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Environmental control of canopy stomatal conductance in a tropical deciduous forest in northern Thailand

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ABSTRACT

Tropical seasonal forests in Southeast Asia are among the most important biomes in terms of global and local hydrologic and carbon fluxes, and their vulnerability to climate change. We conducted eddy flux measurements in a teak (*Tectona grandis* Linn. f.) plantation in northern Thailand over a 6-year period; this forest undergoes a drastic seasonal change in foliage with somewhat constant incident radiative energy. We used a combination of actual evapotranspiration (ET) flux data and an inversed version of a simple two-layer ET model for estimating the mean canopy stomatal conductance (g_s). The main novelty of this analysis is that canopy conductance can be extracted from total surface conductance (including the canopy and forest floor effects), and thus environmental and biological controls of g_s are explicitly compared among seasons and years. The relationship between seasonal variations in the leaf area index (LAI) and g_s revealed an apparent effect of leaf age on leaf gas exchange capacity: within a year, g_s peaked earlier than full-leaf expansion and abruptly declined after the peak of LAI. We used this result to classify three leaf age stages: leaf-out, mid-growing, and leaf-senescence seasons. Then, two ecophysiological parameters, the reference value of g_s (g_{sref}), and the sensitivity of g_s to atmospheric demand (m), as well as their proportion (m/g_{sref}), were derived from the logarithmic response curve of g_s to vapor pressure deficit (VPD) for each season. We showed seasonal variation in g_{sref} as follows: leaf-out season ≈ mid-growing season > leaf-senescence season. m demonstrated little seasonality and little interannual variation was observed in either parameter. This resulted in a value of almost 0.6 for m/g_{sref} during the leaf-senescence season and of less than 0.6 in the leaf-out and mid-growing seasons, which suggests that the teak trees had strict stomatal regulation to prevent excessive xylem cavitation during the leaf-senescence season (i.e., under drought conditions) and less strict stomatal regulation during the leaf-out and mid-growing seasons (i.e., under moist conditions) when little risk of water stress-induced hydraulic failure would occur. In addition, we obtained a simple linear relationship between soil moisture and g_{sref}, which can be a powerful tool for further research of land–atmosphere interactions using global climate and vegetation dynamics models.

1. Introduction

Tropical forests receive high radiative energy and play an important role in the global carbon budget (Melillo et al., 1993; Field et al., 1998; Malhi and Grace, 2000; Grace et al., 2001). They are a major source of global hydrological fluxes, profoundly influencing both global and regional climates (Lean and Warrilow, 1989; Nobre et al., 1991; Kanae et al., 2001; Avissar and Werth, 2005;

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Kumagai et al., 2013). Furthermore, recent evidence shows that unprecedented climates will occur first in the tropics, implying the vulnerability of tropical forest ecosystems (Mora et al., 2013). Although those in Southeast Asia represent only ~11% of the world's tropical forests in terms of area (World Resource Institute, 2007), they have undergone the highest relative deforestation rate in the tropics (Houghton and Hackler, 1999; Laurance, 1999; Malhi and Grace, 2000; Canadell et al., 2007); thus, their impacts on global and regional climates, and on hydrological cycling, are an important concern (Kanae et al., 2001; Malhi and Wright, 2004; Mabuchi et al., 2005; Werth and Avissar, 2005; Spracklen et al., 2012).

Tropical moist deciduous forests and tropical dry forests represent 55.9% of the total area of tropical forests (Food and Agriculture Organization, 2009). Furthermore, the area consisting of tropical deciduous forests is estimated to be larger than that of temperate deciduous forests (see Melillo et al., 1993). In deciduous forests, transpiration and primary productivity are significantly affected by large seasonal changes in leaf area, as well as physiological factors such as stomatal control (e.g., Wilson et al., 2001). Partitioning of net radiation into sensible and latent heat fluxes and the carbon exchange balance are considerably different between the growing and leafless seasons due to the lack of tree transpiration and photosynthesis during the latter (Moore et al., 1996; Schmid et al., 2000; Wilson and Baldocchi, 2000; Saigusa et al., 2002). In deciduous forests of temperate and boreal zones, incident radiative energy and atmospheric evaporative demands are smaller in fall/winter than in spring/summer. However, unlike in temperate and boreal forests, the impact of leaf phenology modification (i.e., the timing of leaf-out and leaf-fall, and the length of the physiological active season) on the annual energy and carbon cycle in tropical deciduous forests is likely to be critical because of the large annual and seasonal energy fluxes.

