A simple framework to analyze water constraints on seasonal transpiration in rubber tree (Hevea brasiliensis) plantations

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Climate change and fast extension in climatically suboptimal areas threaten the sustainability of rubber tree cultivation. A simple framework based on reduction factors of potential transpiration was tested to evaluate the water constraints on seasonal transpiration in tropical sub-humid climates, according pedoclimatic conditions. We selected a representative, mature stand in a drought-prone area. Tree transpiration, evaporative demand and soil water availability were measured every day over 15 months. The results showed that basic relationships with evaporative demand, leaf area index and soil water availability were globally supported. However, the implementation of a regulation of transpiration at high evaporative demand whatever soil water availability was necessary to avoid large overestimates of transpiration. The details of regulation were confirmed by the analysis of canopy conductance response to vapor pressure deficit. The final objective of providing hierarchy between the main regulation factors of seasonal and annual transpiration was achieved. In the tested environmental conditions, the impact of atmospheric drought appeared larger importance than soil drought contrary to expectations. Our results support the interest in simple models to provide a first diagnosis of water constraints on transpiration with limited data, and to help decision making toward more sustainable rubber plantations.

Keywords: potential transpiration model, drought, high evaporative demand, canopy phenology, relative extractable soil water

INTRODUCTION

The rubber tree (Hevea brasiliensis) is a major tree crop in Southeast Asia. Globally, it covers 9.82 million hectares mainly exploited by smallholders (UNCTAD, 2013). The tree is a native from the rainforests of the equatorial region of the Amazon basin (Priyadarshan et al., 2005). Traditionally, it has been cultivated in the equatorial belt and humid zones with a tropical and monsoon climate (Raj et al., 2005). Currently, Thailand is the world’s top producer of natural rubber. The plantations are mainly located where conditions are optimal in southern Thailand. However, in the last 30 years, the rubber plantations have largely expanded into climatically sub-optimal areas in north and northeast Thailand. The dynamic of land use is similar to that in other rubber-producing countries, with expansions also recorded in northeast India, the highlands and coastal areas of Vietnam, southern China, and the southern plateau of Brazil (Priyadarshan et al., 2005). In such areas, rubber can be constrained by drought, low temperature and high altitude or conversely by periodic heavy rainfall. Moreover, with climate change, higher frequencies of extreme events (flooding, drought) in the rainy season and an increase in temperature and evaporative demand in the dry season are expected in both traditional and new areas (Masaki et al., 2011). In addition, despite the large extension of land covered by rubber plantation, little is known of its environmental impacts and particularly about carbon and water balances (Guardiola-Claramonte et al., 2010; Kumagai et al., 2013). To address the sustainability of rubber plantations and to choose appropriate plant material and management practices, it is necessary to forecast rubber tree behavior on a large scale and over long periods of time. Hence the availability of simple models with limited data to analyze water constraints on tree transpiration and consequences on growth, production and soil water balance is a key issue (Guardiola-Claramonte et al., 2010; Boithias et al., 2012; Carr, 2012).

Our final objective is to evaluate, on an annual basis, the relative contributions of soil water shortage and atmospheric drought to the regulation of maximal transpiration in rubber tree stands under various pedoclimatic conditions. The use of a robust and
simple model based on reduction factors of potential transpiration simulation appeared as a reasonable first approach to schematically separate the main controls. Granier et al. (1999) proposed such a model of daily water balance called BILJOU to evaluate water constraints in forest stands. It has been successfully used in temperate and tropical humid forests (Granier et al., 1999; Wagner et al., 2011). Transpiration models based on canopy conductance regulation have been also assessed and used (Jarvis, 1976; Stewart, 1988; Granier et al., 2000, 2007). However, they require an hourly step, more parameters and input data. As a first approach we chose to use the framework of BILJOU99 (Granier et al., 1999). The model assumes, under non-limiting soil water, a linear response of maximal transpiration ($T_{max}$) vs. potential evapotranspiration ($PET$) for a leaf area index ($LAI$) inferior to 6, the slope being the ratio “$rm$” depending on the LAI. The model assumes that under a soil water shortage, $rm$ decreases linearly below a threshold of relative extractable water ($REW$) of 0.4. Like many models, it does not consider direct constraint due to atmospheric drought (Boote et al., 2013). However, Isarangkool Na Ayutthaya et al. (2011) have shown that transpiration in mature rubber trees was strongly regulated above a threshold of evaporative demand, whatever the soil water availability. Such a regulation was related to an isohydric behavior expressed by stability of minimum leaf water potential and maximum whole-tree hydraulic conductance. The idea was to add a reduction factor above a critical climatic demand.

