Agricultural and Forest Meteorology 198–199 (2014) 221–231

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Implications of leaf-scale physiology for whole tree transpiration under seasonal flooding and drought in central Cambodia

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ARTICLE INFO

Article history:
Received 24 March 2014
Received in revised form 20 August 2014
Accepted 28 August 2014

Keywords:
Asia Monsoon
Community forest
Drought
Flooding
Ground water
Sap flux

ABSTRACT

In central Cambodia, rapidly growing non-endemic species are often planted for timber production. The introduction of non-endemic species into stands with native species has been found to alter the forest transpiration characteristics in this region with distinct dry and rainy seasons defined by the different rainfall patterns. However, less is understood about the underlying processes, especially the ecophysiological characteristics of native species that are adapted to the highly seasonal environments and the non-endemic species that acclimate to those environments. Leaf ecophysiological traits were measured for two native and two representative non-endemic tree species in central Cambodia to examine whether species-specific seasonal trends in transpiration could be explained by leaf ecophysiological traits. Photosynthetic capacity as represented by the maximum carboxylation rate (V_{cmax25}) of each species remained constant in the rainy and dry seasons. Native species had high stomatal conductance (g_{sw}) and the parameter for its response to the environments (m) in the rainy season and lower levels in the dry season. Additionally, the seasonal change in g_{sw} for non-endemic species was less clear despite the seasonality in the tree-level transpiration. A multi-layer model that incorporated the measured data related to the leaf ecophysiological traits and their seasonal changes successfully reproduced the daily canopy-scale transpiration rate (E_{canopy}). The modeled E_{canopy} successfully reproduced most of the seasonal and day-to-day changes in measured E_{canopy} using sap flux measurements and showed the strong control of leaf ecophysiological traits over E_{canopy} and the species-specific seasonal trends. Two reduction events in measured E_{canopy} were, however, not explained by the simulation, possibly as a result of species-specific factors that were not considered in this study, i.e., the reduction in water uptake by a native species caused by drought and the hypoxic effects of flooding on the roots of a non-endemic species.

1. Introduction

The Southeast Asian Monsoon creates seasons of contrasting precipitation, i.e., a rainy season as well as a dry season with periods of days without rain. In this seasonally changing environment, transpiration rates are thought to differ among trees and sites because of the site-specific environmental conditions (Pinker et al., 1980; Tanaka et al., 2003, 2008) and species-specific ecophysiological traits (Eamus et al., 2001; Kelliher et al., 1995; Kunert et al., 2010; O'Grady et al., 2009). Transpiration and its relationship with species and environmental conditions have been intensively investigated in regions experiencing seasonal droughts because the water demands of fast-growing plantation species can pose a threat to local water resources (Bruijnzeel, 2004; Calder et al., 1993; Mielke et al., 2000; Whitehead and Beadle, 2004).

Our previous work demonstrated the presence of drastic seasonal changes in soil water environments, characterized by flooding

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http://dx.doi.org/10.1016/j.agrformet.2014.08.013

Table 1
List of abbreviations.

Abbreviations	Units	
A	μmol m^{-2} s^{-1}	Net photosynthetic rate
A_G	m^2	Surface area of the stand
A_s	m^2	Sapwood area
b	mol m^{-2} s^{-1}	Intercept of Eq. (3)
C_i	μmol mol^{-1}	Intercellular CO_2 concentration
C_i/C_a	–	C_i relative to the air CO_2 concentration
E_{canopy}	mm day^{-1}	Daily canopy-scale transpiration rate
E_{l_mod}	mm day^{-1}	Modeled leaf-scale transpiration rates
E_{l_sap}	mm day^{-1}	Measured leaf-scale transpiration rates
F_d	g m^{-2} s^{-1}	Sap flux measured by a sensor
g_{sc}	mol m^{-2} s^{-1}	Leaf-scale stomatal conductance for CO_2
G_{sw}	mol m^{-2} s^{-1}	Leaf-scale stomatal conductance for water vapor calculated based on J_s
g_{sw}	mol m^{-2} s^{-1}	Leaf-scale stomatal conductance for water vapor
Γ^*	μmol mol^{-1}	CO_2 compensation point (40 at 25 °C)
J_s	g m^{-2} s^{-1}	Stand mean xylem sap flux over the total stand sapwood area
K_c	μmol mol^{-1}	Michaelis–Menten constant for CO_2 (404 at 25 °C)
K_o	mmol mol^{-1}	Michaelis–Menten constant for O_2 (248 at 25 °C)
LAI	m^2 m^{-2}	Leaf area density
m	–	Slope of Eq. (3)
SF$_n$	–	Sap flux normalized based on the equilibrium evaporation
V_{cmax25}	μmol m^{-2} s^{-1}	Maximum rate of ribulose-1,5-bisphosphate carboxylation normalized at 25 °C
VPD	kPa	Air vapor pressure deficit
Ψ_{leaf}	MPa	Leaf water potential