Previous studies (Yoshifuji et al., 2006, 2014) suggest that a teak (*Tectona grandis* Linn. f.) plantation as a typical Southeast Asian tropical deciduous forest in northern Thailand has much larger interannual variations in canopy duration and the transpiration (T_r) period (i.e., the periods between leaf-out and leaf-fall, and between the commencement and decline of tree T_r, respectively) than temperate and boreal deciduous forests (Black et al., 2000; Wilson and Baldocchi, 2000; Granier et al., 2002; Barr et al., 2004). Studies have also found that the major determining factor of these tropical deciduous forests is soil moisture, which is affected by interannual variation in rainfall regimes. Notably, a remarkable difference exists in the teak canopy between canopy duration and the leafless season (Fig. 1).

Vourlitis et al. (2008) reported that in a semi-deciduous forest in the southern Amazon basin, T_r was correlated to the leaf area index (LAI) during the dry-wet season transition period, while evapotranspiration (ET) changed little throughout the year. This shows that values of T_r and estimated canopy conductance (G_c) are significantly smaller in the dry season than in the wet season. The authors attributed the difference to the inclusion of an evaporation component in the estimates of ET. In Southeast Asian tropical deciduous forests, the energy balance, and water and material cycling dynamics are less certain. As Vourlitis et al. (2008) pointed out, detailed long-term studies on the vegetation–atmosphere exchange of energy, water, and materials are needed in such ecotonal forests, which are being endangered by both human activity and climate change.

The goal of this study, therefore, was to examine the seasonal and interannual variations in canopy exchange traits of teak, a major tropical deciduous plantation tree, and to determine the environmental and biological factors that cause such variations. Toward this goal, we conducted eddy flux measurements over a 6-year period and compared the estimated mean canopy stomatal conductance (g_s) among seasons and years. Prior to assessing the environmental control of stomatal conductance, a simple two-layer model (Kelliher et al., 1995), which considers a whole ecosystem ET as a sum of canopy ET and vegetation floor evaporation, was first used to extract G_c from surface conductance (G_s).

2. Materials and methods

2.1. Site description

The experiments were carried out in an even-aged teak plantation in Mae Moh district, Lampang province, northern Thailand (18°25′ N, 99°43′ E; 380 m a.s.l.). Teak plantations are widely established throughout the tropics, especially in Indochina and India, due to their market value (Kollert and Cherubini, 2012). In Thailand, as a result of significant decreases in forest area until the 1980s, forest rehabilitation and plantations have been promoted, resulting in the establishment of teak plantations by the Forest Industry Organization (FIO), mainly in northern regions. The Mae Moh teak plantation was established by the FIO in ~1968.

Tree density in the study site was 440 trees ha^{-1} in 2005 and 433 trees ha^{-1} in 2012 due to tree mortality. Mean stem diameter at breast height (DBH) was 22.4 ± 7.3 cm (mean ± SD; n = 308) in November 2005, and increased to 24.2 ± 8.3 cm (n = 303) in February 2012. Mean tree height was 19.9 ± 3.5 m (n = 308) in November 2005, and 23.8 ± 5.4 m (n = 303) in February 2012. Various species of herbaceous plants and shrubs, at a moderate density, occupied the understory. The study site was located on an area of flat land with an almost homogeneous stand structure. The soil was classified as Loamy Paleustults (Thai classification) or Ultisols (U.S. Department of Agriculture Soil Taxonomic Classification), with 35.5% sand, 43.5% silt, and 21.0% clay, and a total porosity of 35–40%. Most fine and coarse roots were detected in the top 0.4 m of soil (Kume et al., 2013).

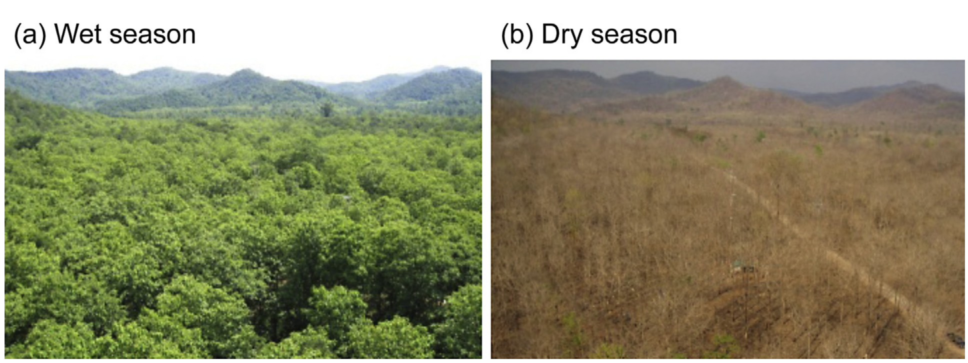

Fig. 1. Photographs of the studied teak plantation canopy in northern Thailand, during a wet season (a) and a dry season (b).