To test our modeling approach based on BILJOU99 framework, we selected a representative mature stand where trees faced the full range of soil and atmospheric drought conditions over a complete annual cycle. Tree transpiration, the evaporative demand and the soil water availability were measured every day over 15 months. The first objective was to test simplified controls of transpiration through evaporative demand, leaf area index and relative extractable water. We hypothesized that the basic relationships hold, except when the evaporative demand becomes too high. The second objective was to test an evolution of the model including sensitivity to atmospheric drought. We assumed that it would provide a reasonable indication of the trend in seasonal transpiration. The third objective was to assess by modeling the hierarchy between soil water and atmospheric constraints on transpiration on an annual basis. We assumed a predominant control by soil drought according to common thinking.

**CLIMATIC MEASUREMENTS**

The local microclimate was monitored automatically in an open field at a distance of 50 m from any trees. An automatic weather station (Minimet automatic weather station, Skye Instruments Ltd, Llandrindod Wells, UK) recorded half-hourly values of air temperature, relative humidity, incoming short wave radiation, wind speed and rainfall. The reference evapotranspiration was calculated according to the FAO 56 formula in Allen et al. (1998).

**SOIL WATER CONTENT MEASUREMENTS**

Volumetric soil water content ($\theta$) was measured with a neutron probe (3322, Troxler, Research Triangle Park, NC, USA) calibrated for the experimental soil with separate calibrations for the upper (0–0.2 m) and lower (below 0.2 m) layers. Twelve 2 m-long tubes were set up in pairs; in each pair, one tube was located in the planting line between two trees, and the other in the middle of the inter-row. Measurements were made every 0.2 m, from a depth of 0.1 to 1.5 m every 2 weeks. Based on observed fluctuations in soil water, the soil profile was separated into two layers: topsoil (0–0.6 m) and subsoil (0.6–1.6 m). The average field capacity and permanent wilting points were measured as 0.21 and 0.07 m$^3$ m$^{-3}$ for the topsoil, and 0.25 and 0.10 m$^3$ m$^{-3}$ for the subsoil, respectively (Isarangkool Na Ayutthaya et al., 2010). Additionally, $\theta$ was estimated from cross-calibration with the neutron probe measurements. For each sensor, $\theta$ was estimated from cross-calibration with the neutron probe measurements. Relative extractable water was calculated for each layer according to Granier et al. (1999):

\[
REW_i = (W - W_{m})/(W_f - W_{m})
\]

where $REW_i$ is the relative extractable water in each soil layer $i$, $W_{m}$ is the minimum soil water content, $W_f$ is the soil water content at field capacity and $W$ is the actual soil water content. To calculate the total $REW$ for the sensitive root zone, $REW$, was weighted by the percentage of fine root length within each layer. As the soil profiles showed low soil water availability and little change in the subsoil (Figure 1B), for modeling purpose the total $REW$ was calculated for the top soil (0–0.6 m). In this site, the top soil contained 83% of the fine root length accumulated down to 1.6 m (Gonkhramdee et al., 2009). The fraction of fine root length used for weighting the $REW$ in the top soil was 0.63, 0.32, and 0.05 for the layers 0–0.2, 0.2–0.4, and 0.4–0.6 m, respectively.
**FIGURE 1 |** Seasonal course of: (A) reference evapotranspiration \((ETo)\); (B) rainfall (solid bar) and relative extractable water of bulk soil \((REW)\) for layers 0–0.6 m \((REW\,0–0.6)\), 0.6–1.6 m \((REW\,0.6–1.6)\) and 0–1.6 m \((REW\,0–1.6)\); and (C) measured transpiration \((T\,mea,\) dotted line) and leaf area index estimated from litterfall \((LAI\,mea,\) triangles) and schematic shape \((LAI\,mod,\) solid line).

