

Evapotranspiration of subtropical forests and tree plantations: A comparative analysis at different temporal and spatial scales

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ABSTRACT

The area of tree plantations in the humid subtropical region of Northern Argentina has recently increased five folds. However, the impact of this land use change on evapotranspiration (ET), one of the main components of the hydrologic cycle, has not been evaluated. We studied the ET at tree and ecosystem levels for native forests and three tree plantations (*Pinus taeda*, *Araucaria angustifolia* and *Eucalyptus grandis*). Water consumption of individual trees was estimated using sap flow measurements. Ecosystem ET was characterized using both remote sensing derived data products (ET_{MODIS}) for 2000–2011 and scaling up from tree sap flow measurements to stand level. Canopy conductance (g_c) was estimated using both sap flow measurements and ET_{MODIS} data. At individual level, transpiration was positively related to the size of the tree, and the relationship was well described by an exponential function when all species (both native and cultivated trees) were included in the analysis. The average annual leaf area index was similar between native forest and tree plantations. The ET estimates obtained from scaling up sap flow measurements and from ET_{MODIS} were relatively similar in most cases and differed by 4–34%, depending on the ecosystem. The tree plantations, regardless of density or age, did not show higher ET_{MODIS} than native forests. The ET ranged from 1161 to 1389 mm per year across native forests and tree plantations according to remote sensing, representing 58–69% of the annual precipitation. Furthermore, the good agreement between ET estimates, with the exception of *E. grandis*, obtained using sap flow and remote sensing provide a good basis for predicting the effects of land conversion from native forest to most non-native tree plantations on regional ET. Monthly ET_{MODIS} increased with increasing monthly air saturation deficit (ASD) up to 0.8 kPa, value at which ET_{MODIS} did not increase further probably due to stomatal control and low values of g_c . Different negative exponential relationships between g_c and ASD were obtained when g_c was calculated by scaling up daily tree sap flow to ecosystem level. Canopy conductance (estimated by remote sensing) declined in a similar negative exponential fashion with increasing ASD, and no differences were observed across ecosystem types. The result of increasing the time step, from daily to monthly, and the spatial scale from individual tree to stand level, had the consequence to lower, even to eliminate differences in annual ET and g_c among ecosystems in their responses to climate drivers. This suggests that the nature of ET regulation at individual and ecosystem levels could be different, which should be taken into account when predicting the effects of changes in land use on regional hydrology.

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Abbreviations: ASD, air saturation deficit; DBH, diameter at breast height; ET, evapotranspiration; ET_{MODIS}, evapotranspiration estimated from remote sensing with MODIS; ET_{upflow}, evapotranspiration at stand level, scaled up from field sap flow measurements; g_c , canopy conductance; GR, global radiation; MODIS, moderate resolution imaging spectroradiometer; SF, total diurnal sap flow; T, transpiration at stand level from field sap flow measurements.

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1. Introduction

One of the major processes regulating water exchange between terrestrial ecosystems and the atmosphere, particularly in forests, is evapotranspiration (ET), which has two different components: evaporation and transpiration. Evaporation in dense forests refers to the exchange of water from the liquid to the gaseous phase mostly from the canopy, while transpiration indicates the process of water vaporization from leaves of trees. Both processes are driven by the available energy and the drying potential of the surrounding air, but transpiration also depends on the capacity of plants to transport water from the roots and internal water storages to the leaves as well as the stomatal control of water losses (Bucci et al., 2008; Giambelluca et al., 2009).

Information on the effects of tree plantations on regional hydrological cycle processes is extremely important in assessing the impact of land use changes and in developing strategies related to sustainable use of water resources. Some information is available about the hydrological impacts of converting grasslands or shrublands to tree plantations (e.g., Jobbágy et al., 2006). In humid regions where forests are the dominant vegetation type, such as in Northeastern (NE) Argentina, the impact of tree plantations on hydrological processes, particularly evapotranspiration, has not been assessed.

These moist subtropical forests maintain high photosynthetic rates during most time of the year because many tree species are evergreen and the winter period during which the deciduous canopy species drop their leaves is short and with infrequent sub-zero air temperatures (Gatti et al., 2008; Tan et al., 2012; Cristiano et al., 2014). Changes in land use, particularly the replacement of native forests by tree plantations may have an impact not only on the water balance but also on the carbon balance at a regional level. Tree plantations are expanding at a rate of 5000 km² per year in South America (Jobbágy and Jackson, 2004; Jobbágy et al., 2006). In NE Argentina, the area dedicated to tree plantations has recently increased five folds (Izquierdo et al., 2008). A paradigm that has not been assessed for humid forest ecosystems is that tree plantations have high productivity with great annual evapotranspiration (Jackson et al., 2005). However, this trade-off between carbon sequestration and water utilization may not be valid for humid subtropical forests (Zhang et al., 2013; Cristiano et al., 2014).

The use of information provided by remote sensing has emerged as a useful tool in studying spatial-temporal dynamics of ecosystem processes. For example, some models allow the estimation of ET from satellite data. The most widely used ET model is the MOD16A2 product from the MODIS-Terra sensor (Mu et al., 2011). This product has been validated using 46 sites with eddy-covariance towers which are mostly located in North America while only two sites are in tropical rain forests close to the equator in Brazil. Currently there is no validation of this model for subtropical Argentinean forests neither using eddy covariance methods nor using sap flow measurements from individual trees. The current study investigates physiological mechanisms regulating transpirational water losses at different scales for native subtropical forests and high yield tree plantations in Northeast (NE) Argentina. The objectives of this study were (1) to understand mechanisms controlling the ET at tree and ecosystem levels including environmental factors such as evaporative demand and incoming solar radiation, and the interaction between canopy structure and the physical environment, described by canopy conductance (g_c), and (2) to determine whether ET and g_c from high yield tree plantations of *Eucalyptus grandis* W. Hill ex Maiden, *Pinus taeda* L. and *Araucaria angustifolia* (Bert) O. Kuntze were comparable to native subtropical forests in the same region. In this regard it was assessed whether the results of scaling up sap flow measurements to ecosystem level ET were consistent with ET estimated from remote sensing. Research on tree and ecosys-

tem level determinants of evaporative fluxes should improve our understanding of how subtropical trees and tree plantations regulate water fluxes. This information will also help to predict the impact of land use changes on ET at a regional scale.

2. Materials and methods

2.1. Study area

Field measurements of stand structure and transpiration were made in tree plantations of *P. taeda*, *E. grandis* and *A. angustifolia*, and in a native subtropical forest stand in the Atlantic Forest within the Iguazú National Park, Misiones Province, NE Argentina (26°25' S, 54°37' W). Mean annual rainfall in the area is about 2000 mm and is evenly distributed throughout the year. Mean annual temperature is 21 °C, and frost seldom occurs in winter, thus, temperatures are favorable for growth during most of the year. Relative air humidity is high throughout the year with mean monthly values ranging from 73 to 85%, from 1961 to 2014. Average monthly wind speed at 10 m ranges from 5.3 to 7.8 km h⁻¹ for the same time period. The soils, which are derived from basaltic rocks containing high concentration of Fe, Al and Si, correspond to the 9a type (Ligier et al., 1990) and include Alfisols, Molisols and Inceptisols (Soil Survey Staff, 1992).

