Supplementary Data for this article are available at *Tree Physiology* Online.

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## Conflict of interest

None declared.

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