**TRANSPIRATION MEASUREMENT**

The xylem sap flow density was measured using the transient thermal dissipation method (TTD, Isarangkool Na Ayuthaya et al., 2010). The TTD method is based on using the same Granier probe design and heating power but uses a cyclic schedule of heating and cooling to assess a transient thermal index over a 10-min rise in temperature. The hourly sap flux density \((J_s;\,\text{kg m}^{-2}\text{h}^{-1})\) was calculated according to the non-species-specific calibration assessed by Isarangkool Na Ayuthaya et al. (2010):

\[ J_s = 12.95 \times K_a \times 10^2 \]  
(2)

where \(K_a\) is the transient thermal index. A temperature signal \((\Delta T_a)\) was defined as

\[ \Delta T_a = \Delta T_{on} - \Delta T_{off} \]  
(3)

where \(\Delta T_{on}\) is the temperature difference reached at the end of the 10-min heating period and \(\Delta T_{off}\) is the temperature difference before heating. To measure \(J_s\) every half hour with a heating period of 10 min, a cycle of 10 min heating and 20 min cooling was applied and the temperature signals were recorded every 10 min. \(\Delta T_{off}\) was interpolated at the time of \(\Delta T_{on}\) from \(\Delta T_{off}\) surrounding measurements. The transient thermal index was calculated as:

\[ K_a = (\Delta T_{0a} - \Delta T_{ua})/\Delta T_{ua} \]  
(4)

where \(\Delta T_{0a}\) is the maximum temperature difference obtained under zero flow conditions and \(\Delta T_{ua}\) is the measured signal at a given \(J_s\), the zero flux signal was determined every night assuming that sap flow was negligible at the end of the night. This
Details of calculation

Potential, climatic or maximal transpiration was first calculated from the following equation:

\[ \text{\(T_{\text{max}}\)} = \text{\(rm \times ETo\)} \quad (7) \]

where \(rm\) depends on \(LAI_{\text{max}}\);

Second, \(T_{\text{max}}\) could be decreased according to the \(LAI\) pattern by the following reduction coefficient:

\[ \text{\(rLAI = (LAI / LAI_{\text{max}})\)} \quad (8) \]

The effect of soil water shortage was simulated by the calculation of a reduction coefficient (\(rREWc\)) as:

\[ \text{\(rREWc = rLAI \quad \text{if REW} > REWc\)} \]
\[ \text{\(rREWc = (rLAI/REWc) \times \text{REW} \quad \text{if REW} \leq \text{REWc}\)} \quad (9) \]

where \(REWc\) is the critical value of relative soil water content.

Hence the transpiration was calculated according to the following formula:

\[ \text{\(T_{\text{mod}} = rREWc \times T_{\text{max}}\)} \quad (10) \]

The expected saturation of transpiration at high evaporative demand was introduced in the BILJOU99 framework by applying a reduction coefficient above a critical value of \(ET0\):

\[ \text{\(T_{\text{mod,ET0c}} = \text{\(\text{\(min\)}\)}(rREWc; rET0c) \times T_{\text{max}}\)} \quad (11) \]

For simplicity of writing we could have included the negative effect of high \(ET0\) in equation [7]. But we have preferred to separate the effects because of functional reasons. Equation [7] represents a general climatic driving effect (positive) on transpiration whatever plant species. While \(ET0c\) in equation [11] expresses a negative effect which varies according species and which is attributed to plant hydraulic limitations (Oren and Pataki, 2001; Bush et al., 2008; Isarangkool Na Ayuthaya et al., 2011; Ocheltree et al., 2014).