2.2. Sap flow

Sap flow was measured in two trees for each of 10 dominant woody species with different leaf phenology in native forests and one palm and two lianas which contribute to 72% of the entire canopy and sub-canopy woody species. Sap flow was measured also in five trees in *E. grandis* and in six trees in *P. taeda* and *A. angustifolia* tree plantations, which were 12, 6, and 28 years old, respectively, at the time of the study. The species selected in the native forest, were *Parapiptadenia rigida* (Benth.) Brenan, *Cedrela fissilis* Vell., *Balfourodendron riedelianum* (Engl.) Engl., *Cabrera canjerana* (Vell.) Mart., *Chrysophyllum gonocarpum* (Mart. & Eichler) Engl., *Ocotea diospyrifolia* (Meisn.) Mez., *Lonchocarpus muehlbergianus* Hassl., *Cordia trichotoma* (Vell.) Arráb. ex Steud., *Holocalyx balansae* (P. Micheli), *Ceiba speciosa* (A. St. -Hil. Juss & Cambessds) Ravenna, *Euterpe edulis* Mart., *Pisonia aculeata* L. and *Amphilophium* Kunth sp. Thirty percent of the trees are deciduous and leaf drop occurs during the cold season (Cristiano et al., 2014). Understory plants were not included in the sap flow measurements across all systems. Sap flow measurements were obtained throughout 2012 and 2013, during the spring–summer and autumn–winter seasons, in order to have a good representation of annual variations in diurnal sap flow patterns (142 days in ten native forest species, 44 days in *P. taeda*, 46 days in *A. angustifolia* and 56 days in *E. grandis*). The heat dissipation method (Granier, 1985, 1987) was used for sap flow measurements. A pair of hypodermic needles 20-mm long and 2-mm in diameter, which contain a copper–constantan thermocouple inside a glass capillary tube and a heating element of constantan coiled around the tube, were inserted into the sapwood at 1.5 m from the ground in the main stem in each tree. The probes were installed in the same azimuthal position for all trees. Measurements in the outer 20 mm of sapwood may overestimate sap flow in few tree species because flow rates may decrease with sapwood depth in large trees. The upper (downstream) probe was continuously heated at a constant power by the Joule effect, while the unheated upstream probe served as a temperature reference. Temperature differences between the upstream and downstream probes were recorded every 10 s and 10-min averages were recorded using dataloggers (CR 10X, Campbell Scientific, Logan, Utah, USA). Sap flux density was calculated from the temperature difference between

the two probes using an empirical calibration (Granier, 1987). The temperature differences were corrected for natural temperature gradients between the probes (Do and Rocheteau, 2002). Mass flow of sap per individual was obtained by multiplying sap flux density by active sapwood cross-sectional area. Sapwood cross-sectional area was obtained by injecting a dye near the base of the main stem for each of the trees studied and a wood core was obtained 5 cm above the injection point with increment borers 1 h after injection (Meinzer et al., 2001). Even though it has been suggested that each species requires an individual calibration to obtain adequate estimates of sap flow using the heat dissipation method (Steppe et al., 2010), the empirical model was validated for diffuse porous tropical trees with similar xylem anatomy as the ones we are using in this study (Clearwater et al., 1999; McCulloh et al., 2007). One of the important issues for obtaining good estimates of sap flow is to minimize the wounding effects (Wiedemann et al., 2013). Consequently we drilled new holes and replaced the sensors frequently, and thus, continuous measurements were limited to short periods following installation because it is difficult to know if wound effects progress in all individuals of a given species at a similar rate. The diameter at breast height (DBH) of each studied tree and mean annual leaf area index (LAI) in each studied site were measured in a previous work (Table 2, Cristiano et al., 2014). The daily average sap flow per tree in the native forest was calculated taking into account both the DBH of the measured trees and the DBH of all the trees in the stand. For example, the daily average sap flow of *B. riedelianum* trees measured with an average DBH of 48.6 cm was 112.61 day^{-1} , but the average DBH of all individuals of this species in the native forest was 32.6 cm, resulting in an average daily sap flow of 75.61 day^{-1} . The DBH of the measured trees in the tree plantations were similar to the average DBH of all individuals in the stand.

2.3. Stand transpiration

The daily average sap flow per individual was scaled up to obtain transpiration at stand level (T , mm day^{-1}), multiplying the daily average sap flow per tree (1 day^{-1}) obtained from field measurements by tree density. The tree density of plantations was estimated on a 1000 m^2 square plot, while in the native forest 4 transects of $100 \times 10 \text{ m}$ were used. In each transect, all individuals with diameter at breast height (DBH) greater than 10 cm were identified and measured. The total evapotranspiration of each stand (native forest or tree plantation) ($\text{ET}_{\text{upflow}}$, mm day^{-1}) was calculated using the T values obtained from field measurements plus the water intercepted by the canopy obtained from the literature for similar ecosystems (Miralles et al., 2010). For the native forest and *E. grandis* plantation, an average annual interception value of 18% of annual precipitation corresponding to broadleaf evergreen forests was used. For *P. taeda* plantations an average value of 29% corresponding to coniferous forests was used (Miralles et al., 2010). These values were close to preliminary results on canopy interception measurements in our study sites.

2.4. Remote sensing evapotranspiration and meteorological variables

Satellite images of Terra-MODIS sensor (MOD16A2 product) were used to analyze the monthly actual evapotranspiration (ET) during a period of 12 years (2000–2011). The MOD16A2 product is a land surface ET product that represents all transpiration by vegetation and evaporation from understory and soil surfaces, expressed in 1-dimensional vertical units (mm day^{-1}). The MODIS ET product has a spatial resolution of 1 km^2 and a temporal resolution of 16 days. The MOD16 algorithm (Mu et al., 2007, 2011) used in this study is a revision of an algorithm proposed by Cleugh et al. (2007) based on the Penman–Monteith equation (Monteith, 1965). The

Table 1

Central geographic coordinate and number of pixels (1 km^2) used to characterize ET in each site from MODIS-Terra product.

Study sites	Latitude (S)	Longitude (W)	N° pixels
Native forest	25°41'28.51"	54°29'9.59"	4
	25°44'30.78"	54°21'39.17"	6
	25°48'16.13"	54°15'6.77"	1
<i>P. taeda</i>	26°9'50.20"	54°26'50.08"	2
	25°47'54.14"	54°25'11.57"	2
<i>E. grandis</i>	26°6'34.80"	54°26'10.68"	4
	26°7'43.13"	54°34'33.16"	2
<i>A. angustifolia</i>	26°14'48.92"	54°30'38.73"	1