from the middle to the end of the rainy season and a lowered groundwater table late in the dry season in central Cambodia (Miyazawa et al., 2014). In the studied forest, sap flux was normalized based on the equilibrium evaporation (Jarvis and McNaughton, 1986) of each species that differed for each species in terms of the responses to the changing groundwater table. One species, eucalyptus (*Eucalyptus camaldulensis* Dehnh.) exhibited a decline in the ratio of sap flux to the equilibrium evaporation (SF$_n$, Table 1) under flooding in the rainy season. Another species, Popel (*Shorea roxburghii* G. Don.) did so in dry season with the progression of lowering of the water table and a third species, Tbeng (*Dipterocarpus obtusifolius*) did not show clear decline. Such varied responses to changing soil water environments have been observed in previous studies and were considered to have been caused by differences in the depth in root water uptake (Becker, 1996; Cleverly et al., 2006; Kume et al., 2007), leaf photosynthetic traits (Herbst et al., 2008) and hydraulic properties (Katul et al., 2003; Williams et al., 1996, 1998).

Information related to the leaf ecophysiological traits and their seasonal trends would provide insight into the basis underlying the species-specific responses in transpiration that occur in response to changes in the groundwater table. Leaf ecophysiological traits are known to change as the driver for changing transpiration (Baldocchi, 1997; Law et al., 2000; Wilson et al., 2001; Xu and Baldocchi, 2004). Stomatal conductance for water vapor (g_{sw}) changes in response to the atmospheric evaporative demand and the soil water content especially in the presence of drought to balance canopy transpiration and root water uptake (Katul et al., 2003). Many species in regions with pronounced rainy and dry seasons are known to reduce leaf gas exchange rates during the dry season (Aranda et al., 2012; Ishida et al., 2006; Liu et al., 2004; Pereira et al., 1987). These studies imply that species in central Cambodia should show similar seasonal trends in leaf ecophysiological traits, such as in the photosynthetic capacity V_{cmax25} (maximum rate of ribulose-1,5-bisphosphate carboxylation normalized at 25 °C, Farquhar et al., 1980), and a parameter for stomatal control (m, the slope of stomatal conductance and the function of photosynthetic rate and leaf surface environments, Ball et al., 1987). Results for some species, however, did not show the expected remarkable reduction in these leaf ecophysiological traits during dry season because of the species-specific ecophysiological traits (Ferrio et al., 2003; Martinez-Ferri et al., 2000) and/or site-specific edaphic conditions (Prior et al., 2004; Tanaka et al., 2003), making it difficult to predict transpiration rates of forests with clear seasonality in rainfall without in situ measurements. In the Indochina Peninsula, research studies have been conducted related to leaf ecophysiological traits in hill evergreen forests (Tanaka et al., 2003) and lowland evergreen forests (Ishida et al., 2006; Kenzo et al., 2012; Norisada and Kojima, 2005); these showed variations in their seasonal trends among species and sites. However, no research studies have been conducted for co-occurring tree species in forests whose productivity and water use are affected by seasonal flooding and drought.

The goal of this study is to investigate the leaf ecophysiological traits of the co-occurring tree species and to clarify how the seasonality in transpiration of each species is controlled by species-specific leaf ecophysiological traits. Toward that goal, field measurements were conducted in a community forest in central Cambodia, which had been established as a conservation area under the non-timber producing management by nearby villagers. The community forest is composed of various naturally regenerated Popel, Tbeng and other native tree species and non-endemic eucalyptus and acacia (*Acacia auriculiformis*) that had been planted for timber production. Interspecific variation in the canopy-scale transpiration rate (E_{canopy}) and its response to the changing environments is thought to be caused by variations in g_{sw} and its seasonality specific to the species. Therefore, among leaf ecophysiological traits with a close relationship to g_{sw}, V_{cmax25} and m of two native and two non-endemic tree species were periodically measured. Canopy-scale transpiration rate (E_{canopy}) was computed using a multilayer model (Leuning et al., 1995). This model was used both as a tool for scaling up the observed leaf-scale gas exchange rates and as a way to investigate the role of seasonal changes in the leaf ecophysiological parameters on E_{canopy} in rainy and dry seasons. For these purposes, we examine whether the modeled E_{canopy} successfully captures the patterns of seasonal and day-to-day changes in measured E_{canopy} by taking seasonal changes in leaf ecophysiological traits into consideration.

We examine the following hypotheses. First, V_{cmax25} and m of each species are high during the rainy seasons and are low under drought conditions during the dry season, which effectively reduces E_{canopy}. Additionally, V_{cmax25} and m show species-specific seasonal trends corresponding to those in the SF$_n$. Finally, seasonal changes in V_{cmax25} and m strongly influence E_{canopy}, i.e., input of data obtained in different season results in large changes in E_{canopy}.

2. Materials and methods

2.1. Study site and meteorological observation

The study was conducted at the study site of Miyazawa et al. (2014) (Svay Bakav water cycle study site), Kampong Chhnang in central Cambodia (11°59′20″ N, 104°44′27″ E, 50 m a.s.l.) starting in March 2008. The site was located in a reforested area, which had been established on heavily degraded land in 1998. The Cambodian government designated the area as a 'community forest', which is managed by the villagers for the purpose of forest conservation. Community forests are used by villagers for the production of non-timber forest products, and presently, timber cutting is forbidden.