Diagnosis of hierarchy between water constraints

The approach was to use the calibrated framework to simulate independently or in combination the factors that control the regulation of transpiration on an annual basis and to separate the rainy season and dry season. The regulations of transpiration was expressed as the ratio between the cumulated potential transpiration, driven by evaporative demand and stand characteristics under full canopy conditions (\(LAI_{\text{max}}\)), and the cumulated actual transpiration possibly reduced by defoliation, soil water availability or sensitivity to air dryness. Such a calculation assumes that reduction factors act independently which is certainly not true in the details. The annual cycle of transpiration was considered from January 1 to December 31, and the rainy season from May 1 to October 31. The few gaps in the daily transpiration were interpolated from \(ET0\) using an average ratio \(T/ET0\) measured on surrounding data (at least 4 days).
DATA ANALYSIS
Statistics were performed using the XLSTAT software (Addinsoft, Paris, France). The agreement between measured and simulated data was quantified by using the coefficient of determination \((R^2)\), root mean square error \((RMSE)\) and relative root mean square error \((RRMSE)\). Absolute and relative root mean square errors were calculated according to the following formulas:

\[
RMSE = \sqrt{\frac{\sum_{i=1}^{n} (x_{\text{mea},i} - x_{\text{mod},i})^2}{n}},
\]

\[
RRMSE = \sqrt{\frac{\sum_{i=1}^{n} (x_{\text{mea},i} - x_{\text{mod},i}/x_{\text{mea},i})^2}{n}}.
\]

where \(x_{\text{mea},i}\) is the measured value, \(x_{\text{mod},i}\) is the simulated value at place \(i\) and \(n\) is the number of values.

RESULTS
SEASONAL VARIATIONS OF ENVIRONMENTAL WATER CONSTRAINTS, LAI, AND TRANSPIRATION
The evaporative demand as expressed by \(ET0\) largely fluctuated between 1 and 9 mm d\(^{-1}\) with a cumulative value of 1247 mm year\(^{-1}\) (Figure 1A), 23\% above the cumulative rainfall (965 mm) in 2007. \(ET0\) values were particularly high during the 6 months of the dry season, from 3 mm d\(^{-1}\) in November up to 9 mm d\(^{-1}\) in March, corresponding to a VPD value above 1.0 kPa. The evaporative demand remained relatively high in the first part of the rainy season (from May to July) and decreased markedly in August, September and October, with \(ET0\) and VPD values below 2.0 mm d\(^{-1}\) and 0.7 kPa, respectively.

The water availability of the bulk soil or \(REW\) logically followed the rain occurrence (Figure 1B), with values close to 1.0 at the start of the rainy season in the topsoil (0–0.6 m). The availability decreased sharply to 0.2 in July, in the middle of the rainy season. The \(REW\) again reached high values (above 0.5) from August to October. \(REW\) values above 1 at the end of October suggested temporary water logging in the topsoil which was confirmed by observations. The \(REW\) quickly decreased in the dry season, reaching 0.2 in January. In the deep soil (0.6–1.6 m), the \(REW\) value indicated low water availability with little change over the year (maximum 0.26).

As represented by the schematic change in the LAI (Figure 1C), leaf shedding occurred in January and February, immediately followed by leaf flushing, with the latter occurring when the evaporative demand was the highest. The maximum LAI deduced from litterfall measurements averaged 3.9 at the end of 2007 \((n = 9, SD = 0.7)\). The period with full canopy included approximately the period of highest soil water availability and lowest evaporative demand.