MODIS ET algorithm uses global MODIS land cover, the fraction of photosynthetically active radiation/leaf area index data (Myneni et al., 2002), albedo data (Jin et al., 2003; Salomon et al., 2006) and global surface meteorology from the Global Modeling and Assimilation Office (GMAO) meteorological data. Aerodynamic resistance (r_a , the inverse of aerodynamic conductance) is calculated as a parallel resistance to convective and radiative heat transfer following the Biome-BGC model. Finally ET is estimated using r_a and a highly improved algorithm from the previous MODIS model which includes daytime and nighttime transpiration, soil evaporation and several parameters that now are a function of different biome types (e.g., the mean potential stomatal conductance per unit leaf area) (Mu et al., 2011). Evapotranspiration values were averaged monthly to obtain a value of average daily ET for each month. Using Google Earth, homogeneous continuous areas larger than 10 ha were selected for native forest stands ($n=3$) and tree plantations: *P. taeda* ($n=2$) and *E. grandis* ($n=2$). Only one plantation of *A. angustifolia* was found with an area larger than 10 ha. Even though ET estimates for *A. angustifolia* plantation using MODIS images were obtained, the results were not included in tables and figures containing stand level information because replications were not possible in the study area. These sites had the same soil type (Ligier et al., 1990) and topography (200–300 m asl). The landscape in the study area is fragmented with remnants of native forests and tree plantations. Most of the plantations have areas smaller than 1 pixel, which is 1 km^2 for the MODIS Terra ET product. The sites were inspected in the field and those sites with pixels containing at least 85% of the target vegetation/tree plantations coverage were selected. The number of pixels used to characterize ET and the geographical coordinates of the center of each site is included in Table 1. The largest distance between the most southern and the most northern study site was about 60 km. Cumulative daily rainfall values obtained from the nearest meteorological station (Puerto Iguazú-Aero) were used to calculate monthly precipitation, and hourly temperature and relative humidity values were averaged to obtain monthly values. These variables were used to calculate monthly air saturation deficits (ASD). Canopy conductance (g_c , m s^{-1}) was estimated according to Morris et al. (1998) using remote sensing monthly evapotranspiration data (ET_{MODIS} , mm s^{-1}) and mean monthly air saturation deficit (ASD, Pa) as:

$$g_c = \gamma \lambda \text{ET}_{\text{MODIS}} / \rho C_p \text{ASD} \quad (1)$$

where γ is the psychrometric constant (Pa K^{-1}), λ is the latent heat of evaporation of water (J m^{-3}), ρ is the atmospheric density (kg m^{-3}) and C_p is the specific heat of dry air at constant pressure ($\text{J kg}^{-1} \text{K}^{-1}$). To express g_c in molar units, values in m s^{-1} were divided by $(V_0 T^\circ P_0)/(T_0 P)$, where V_0 is the molar volume of air ($0.0227 \text{ m}^3 \text{ mol}^{-1}$), P_0 and T_0 are atmospheric pressure and temperature at standard conditions (100 kPa and 273 K, respectively), T° is daily mean temperature and P is atmospheric pressure, assumed constant at 98.9 kPa in the study area, which correspond to 200 m above sea level. The validation of this method for estimating g_c

Table 2

Information on: tree density; average DBH (diameter at breast height) per tree; mean annual LAI from MODIS data and field measurements; water consumption per tree, transpiration at stand level (T_{stand}); evapotranspiration at stand level (ET_{upflow}) calculated as T_{stand} + canopy interception; evapotranspiration from remote sensing (ET_{MODIS}). Final T_{stand} of native forest (954 mm year^{-1}) to calculate ET_{upflow} includes contribution of trees (841 mm year^{-1}), palms ($110.5 \text{ mm year}^{-1}$) and lianas (2.5 mm year^{-1}). Percent differences [%] between ET_{upflow} and ET_{MODIS} estimates are included. Different letters indicate significant differences ($p < 0.05$) between systems. Leaf Area Index values were obtained from Cristiano et al. (2014).

	Native forest	<i>P. taeda</i>	<i>A. angustifolia</i>	<i>E. grandis</i>
Tree density (ind ha ⁻¹)	480	1300	240	500
DBH ± SE (cm) (n)	23.9 ± 1.13 (192)	16.5 ± 0.2 (138)	37.5 ± 1.0 (24)	29.1 ± 0.6 (26)
Mean annual LAI _{MODIS} ± SE	5.6 ± 0.01 (3)	6.0 ± 0.08 (2)	5.2 (1)	5.6 ± 0.07 (2)
Mean annual LAI _{FIELD} ± SE	6.0 ± 0.29 (10)	4.5 ± 0.06 (10)	6.5 ± 0.1 (10)	3.9 ± 0.06 (10)
Water consumption ± SE (l day ⁻¹)	41.1 ± 5.6(30) ab	13.3 ± 4.7(6) bc	64.04 ± 8.3(6) a	30.66 ± 4.7(5) ab
T_{stand} (mm year ⁻¹)	841	633	561	560
ET_{upflow} (mm year ⁻¹)	1314	1211	1141	920
ET_{MODIS} ± SE (mm year ⁻¹)	1372 ± 31.32 a	1161 ± 66.14 b	1356	1389 ± 12.24 a
[%]	4	4	16	34

applying the Penman–Monteith combination equation is discussed in Morris et al. (1998). The same equation as above (Eq. (1)) was used to estimate g_c from field measurements of sap flow on a daily basis. Instead of ET_{MODIS} , T (stand level transpiration) calculated from up-scaling sap flow measurements to stand level were used in Eq. (1).

2.5. Data analysis

In conjunction with meteorological data, the determinants of seasonal variations of ET were analyzed using time series analysis. Cross-correlations were performed between the time series of ASD and ET in native forests and in *P. taeda* and *E. grandis* plantations. Annual ET values from remote sensing were compared between native forest and two tree plantations: *P. taeda* and *E. grandis* by a one way ANOVA analysis, after their assumptions of normality and homoscedasticity were assessed. Multiple comparisons were made using Scheffé contrasts. To test for statistical differences between g_c and ASD relationships, the ASD axes were ln transformed to linearize the relationships. The slopes of the linearized relationships were compared in pairs with t -tests using a 95% confidence.

3. Results

3.1. Tree water consumption and stem size across species

Species-specific water consumption (total daily sap flow, SF) was influenced by the average tree size and by species identity. A significant exponential relationship was observed between stem diameter at breast height (DBH) and SF with increasing SF as DBH increases, when all species (both native and cultivated trees) were included in the regression analysis (Fig. 1, $p < 0.0001$). Annual leaf area index (LAI) calculated by field measurements and by the MODIS sensor were similar and ranged from 5.2 to 6.0 (according to MODIS) across native forest and tree plantations. The LAI in the native forest decreased 35% during the cold season according to field data because the deciduous canopy species drop their leaves. Daily water consumption of *A. angustifolia* was significantly higher than *P. taeda*, with intermediate values for *E. grandis* and the native forest ($F = 3.85$, $fd = 3$, $p = 0.022$) (Table 2). The differences in daily water consumption between *P. taeda* and *A. angustifolia* trees were consistent with the average DBH differences (16.5 cm and 37.5 cm for *P. taeda* and *A. angustifolia*, respectively).

Daily cycles of sap flow during two days with different evaporative demand (high and low ASD) were depicted in Fig. 2. All species exhibited the typical diurnal sap flow pattern, with an increase in the early morning when global radiation (GR) and ASD increases to reach their maximum value near midday, after which sap flow began to decrease. Native forest trees tended to exhibit lower total daily sap flow at high ASD than the trees in the plantations (Fig. 2).

