Biophysical limits to responses of water flux to vapor pressure deficit in seven tree species with contrasting land use regimes

Jianguo Gao, Ping Zhao*, Weijun Shen, Junfeng Niu, Liwei Zhu, Guangyan Ni

Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, PR China

ABSTRACT

Quantifying the sensitivity of trees to environmental variables such as vapor pressure deficit (D) is important for understanding the hydrological responses to land use changes and the role of underlying physiological mechanisms. Sap flux (J_s), water transport, and sensitivity of canopy stomatal conductance (G_s) to D (m) were determined during the early dry season in 2012 and 2013 for young timber trees (5 years), secondary forest trees ($\sim$25 years), and mature forest trees ($\sim$50 years) at three sites of lower sub-tropical China. The J_s was found to be negatively correlated with tree biometric parameters, and whole tree water transport for a given tree size decreased with age or size, which was partially attributed to the lower sapwood quantity for a given diameter. The m and reference G_s at 1 kPa (G_{sref}) of the seven tree species decreased from young timber to mature trees, although not significantly. The D, which is the extrapolated value when stomata closure ($e^{b/m}$), significantly varied among species, which decreased from isohydric *Eucalyptus grandis × urophylla* to more anisohydric *Acacia auriculiformis* and *Eucalyptus citriodora*. J_s and maximum sap flux ($J_{s,max}$) decreased with wood density, suggesting that water flux was regulated by biophysical constraints. Wood density was a good predictor of G_{sref} ($r^2 = 0.664$, $P = 0.026$), indicating that water flux to D is an intrinsic adaptive characteristic. To the best of our knowledge, this is the first study linking wood density and G_{sref}. The responses of water flux to D varied among species, size or age, and hydraulic architecture, which highlights that modeling water budget to land cover transition based on the same hydraulic parameter from one land use scenario can potentially cause extensive errors in model prediction. Our empirical research could be used for the evaluation of the consequences of land use changes on the hydrological process of forest ecosystems.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Land use alterations and global climate changes could exert profound influences on terrestrial ecosystem hydrological regimes (Foley et al., 2005). Land cover transition can greatly change the patterns of runoff, evaporation, and soil water content, and in turn, these changes could influence serious regional water budget across broad spatial scales, as well as consequences for ecosystem goods and services upon which society depends (DeFries and Eshleman, 2004; Schlesinger and Jasechko, 2014). The effects of land use changes on regional water budget are influenced by tree species, climatic variables, soil nutrients, and forest managements; it also plays a crucial role in predicting consequences from the perspective of tree physiology. Stomata coordinate the carbon gain and water loss, playing an important role in the water balance of the forest

ecosystem (Meinzer et al., 2013). By qualifying the responses of tree transpiration to environmental variables such as vapor pressure deficit (D), the underlying physiological mechanism can be elucidated. The sensitivity analysis of canopy stomatal conductance (G_s) to D excluded the influences of species, site, or land use scenarios (Oren et al., 1999), which is convenient for scaling and predictive understanding of water fluxes regardless of meteorological variables.

Stomata close under high D to avoid hydraulic failure caused by a decrease in leaf water potential that is caused by high transpiration rates. The growth of plants can be determined by the sensitivity of stomata to D (m); plants with higher m always have higher carbon assimilation rates and quantum yields of photosynthesis (Franks and Farquhar, 1999). Higher m also assists plants in maintaining the lowest leaf water potential, thus preventing the decrease of hydraulic conductance (Addington et al., 2004). m is affected by intrinsic biological factors; for example, the m increased with age in conifers inhabiting xeric environments (Hubbard et al., 1999); however, for the seedlings of red spruce, the m is higher than
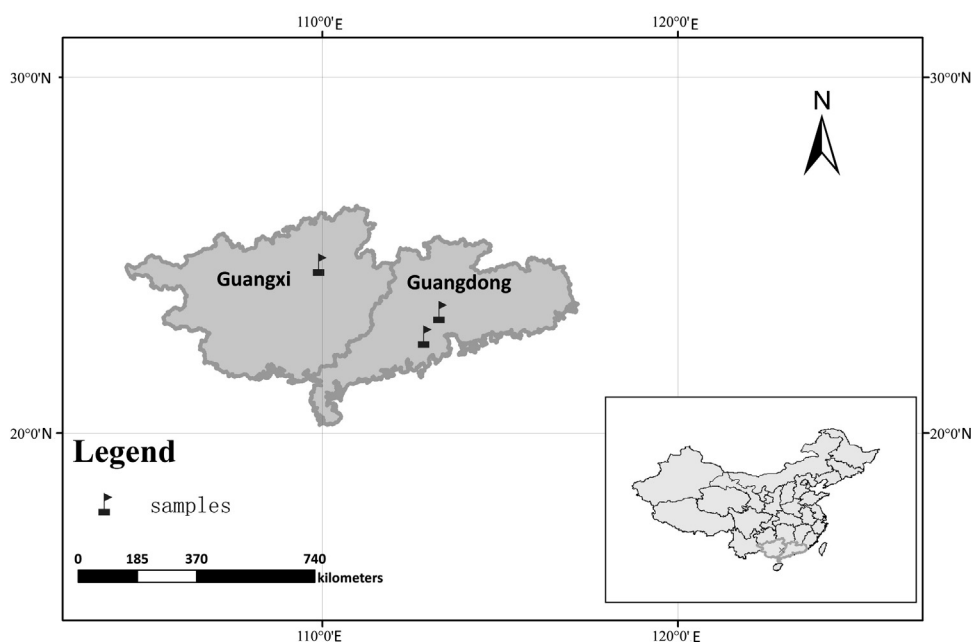
Fig. 1. Geographical research sites in this study, including one site in Guangxi Province and two sites in Guangdong Province. More details in Table 1.