The maximum transpirations estimated by sap flow measurements \((T_{\text{mea}})\) were steady (approximately 2.0 mm d\(^{-1}\)) throughout the period with full canopy (Figure 1C). The intermittent decreases evident in June and July related to the evolution of the \(REW\) in the topsoil (Figure 1B). The lowest transpiration corresponded to the time of leaf shed. However, it never reached zero values despite almost complete defoliation. However, the sap flow measurement using the TTD method has low accuracy at very low flow rates (Isarangkool Na Ayuttthaya et al., 2010). The minimum recorded transpiration was 0.1 mm d\(^{-1}\) on April 11, 2007 and the maximum value was 2.2 mm d\(^{-1}\) on May 31, 2007.

TRANSPIRATION vs. \(ET0\), \(REW\), AND LAI

\(ET0\)
Under conditions of full canopy and non-limiting soil water (\(REW > 0.5\)), transpiration plotted vs. \(ET0\) showed a linear response at low evaporative demand but it exhibited a pseudo-plateau above approximately 2.3 mm d\(^{-1}\) (Figure 2A). The average slope of the linear section crossing the origin was estimated as 0.9 (± 0.052). Such a slope corresponds to \(rm\), the \(T_{\text{max}}/ET0\) ratio, in the model framework (Equation [7]). Several values of \(T_{\text{max}}/ET0\) were above 1.0 at low \(ET0\). First, \(ET0\) is a reference value which does not necessarily represent the maximum \(ET\) for this particular stand. Second, transpiration could have been overestimated by sap flow measurement, particularly for rainy days and low flow rates. In Figure 2B, \(T_{\text{max}}/ET0\) was plotted vs. \(ET0\) discarding y values above 1. The relationship fitted well a Lohammar’s function \((y = -0.585\ln(x) + 1.2492; R^2 = 0.87)\). The \(R^2\) has little meaning here because the variables were directly related by \(ET0\) in the calculation. However, Lohammar’s function provided better results of \(T_{\text{mod}, ET0c}\) than a linear adjustment. The plot of midday canopy conductance \((G_{c_{\text{mid}}})\) vs. VPD\(_{\text{max}}\) confirmed the underlying mechanism of stomatal regulation at increasing VPD (Figure 3). According to the fitted Lohammar’s function (Lohammar et al., 1980), the reference \(G_c\) at 1 kPa and the sensitivity term equal 4.74 mm s\(^{-1}\) and 7.6, respectively.

LAI
Transpiration estimated by sap flow measurements \((T_{\text{mea}})\) followed in the expected manner the LAI seasonal pattern (Figure 1C) which supports a strong control of transpiration by the LAI. However, the soil water availability decreased at the same time in the dry season.

REW
The plot of \(T/ET0\) vs. \(REW\) showed scatters of points consistent with the assumption of a threshold around \(REW = 0.4\) (Figure 4). Above a threshold between 0.4 and 0.5, \(T/ET0\) exhibited a pseudo-plateau averaging 1.0, with large variability. Below the critical \(REW\), a linear decrease toward 0.0 crossed the scatter of points. However, the assessment of the value critical \(REW\) was approximate due to the lack of soil data between 0.4 and 0.5 \(REW\).

SIMULATION OF TRANSPIRATION
Conditions of simulation
For the calculations described in the Modeling paragraph of Material and Methods:

- \(rm\) was tested between 0.9 and 1.0 according to Figures 2A, 4, and finally 1.0 was kept.
- \(LAI_{\text{max}}\) was taken equal to 3.9 as measured.
- \(REW\) was calculated for the top soil (0–0.6 m) with weighting by percentage of fine root length distribution as described in paragraph 2.3.
- The active soil depth and weighting by root distribution were kept constant over the annual cycle.
- $REW_c$ was taken equal to 0.4 according to BILJOU99 framework and Figure 4.
- $rET0c$ was calculated according the function deduced from Figure 2B:
  
  If $ET0 \leq ET0c$, $rET0c = 1$
  
  If $ET0 > ET0c$, $rET0c = a \cdot \ln(ET0) + b$
  
  with $ET0c = 2.3$ mm d$^{-1}$, $a = -0.585$ and $b = 1.2492$.