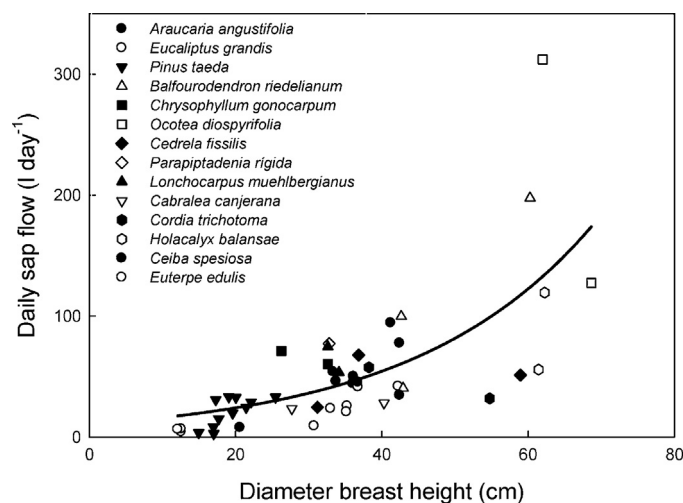


Fig. 1. Relationship between total daily sap flow (SF) and the diameter at breast height (DBH) in trees of native forest and tree plantation species. An exponential function was fitted to the data with $R^2 = 0.48$ ($SF = 10.7442 \text{ Exp}^{(0.0406\text{DBH})}$). Each point represents one individual per species.

The inset in each panel shows the relationship between daily SF and daily ASD for many days of measurements (Fig. 2). Daily SF increased with increasing ASD in three dominant native forest species and in the three plantations (Fig. 2 inset). Asymptotic functions were fitted to the scatter diagrams ($p < 0.0001$) for the three native forest species and for *E. grandis*. Sap flow kept increasing until ASD reached 0.8–1.0 kPa.

Another potential factor controlling sap flow is the incoming solar radiation. Water consumption increased as GR increased for three native species and most tree plantations, but the relationships could not be adequately described by any regression for two of the ecosystems (native forests and the *A. angustifolia* plantation). The scatter diagram of sap flow versus GR of *E. grandis* and *P. taeda* plantations, on the other hand, could be well described by a linear relationship having a R^2 of 0.74 and 0.45, respectively (results not shown).

3.2. Water consumption of native forests and tree plantations estimated with sap flow and remote sensing

Both estimates of ET, scaling up from the sap flow measurements to ecosystems (ET_{upflow}) and the ET estimated using remote sensing (ET_{MODIS}) were very similar for native forests and *P. taeda* plantations (Table 2). In contrast, *E. grandis* and *A. angustifolia* had lower values of ET_{upflow} compared to ET_{MODIS} . ET_{MODIS} was similar between native forests and *E. grandis* plantations, and both were

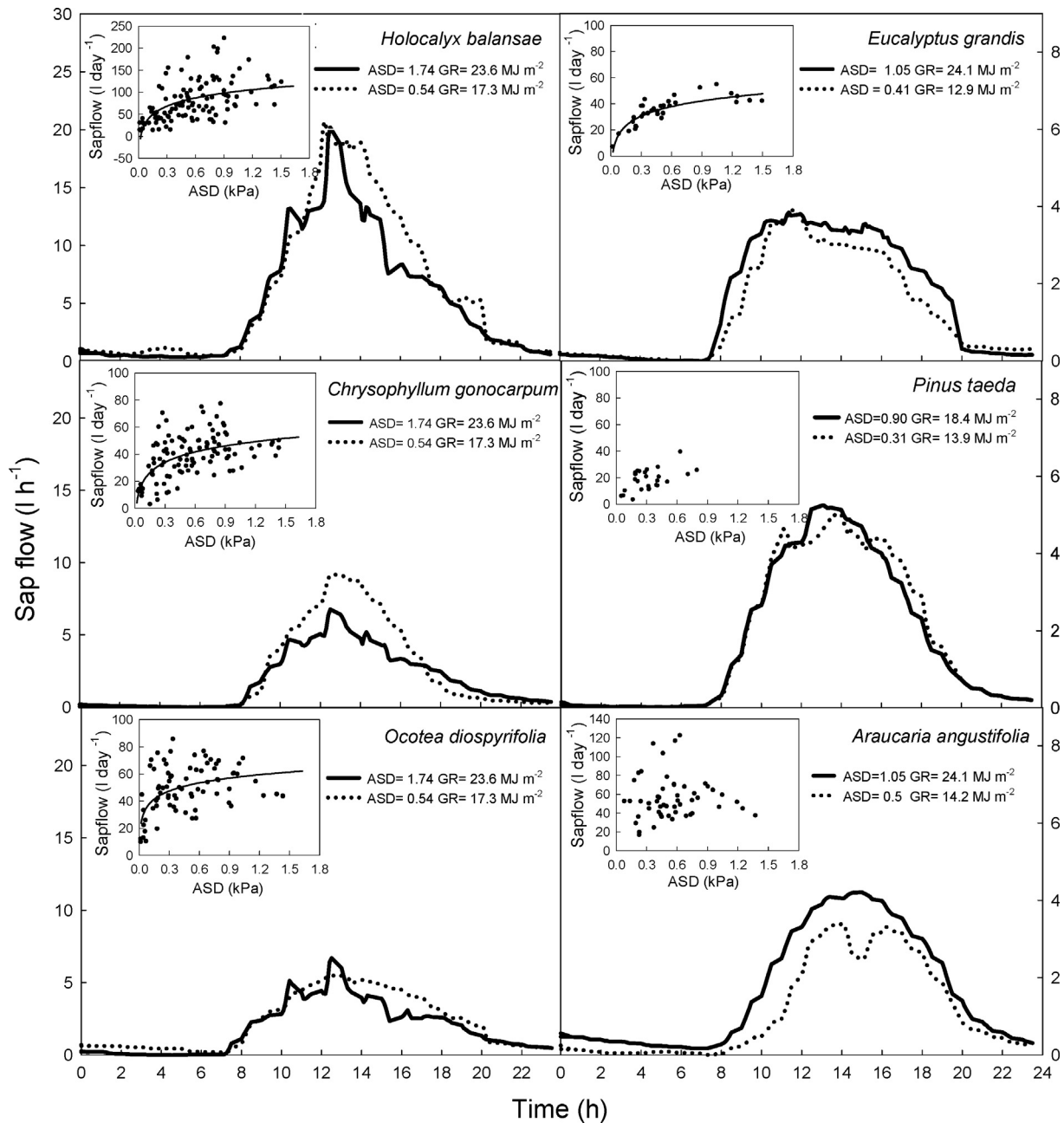


Fig. 2. Diurnal patterns of sap flow for two days with contrasting air saturation deficit (ASD) in the same tree for three dominant species of the native subtropical forest (left panels) and for each species from the three tree plantations, *Pinus taeda*, *Araucaria angustifolia* and *Eucalyptus grandis* (right panels). Average daily values of ASD and global solar radiation (GR) were also included. Insets: Total daily sap flow in relation to average daily ASD for all days of measurements.

significantly higher compared to *P. taeda* plantations ($F=12.51$, $fd=2$, $p=0.019$, Table 2).