mature trees inhabiting mesic environments (Day and Greenwood, 2011). Oren et al. (2001) showed that reference G_s at 1 kPa (G_{sref}) and m increased in *Taxodium distichum* trees after reduction in its leaf area due to hurricane. In addition, canopy height, sapwood area, and the competition for light could influence G_{sref} and m (Novick et al., 2009; Loranty et al., 2010; Ewers et al., 2011), thus, G_{sref} and m exhibit some plasticity, which varies with tree biometric parameters, age, or environment.

The hydraulic resistance would increase with flow-path length because of tree size or age, especially for bigger trees that probably undergo more water stress than smaller trees. For example, Meinzer et al. (2001) reported that sap flux (J_s) decreased with the diameter. Bigger trees close their stomata faster than that by smaller trees even under similar water stress, to minimize the intrinsic moisture deficit, which was first proposed by Yoder et al. (1994) and Ryan and Yoder (1997). Since then, the Hydraulic Limitation Hypothesis (HLH) was tested and verified in plant physiology research studies. Apart from tree size and age, tree transpiration is also influenced by hydraulic architecture such as wood type, vessel scattering, sapwood, or leaf area (Sperry, 2000; Oren et al., 2001). These factors diversified tree transpiration resulting in species-specific rates of transpiration. For example, Kagawa et al. (2009) reported that native *Metrosideros polymorpha* had the lowest values of J_s and whole-tree water use, which was substantially less than the timber species *Eucalyptus saligna* or *Fraxinus uhdei*. The biophysical and biological mechanisms of species-specific water use differences was examined in relation to tree size and age (Ewers et al., 2011), as well as its origin (native or exotic), succession stage (early or late), wood type, wood density (Sperry, 2000). For instance, species- specific water use differences always mirrored differences in ring-porous or diffuse-porous wood. Bush et al. (2008) reported that the sensitivity of water flux to D varied between ring-porous or diffuse- porous trees; diffuse-porous trees are more resistant to embolism, although these showed low sensitivity to D.

The capacity of resisting embolism is correlated to conduit diameter, vessel length, pit area, and wood density. Furthermore, wood density is highly correlated with hydraulic conductance (Jacobsen et al., 2005, 2007; Hacke et al., 2009; McCulloh et al., 2012). The relationship between wood density and water flux has gained recent

attention around the world, because of the effects of wood density on tree growth rate, hydraulic capacitance and conductance, and the resistance to drought-induced embolism (McCulloh et al., 2012). A recent meta-analysis showed that the effect of wood density on J_s is convergent, and the most efficient water transport wood density is 0.51–0.65 g cm^{-3} (Kallarackal et al., 2013). In a study on J_s of the conifer *Dacrydium cupressinum*, a good negative relationship was established with wood density (Barbour and Whitehead, 2003). Trees with higher wood density always have low water transport efficiency and narrow conducting area (Hacke et al., 2001). Wood density also reflects the growth strategy of trees; for example, trees with low wood density are likely to be at the early stage of succession with high growth rates, whereas understory trees with high wood density are generally more shade tolerant, thus, having lower sensitivity to environmental variables (van Gelder et al., 2006).

Quantifying the effects of land use changes on tree transpiration is constrained by various logistical issues, thus, requiring the cooperation between hydrologists and plant physiologists (Jones et al., 2009). The present study utilized three research plots with contrasting species, tree age, and forest management, which provided an opportunity to study the mechanism of tree transpiration in response to D.

The following study has been conducted to test three hypotheses: (**H1**) J_s would decrease with tree size and age because of the negative effect of increased flow-path length; (**H2**) m and G_{sref} would decrease with tree size and age and species-specific variation occurs even when no apparent soil water stress was detected during our experiments; and (**H3**) considering the high association between wood density and water flux, theoretically and empirically (Roderick and Berry, 2001; Barbour and Whitehead, 2003), we hypothesize that wood density is the intrinsic character of lowering the m and G_{sref}, these links might help determine the underlying mechanism responsible for stomatal regulation.

2. Materials and methods

2.1. Site description and tree species

Three research plots with contrasting land use regimes were employed in this study. The first plot, the Huangmian state forest