**Simulated transpiration**

The transpirations simulated with the original framework of BILJOU99 ($T_{mod}$), largely overestimated during the full canopy period, particularly in April, May, June, August and November, during periods of high evaporative demand (Figure 5). The values simulated with regulation at high evaporative demand ($T_{mod, ET0c}$) logically better expressed the seasonal change of transpiration; however substantial inaccuracy remained in the dry season with overestimates in November and underestimates in other periods (Figure 5). Table 1 summarizes the previous observations: large errors with $T_{mod}$ and the substantial improvement with regulation at high evaporative demand in the rainy season ($RRMSE < 35\%$). In the dry season, the errors were substantial ($RRMSE >$...
Hevea stand daily transpiration model

HIERARCHY BETWEEN REDUCTION FACTORS OF ANNUAL TRANSPIRATION

On an annual basis, the cumulative measured transpiration (430 mm) was 66% lower than the potential annual transpiration (1247 mm). The regulation was substantial in the rainy season (−39%) and twofold higher in the dry season (−81%). The simulated data provided close estimates of transpiration reduction (−64.5%) when all constraints were considered (LAI × REWc × ET₀c in Figure 6). When considering only one reduction factor, the LAI variation induced the lowest reduction, logically located in the dry season, at the time of defoliation. The impacts of REWc and ET₀c were similar with substantial reduction around −45%, slightly higher for ET₀c (−50.1%). The ET₀c constraint was significantly higher than the REWc constraint in the rainy season (Figure 6B). It was noteworthy that the overall effect of the ET₀c constraint alone already represented 76% of the total reduction with the combination of the three factors of constraint. The combination with two factors of constraints supported the proposal that ET₀c had a larger impact than REWc. The small difference in the simulation between REWc and REWc × LAI suggested that the REWc constraint included already the LAI effect. The REWc × ET₀c interaction induced a reduction equivalent to the reduction with three factors, which confirmed the previous suggestion.

DISCUSSION

BASIC RELATIONSHIPS OF BILJOU99 FRAMEWORK

Our results confirmed that the basic relationships of the original framework (Granier et al., 1999) hold except that the regulation of transpiration at high evaporative demand was not well simulated. ET₀c

Experimental data showed a strong regulation of transpiration under non-limiting soil water at high evaporative demand, when the ET₀ was approximately above 2.3 mm d⁻¹. The analysis of the corresponding canopy conductance confirmed a dramatic decrease above VPD values equal to 1 kPa. This result supports the previous analysis of Isarangkool Na Ayutthaya et al. (2011) where such a response was related to isohydric behavior with a stable maximal value of the whole tree hydraulic conductance.

Table 1 | Evaluation metrics of simulations of transpiration according to two frameworks: original BILJOU (Tₘ₉₀), simulation with reduction coefficient of ET₀ (Tₘ₉₀ ET₀c).

<table>
<thead>
<tr>
<th>Model</th>
<th>Observation</th>
<th>R²</th>
<th>Whole year RMSE(RRMS)/(mm.d⁻¹)</th>
<th>Wet season RMSE(RRMS)/(mm.d⁻¹)</th>
<th>Dry season RMSE(RRMS)/(mm.d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tₘ₉₀</td>
<td>379</td>
<td>0.56</td>
<td>1.06 (1.01)</td>
<td>1.00 (0.67)</td>
<td>1.10 (1.19)</td>
</tr>
<tr>
<td>Tₘ₉₀ ET₀c</td>
<td>379</td>
<td>0.77</td>
<td>0.39 (0.56)</td>
<td>0.30 (0.31)</td>
<td>0.45 (0.68)</td>
</tr>
</tbody>
</table>