3.3. Seasonal and inter-annual differences in ET_{MODIS} across native forests and forest plantations

Precipitation exhibited month-to-month differences during the 2000–2011 period, but no clear seasonal pattern was detected. The average monthly precipitation was 171 mm and ranged from 75 to 273 mm, but for most of the 2000–2011 periods, monthly precipitation was within 100 and 220 mm (Fig. 3a). There were strong seasonal changes in the air saturation deficit (ASD), with lower monthly ASD values (0.2 kPa) during the short winter season, particularly during June and July (Fig. 3b). The mean ASD values attained during the summer ranged between 0.8 and 1.0 kPa. The

panel c of figure 3 shows the seasonal variations in ET_{MODIS} of the native forest and *E. grandis* tree plantations which had similar patterns of variations compared to ASD variations. ET_{MODIS} decreased during the winter and increased during the summer consistent with the seasonal changes in ASD. Even though the temporal series of ET_{MODIS} in *P. taeda* plantations was shorter, strong temporal variations in ET_{MODIS} were also observed (Fig. 3d).

Cross-correlation analysis is a measure of similarities of two waveforms as a function of a time lag in months applied to one of them, in this case ET_{MODIS} with respect to ASD. The cross-correlation functions of the time series between these two variables showed the highest positive correlation when the analysis was performed with one month lag between ET_{MODIS} and ASD for the native forests (0.79), followed by *E. grandis* (0.77) and lastly by *A. angus-*

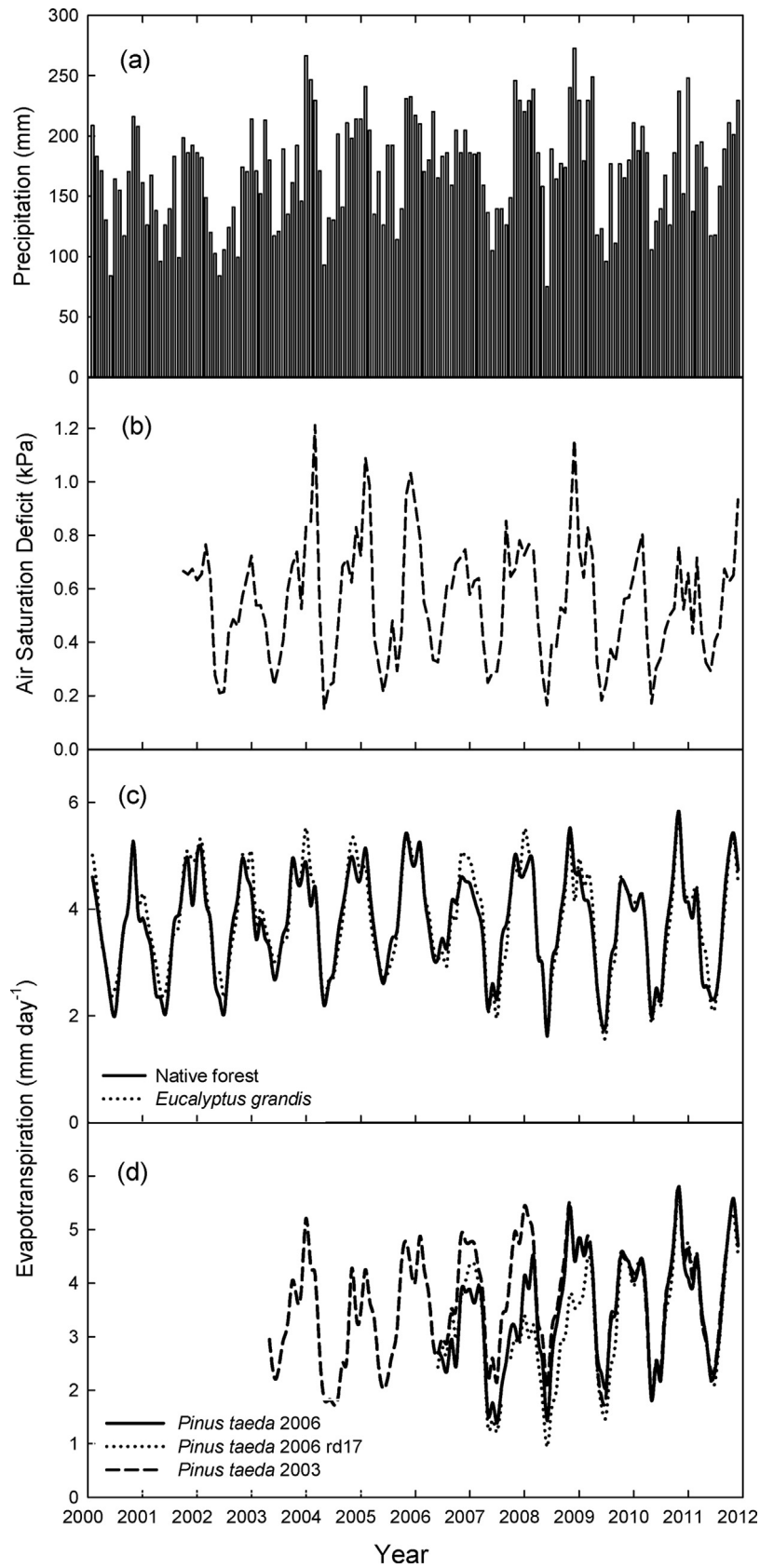


Fig. 3. (a) Monthly precipitation, (b) average monthly air saturation deficit (ASD), (c) monthly evapotranspiration on a daily basis obtained using MODIS-Terra (ET_{MODIS}) for native forests and tree plantations of *Eucalyptus grandis*, and (d) monthly evapotranspiration on a daily basis obtained using MODIS-Terra for three tree plantations of *Pinus taeda*.

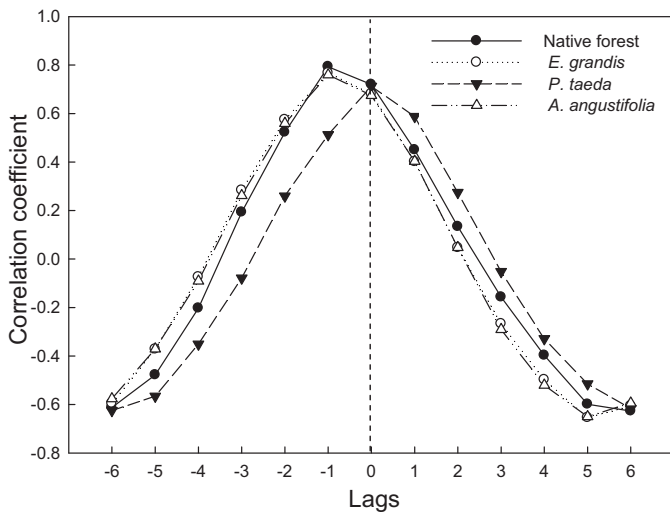


Fig. 4. Cross-correlation coefficients as a function of different lags (in months) between monthly ET_{MODIS} with respect to monthly ASD. Negative lags indicate that ET_{MODIS} peak before ASD. When there is no lag, the seasonal patterns of ET_{MODIS} and ASD are synchronized.

tifolia (0.76) (Fig. 4). The ET_{MODIS} and ASD time series for *P. taeda* were fully synchronized without lags (0.71) (Fig. 4).

Both the native forests and the tree plantations exhibited a significant asymptotic pattern of ET_{MODIS} versus ASD ($p < 0.0001$), regardless of the species composition and the structure (Fig. 5). The daily ET_{MODIS} for each month increased with increasing ASD, approaching the maximum values at around 0.8 kPa in all the systems studied (Fig. 5). It is necessary to point out that the values of ASD depicted in Fig. 5 are monthly average values, while the instantaneous ASD values were substantially higher approaching values of up to 4.5 kPa at midday during summer and spring seasons (unpublished information).

3.4. Canopy conductance at species and ecosystem level

Canopy conductance (g_c) of the native forest and plantations calculated using sap flow data decreased exponentially with increasing ASD (Fig. 6a). The shapes of the relationships were similar, but the native forest trees and *E. grandis* trees exhibited a steeper decrease with increasing ASD compared to *P. taeda* and *A. angustifolia*. All these relationships were well described by exponential functions with R^2 ranging from 0.42 to 0.89 ($p < 0.05$). The g_c versus ASD functions were not statistically different ($p < 0.05$) neither between native forest and *P. taeda* plantation, nor between *A. angustifolia* and *E. grandis* tree plantations. These two groups (native forest–*P. taeda* versus *A. angustifolia*–*E. grandis*), however, were statistically different. When a negative exponential function was fitted to the scatter diagram between g_c and GR calculated using sap flow data, the R^2 were 0.2 for the native forest, 0.53 for *E. grandis*, 0.05 for *P. taeda* and 0.54 for *A. angustifolia*. These relationships were statistically significant at $p < 0.001$, with the exception of *P. taeda* (results not shown). The g_c versus ASD functional relationships were similar across native forests and tree plantations when g_c was estimated by remote sensing (Fig. 6b); g_c decreased exponentially with increasing ASD and the functions were not statistically different among ecosystems ($p < 0.05$). The lack of statistical difference among ecosystems was also observed when one year data were used at a time (results not shown) instead of using all data from the 11 years period.

4. Discussion

4.1. Water consumption at individual level

At individual level, water consumption (daily sap flow) was positively related to tree size regardless of species. This pattern was similar to that found by Meinzer et al. (2001) across 107 tropical tree species. In our study, sap flow was measured in 26 individuals of 13 species in the native forest and in 5–6 individuals per species in each plantation. The diurnal patterns of sap flow of the native forest trees and trees in plantations were similar, but the native forest trees showed lower total daily sap flow at high ASD than the trees in plantations, suggesting that native forest trees have stronger stomatal control on water losses than tree plantation species. For the tree species in the native forests, the total daily water consumption per species was 15 to 20% lower under high (1.74 kPa) than low (0.54 kPa) daily average ASD. The tighter stomatal control on transpiration under high ASD is consistent with the species-specific relationship between total daily sap flow and daily ASD for the native tree species because sap flow did not increase further with ASD above 0.8 or 1 kPa. The large scatter observed in the relationship between sap flow and ASD of the native forest trees was probably because (1) the incoming solar radiation differences experienced by individual trees, and (2) the trees used in sap flow estimates differ in size and height. In contrast, the size of the trees in the plantations was relatively similar.

4.2. Scaling up sap flow of trees to stand level and remote sensing estimates of evapotranspiration

Evapotranspiration (ET) estimated by scaling up sap flow to ecosystems needs to include canopy interception, an important component of water loss to the atmosphere. Canopy interception is considered here to be a constant proportion of annual rainfall for the native forest and the tree plantations. The canopy interception depends not only on structural features of the vegetation but also on the rainfall temporal patterns. While some aspects of the forest and plantations differ, others such as LAI were relatively similar (Cristiano et al., 2014). It is well established that interception decreases with increasing rainfall intensity (e.g., Bahmani et al., 2012), however a yearly canopy interception value was used which average-out canopy interception over different types of rainfall patterns. Preliminary results of actual measurements of canopy interception in the study area (*P. Campanello unpublished results*) agree well with the values obtained from the literature. There are other uncertainties in canopy transpiration obtained from scaling up sap flow measurements to whole ecosystems such as the abundance and the number of species measured compared to the total number of species in the native forest stands (Bucci et al., 2008). The values of annual ET_{upflow} ranged from 920 mm to 1314 mm across all systems that represents between 46 and 66% of mean long term annual precipitation (2000 mm year⁻¹). A recent study in a tropical rainforest using a big-leaf model, eddy covariance fluxes and sap flow measurements has shown that average annual ET was 1323 mm, representing 51% of the annual precipitation (Kume et al., 2011). Compared to the forest ecosystems in our study sites, ET were similar but precipitation was substantially higher in the tropical site (2600 mm). Kume et al. (2011) summarized that ET and precipitation data from 138 tropical forests including both seasonal forests and various types of rainforests. According to Kume et al. (2011), ET increases linearly with increasing precipitation up to 1500 mm. At higher precipitation, ET remains fairly constant. The ET estimates across native forests and tree plantations obtained in our study fit well in the ET versus precipitation relationship described by Kume et al. (2011). In contrast, ET of tropical and sub-

tropical forests is substantially higher than for temperate forests (e.g., Wilson et al., 2001; Verstraeten et al., 2005).

Values of ET for each system calculated by sap flow + canopy interception (ET_{upflow}) and by remote sensing (ET_{MODIS}) were within the same order of magnitude for the native forest and *P. taeda* plantation. ET_{upflow} was 16% and 34% lower than ET_{MODIS} in *A. angustifolia* and *E. grandis*, respectively. There is abundant understorey woody vegetation in these plantations, which may account for the relative low estimates of ET_{upflow} . No abundant understorey woody species were found in the young *P. taeda* plantation. Furthermore, the width of the active xylem area in *E. grandis* is very small, which may account for relatively low sap flow estimates if the length of the sap flow sensor is shorter than the sapwood area. However, the ET value estimated in this study for *E. grandis* is within the range observed (781–1334 mm) for this species in other study within the same ecological region in Brazil (Almeida et al., 2006). An alternative explanation for the 34% of ET_{upflow} underestimation in relation to ET_{MODIS} in this plantation may be in part the soil evaporation, which was not included in the scaling up algorithm. Although soil evaporation from the native forest probably accounts for a very small percentage of total ET due to the multiple canopy layers, this may have a large contribution in the *E. grandis* plantation which has a relatively low LAI. Simulation based on the relationship between soil evaporation and the forest canopy cover predicts that the ratio of soil evaporation to precipitation will be very small (less than 50 mm per year) in a forest at full canopy closure (Raz-Yaseef et al., 2010). If we do not take into account the ET_{upflow} for *E. grandis*, the ET ranged from 1141 to 1314 mm/year (a 15% range), relatively close to the ET_{MODIS} range (20%). Thus, the agreement between the sapflow-based and MODIS-based estimates suggest that the remote sensing values provide a good basis for predicting the effects of land cover conversion from native forest to non-native tree plantations on regional ET. The extrapolation of

the effects of conversion from native forests to *E. grandis* plantations appears to be more uncertain.

Across the native forest and tree plantations, ET_{MODIS} increased with increasing average daily ASD, but no further increases were observed beyond 0.8 or 1.0 kPa. This pattern agrees with most of the relationships between species-specific tree sap flow and ASD, reflecting the degree of stomatal control at the individual level. Scaling sap flow measurements from individual trees to ecosystem ET and remote sensing ET estimates were well correlated for native subtropical forests. Thus, ET estimates from the MODIS product can be used as an input variable in hydrological modeling of subtropical forests without strong seasonality in precipitation. While ET and ASD were well correlated, ET and GR were only correlated in two of the four ecosystem types studied. However, in Penman–Monteith equation ET is mainly driven by both ASD and radiation. One plausible explanation of this partial agreement might be that in humid subtropical forests the high relative humidity limits ET and therefore the relationship between ET and radiation may not be significantly correlated.