RMSE: root mean square error and RRMS: relative root mean square. Wet season from May 1 to October 31, 2007 and Dry season from December 18, 2006 to April 4, 2007 and November 1, 2007 to February 22, 2008.
and a stable minimum value of the leaf water potential. Such regulation of transpiration vs. high evaporative demand is known for several species (Pataki and Oren, 2003; David et al., 2004; Ocheltree et al., 2014). However, the sensitivity of this response appears dependent on wood anatomy and hydraulic conductivity. *Hevea brasiliensis* is a diffuse-porous species (Richter and Dallwitz, 2000). And our results follow the general trend that stomatal control vs. high evaporative demand is stricter in diffuse-porous species than in ring-porous species. (Oren and Pataki, 2001; McCulloh and Woodruff, 2012).

### T\textsubscript{max}/ET\textsubscript{0}

Below the threshold of critical evaporative demand, the simple and common concept of a stable \( rm \) ratio between maximal transpiration and reference evapotranspiration under non-limiting conditions held with our data, as \( rm \) ranged around 1.0 for a maximum \( LAI \) estimated at 3.89. These values appear relatively high compared to the range of 0.70–0.80 quoted by Granier et al. (1999). However, the latter quotation concerned the ratio vs. \( PET \) (Potential Evapotranspiration with the Penman equation) which should be higher than \( ET0 \), the reference evapotranspiration using the Penman-Monteith formula and FAO56 coefficients (Allen et al., 1998). Moreover the accuracy on absolute value of transpiration by sap flow measurement including scaling from tree to stand level is estimated around 20% (Isarangkool Na Ayutthaya et al., 2010).

###REWc

Our data supported the general assumption of a linear decrease of \( T_{\text{max}}/ET0 \) below a critical value around 0.4 for the \( REW \) (Granier et al., 1999; Bréda et al., 2006). This threshold of 0.4 was also quoted for other classical expressions of soil water availability.
i.e., the plant available soil moisture or PAW (Sadras and Milroy, 1996) or the fraction of transpirable soil water or FTSW (Sinclair et al., 2005).

LAI
The seasonal pattern of transpiration followed remarkably the main trend in the LAI. However, this observation did not confirm here the well-known control of transpiration by the LAI because the REW was also decreasing in the dry season. Moreover, simulations in paragraph 3.3 have shown that the decrease in the REW was already sufficient to reduce transpiration.

SIMULATION OF TRANSPERSION WITH MODEL EVOLUTION

Transpiration
Our results confirmed that including regulation by high evaporative demand in the model largely improved the accuracy in simulation of transpiration. However, substantial errors remained and particularly in the dry season. Besides inaccuracy on estimate of absolute transpiration by sap flow measurement, several points could explain this result with such a simple model. The model relationships were mainly tested in the rainy season and under full canopy conditions and they were applied on the annual cycle. The change in the LAI was estimated roughly from litter fall measurements and canopy fullness observations. Temporary water logging could have decreased transpiration in November. Also, stomatal regulation could change with leaf age, particularly during senescence and refoliation (Kositsup et al., 2010). Moreover, the profile of fine root length activity changes in the dry season as shown by Gokkhamdee et al. (2009) while in the simulation, the REW calculation used the same soil depth and root profile for weighting. However, at the end, the simulation provided a reasonable indication of trends in seasonal regulation of transpiration which was the objective of the tested framework.

Several models of water balance previously used for rubber tree did not consider atmospheric constraints on transpiration: CROPWAT (Allen et al., 1998), WANULCAS (VanNoordwich and Lisiana, 1999; Guardiola-Claramonte et al., 2010; Boithias et al., 2012). The consequences could be (1) an overestimate of transpiration and root water uptake and (2) a further underestimation of stomatal regulation and consequently an overestimation of assimilation. In a recent review, Boote et al. (2013) included this process as a current limitation of many crop models. Bregaglio et al. (2014) reported the good performance of a simple approach in arid environments based on transpiration use efficiency that explicitly accounts for the negative impact of vapor pressure deficit on photosynthesis.