The ET_{MODIS} of the tree plantations ranging between 1161 and 1389 mm per year were not higher than the studied native forests. There are few uncertainties in calculating ET from the satellites signal (Heinsch et al., 2006) including simplifying hypothesis in the model construction and variable estimation, such as LAI calculation with the MODIS sensor. In our study sites, a comparison was done between LAI estimates from MODIS and field measurements of LAI. The MODIS LAI and field measured values were relatively similar for different ecosystems in this region (Table 2 and Cristiano et al., 2014).

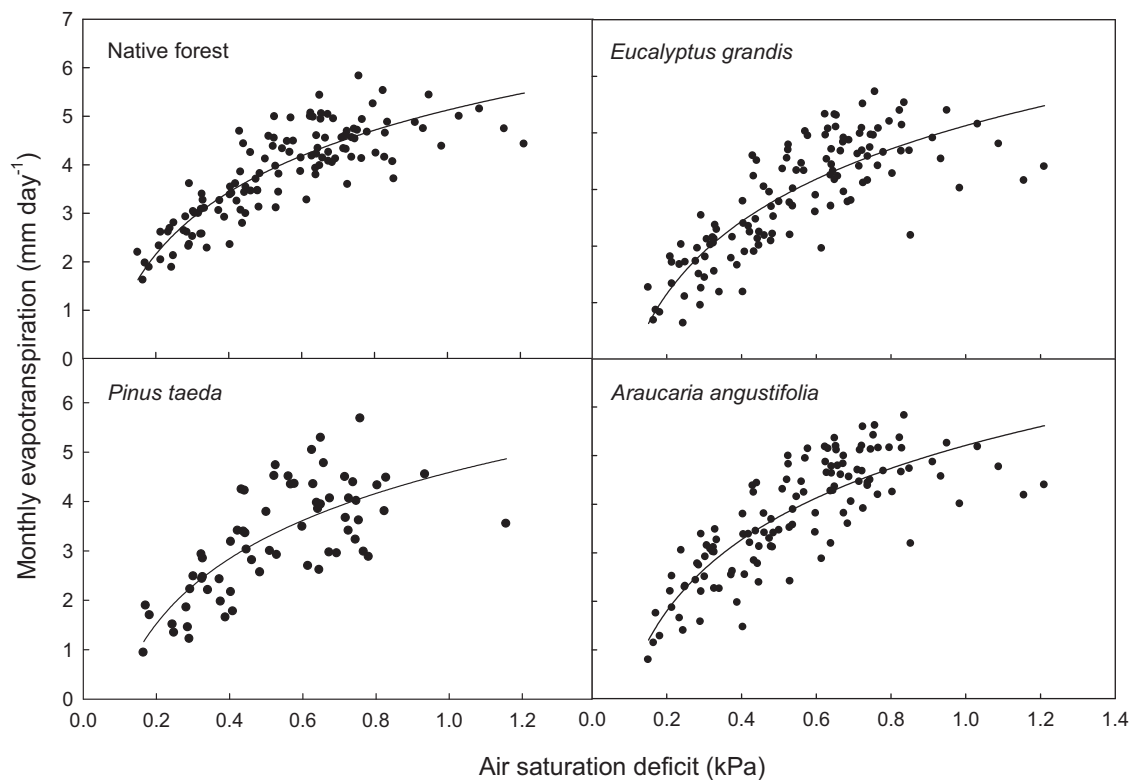


Fig. 5. Relationship between monthly evapotranspiration on a daily basis obtained using MODIS-Terra (ET_{MODIS}) and average monthly air saturation deficits (ASD) for native forests and tree plantations of *Eucalyptus grandis*, *Pinus taeda* and *Araucaria angustifolia*. The asymptotic relationships were significant at $p < 0.0001$ with $R^2 = 0.73$ for the native forest, 0.68 for *E. grandis*, 0.54 for *P. taeda* and 0.68 for *A. angustifolia*. *Pinus taeda* has a smaller n than the other systems because the plantation is relatively young.

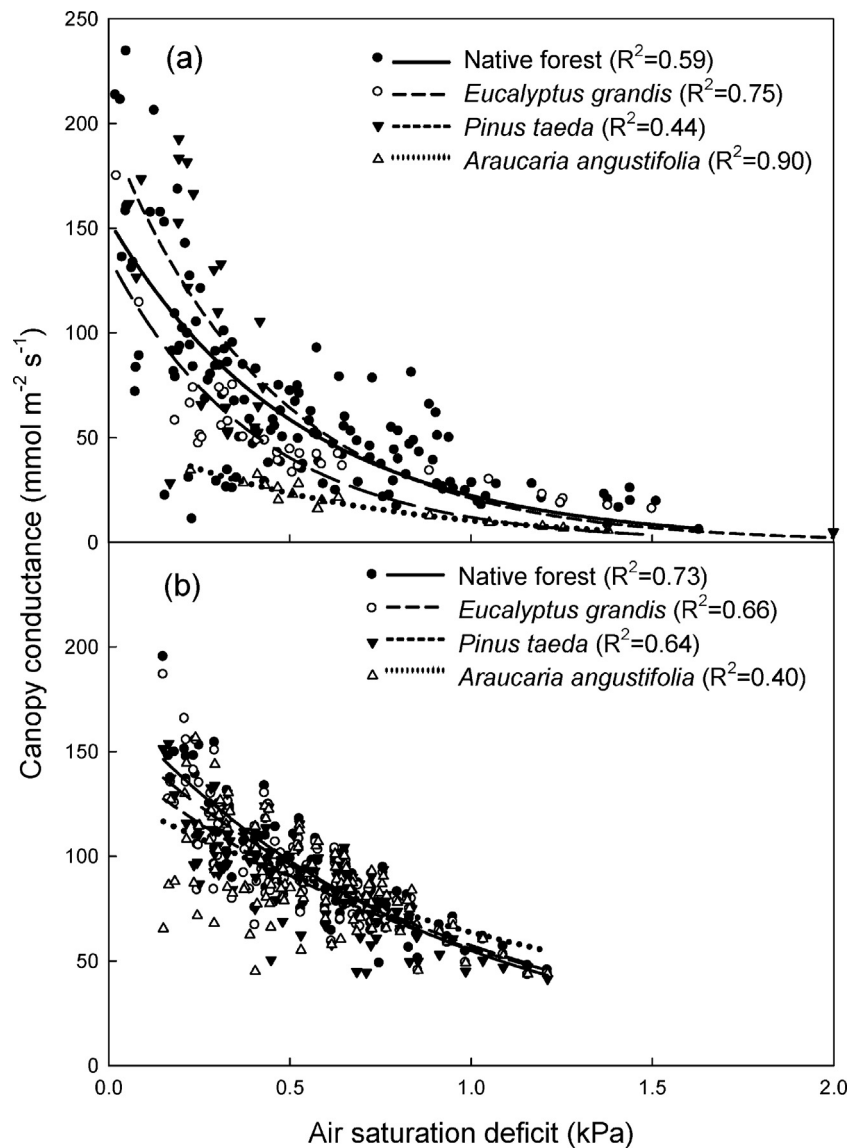


Fig. 6. Functional relationships between canopy conductance (g_c) and air saturation deficit for native forests and tree plantations of *E. grandis*, *P. taeda* and *A. angustifolia* (a) from daily field measurements and (b) from monthly remote sensing data. A negative exponential function ($g_c = a \text{Exp}(-b \text{ASD})$) was fitted to the scatter diagram between both variables in each system. All the functions fitted to the scatter diagrams were significant at $p < 0.0001$. In panel a, each symbol represents one species in the case of tree plantations. In the case of the native forest, one symbol represents the average canopy conductance from all measured species.