A limitation of the reduction factor based on ET0c is likely the generality of the relationship and value of ET0c which has to be tested in different experimental conditions.

DIAGNOSIS OF THE HIERARCHY BETWEEN WATER CONSTRAINTS
The simple framework of simulation has allowed comparing the relative impact of the different constraints on annual and seasonal transpiration. The soil water shortage did not appear as the major water constraint on transpiration in the studied area. High evaporative demand, as expressed by ET0, appeared at least of similar importance, if not higher, than soil water shortage. The provided hierarchy is contrary to expectations in this growing area known as climatically under-optimal due to the low amount and variability of rainfall. Clermont-Dauphin et al. (2013) recently provided evidence that soil water shortage was not the main cause of low growth rates in young rubber plantations of North East Thailand and they suggested the importance of high evaporative demand and temporary water logging.

The results from the simulation are directly due to the fact that the sensitivity to air dryness was taken into account in the model. Such a type of response is dependent on the species or variety. We studied the most-planted clone in Thailand (RRIM 600) and the response may change with other varieties of Hevea brasiliensis. But the recent work of Kobayashi et al. (2014) in Cambodia confirmed the sensitivity of canopy stomatal conductance to VPD for mature rubber trees of another clone (RRIC 100). However, the details of the response may likely change according to the clone, age and stand characteristics, root development (Devakumar et al., 1999), spatiotemporal acclimation and root proliferation (Liu et al., 2014). We doubt in the generality of the relationship and critical ET0 used in the framework to simulate sensitivity to air dryness. The results of Sangsing et al. (2004) on young plants of RRIM 600 and RRIT 251 did not show isohydric behavior under water constraints as observed in mature trees. The variability of water relations and sensitivity to air dryness certainly deserves more study.

On the other end, the lower influence of soil water shortage vs. evaporative demand cannot be attributed to a relatively low soil water constraint in the experiment. The growing area of Buri Ram (south of Northeast Thailand) is known as soil water limited with an average annual rainfall of around 1150 mm, which is far below the recommended threshold of 1500 mm. Moreover, the year of study was particularly dry with a rainfall amount of 965 mm. The measurements of soil water availability confirmed the severity of water shortage in both the top soil and deep soil, in the dry season as in the rainy season (Figure 1B).

Defoliation is usually limited to 1–2 months, with the defoliation peak between mid-January and mid-February. However, in dry years such as in the year of study, the period of defoliation could last over 3 months, from January to March. In addition to internal controls, canopy phenology can be influenced by both soil and atmospheric droughts (Eamus and Prior, 2001; Do et al., 2005). These relationships were not taken explicitly into account in the model. It is likely that such inclusions could have changed the results of simulation in the details. However, it is doubtful that they could change completely the conclusion and particularly the fact that impact of atmospheric drought on transpiration regulation was at least of similar importance than soil drought.

CONCLUSION
In conclusion, the adapted framework of BILJOU99 had allowed analyzing the relative contribution of soil water shortage and atmospheric drought to the regulation of transpiration on a seasonal scale. This paper provides two main insights. The first stresses the importance of taking into account the direct regulation of transpiration vs. high evaporative demand which often is omitted in simple agro-climatic models. According species, water constraint due to evaporative demand could have been
underestimated in previous studies in the sub-humid tropics. The second relies on the interest in simple agro-climatic models to provide a first diagnosis of water constraints on transpiration, in order to help the evolution of cultural choices and practices toward greater sustainability.

**AUTHORS CONTRIBUTION**


**ACKNOWLEDGMENTS**

This work was carried out as part of a PhD and was supported by the Higher Education Research Promotion and National Research University Project of Thailand (NRU), Office of the Higher Education Commission and the Graduate School, Prince of Songkla University. In particular, the field experiment was supported by funding from the French Institute for Rubber (IFC) and associate companies (Michelin, Socfinco, SIPH).

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Hevea brasiliensis


Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 29 September 2014; accepted: 08 December 2014; published online: 06 January 2015.


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