4.3. Determinants of evapotranspiration at different scales

Forests are better coupled to the atmosphere above and are aerodynamically efficient in turbulent transport compare to short grass and crop lands. As a result, transpiration from forests is mainly controlled by ASD and canopy conductance (Jones, 1992; Zhang et al., 1999). Significant negative exponential relationships were observed between g_c estimated from sap flow and ASD, probably because of partial stomatal closure when ASD increases. Partial stomatal closure could down regulate photosynthesis and result in photoinhibition at high ASD. There are previous evidences that support this type of findings (e.g., Ripley et al., 2007; Launiainen et al., 2011). Furthermore, similar negative exponential patterns of g_c decline with increasing ASD were observed in two Neotropical savannas with different tree density (Giambelluca et al., 2009). Different g_c versus ASD functional relationships were observed when sap flow data of dominant trees were used (in the case of tree plantations, only one species per ecosystem was measured). This approach does not take into account other species that may

have impacts on the aerodynamic resistance beyond the individual canopy of each tree, such as large understory, subcanopy trees and lianas (Blanken et al., 1997).

The relationship between g_c estimated by remote sensing and ASD, even exponential, showed a much lesser curvature than sap flow based g_c . Additionally, the decrease in remote sensing based g_c with increasing ASD was similar across all systems, while sap flow based g_c differed among ecosystems in response to increasing ASD. Remote sensing algorithms were not able to separate the differences that are observed in the estimates based on sap flow measurements. Apparently, one possible consequence of increasing the time and spatial scales (from daily to monthly and from individual to ecosystem level) is to decrease and even eliminate differences among species and among ecosystems in their response to climate drivers. This is likely the effect of averaging or aggregating non-linear phenomena like stomatal conductance response to ASD and/or to incoming solar radiation. Another non-exclusive explanation may be related to new emergent properties which belong to the new organization level regulating the magnitude of the stud-

ied process (e.g., water fluxes). Meinzer et al. (1997) also found similar g_c versus ASD negative exponential relationships in four different tropical canopy species, but only after g_c was normalized by variations in the ratio of leaf area to sapwood area and when the appropriate external reference point (the leaf surface) was used for determining evaporative demands. Their results raise a question concerning the interpretation of apparent interspecific differences in stomatal behavior, boundary layer conductance, and transpiration if precautions are not taken during data analysis. The findings of Meinzer et al. (1997) can help to understand why, in the present study, native subtropical forests and tree plantations had similar patterns of g_c decline with increasing ASD when ecosystem level resolution is used. In a previous study with savanna physiognomies of different LAI along topographic gradients in central Brazil, LAI was a good predictor of ET and g_c (Bucci et al., 2008). In general, as total leaf surface area increases in an ecosystem (high LAI), ET first increases linearly and then approaches an asymptotical value at high LAI (Rocha et al., 2012). However in the present study, moist subtropical forests and plantations exhibited similar LAI, and thus, ASD appear to be the main factor controlling ET and g_c (Kelliher et al., 1995).

Although ET_{MODIS} algorithm has been widely tested in different biomes in the Northern Hemisphere (e.g., Mu et al., 2011; Sun et al., 2007), the use of ET estimates from remote sensing (in this case MODIS) to calculate g_c is a novel procedure. The values of g_c estimated in our study ranged from 30 to 250 mmol m⁻² s⁻¹ which are within the range of g_c values observed elsewhere (e.g., Meinzer et al., 1997). Canopy conductance estimates using eddy covariance ranged from 100 to 350 mmol m⁻² s⁻¹ in savanna ecosystems (Giambelluca et al., 2009) and from 50 to 500 mmol m⁻² s⁻¹ on a daily basis in boreal forests (Blanken et al., 1997). The lack of differences among ecosystems when using remote sensing algorithm to estimate ET and g_c , such as observed in the present study, should be tested in ecosystems under drier environmental conditions. Canopy conductance models such as those developed by Wang and Leuning (1998) and Granier et al. (2000) have been increasingly used in land surface studies. In a recent study, a new diagnostic index was developed by Wang et al. (2009) to examine the response of g_c to humidity. This approach is theoretically sound, but relies on canopy latent heat and CO₂ fluxes and environmental variables at the leaf surface which are not always available.

4.4. Cross-correlation between ASD and ET and management practice effects on water cycle regulation

Air saturation deficit was mainly involved in the regulation of transpiration losses at the temporal and spatial scale used in this study, while solar radiation did not influence ET losses as much as ASD. Soil water availability in the study area does not exhibit obvious seasonal changes consistent with the lack of rainfall seasonality (Montti et al., 2011). The seasonal variations in ET_{MODIS} were mostly correlated with seasonal variations in ASD, although ASD tended to lag one month with respect to ET_{MODIS} variations (ET peaked one month before ASD) for the native forests and two of the tree plantations. This suggests that very high ASD had a detrimental effect on ET of the following month due to partial stomatal closure. This lag between ET and ASD appears to be present in ecosystems with strong seasonal changes in environmental conditions which require acclimation in photosynthesis or gross primary productivity (Mäkelä et al., 2004; Gea-Izquierdo et al., 2010; Brümmer et al., 2012). Contrary to evergreen conifers in boreal regions that exhibited strong lag effects, the ET_{MODIS} and ASD time series for *P. taeda* in this study were fully synchronized without lags. Evapotranspiration is one of the most important components of the hydrological cycle. The ET_{MODIS} and ET_{upflow} exhibited similar seasonal patterns and fairly similar average annual ET values in native forests and

some tree plantations. Therefore, the shift from native forests to tree plantations may have limited impact on ET at a regional scale. It is important to distinguish the response of ET at different scales because at the individual level, different tree sizes will transpire different amount of water while at the stand level, larger trees with lower tree density will not necessarily result in higher total water consumption. Additionally, there are other components of the hydrological cycle such as infiltration and runoff, which have not been considered in the present study and should be determined before fully assessing the impact of native forest replacement by tree plantations on the hydrological cycle.

In our study, tree plantations did not have higher annual ET than native forests, regardless of density or age. An average of 1275 mm per year across forests and tree plantations was estimated using remote sensing, which constitutes approximately 64% of the total annual precipitation. Canopy conductance, an important control of evaporative fluxes at ecosystem level, declined in a similar pattern with increasing ASD in native forests and tree plantations in NE Argentina. The regulation of water balance at the individual and ecosystem levels are different and an overall understanding of the regulatory mechanisms at different levels of organization is thus very important for estimating evapotranspiration at landscape level and for predicting the effect of changes in land use on regional hydrology.

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