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Spatial heterogeneity in stand characteristics alters water use patterns of mountain forests

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ABSTRACT

Mountain landscapes have complex and rugged topographies, with abrupt spatial and temporal changes in microclimate and soil properties, factors that directly affect tree growth and canopy processes. These may alter functional relationships over short spatial scales, rendering the use of allometry in scaling tree water use (TWU) from single trees to stand level less accurate. On the other hand, canopy processes, especially stomatal conductance are sensitive to the environmental conditions prevailing above the canopy. Given that these also change rapidly in a mountain landscape, we speculate that patterns of water use in a complex landscape are determined by the interaction between stand structure and canopy conductance. We examined forest stand structure, microclimate and sap flux density (Js) in two forest stands distributed at 50 m and 330 m elevations of the Dinghushan Mountain in south China to determine how they influence tree functional allometry for scaling up stand water use. Tree sapwood area (SA) was correlated with the diameter at breast height (DBH) irrespective of species and location within the forest catchment. The maximum sap flux density (Js) on a clear sunny day ranged from 18 ± 9 to 48 ± 12 and 25 ± 8 to $64 \pm 11\ \mathrm{g\,m^{-2}\,s^{-1}}$ in the 330 m and 50 m forest stands, respectively. Differences among trees and between forest stands were significant ($p < 0.05$). Daily maximum tree water use (TWU) ranged from 2 ± 4 to $36 \pm 12\ \mathrm{kg\,d^{-1}}$ and 4 ± 3 to $42 \pm 11\ \mathrm{kg\,d^{-1}}$ in the 330 and 50 m, respectively. Differences between the stands were significant. Within a stand, TWU was correlated with DBH irrespective of species. This functional relationship was, however, different between the forest stands, resulting in different E estimates for the respective stands. Cross-site variations were due to differences in vapor pressure deficit (VPD), photosynthetic photon flux density (PPFD) and leaf specific canopy conductance (g_t). While trees responded in a similar manner to the microclimatic environment, between-site differences in stand characteristics shifted the functional relationships. Thus, in this complex mountain terrain, using a universal, site-specific allometric equation in scaling up sap flow from single trees to catchment-scale can lead up to 30% inaccuracy.

1. Introduction

In lowland forests, allometric relationships are a useful tool in the estimation of tree and stand water use given that tree allometric structures that relate to water transport in forest trees are independent of forest type, tree species and site-dependant adaptations (Hatton et al., 1998; Meinzer et al., 2001; Meinzer, 2003; O'Grady et al., 2009). In such forests, trees tend to develop a common pattern of water use that relates to tree size (diameter at

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breast height – DBH) (Enquist et al., 1998; Wullschleger et al., 1998; Meinzer et al., 2001, 2005). The establishment of such allometries has made it possible to scale up forest water use from single tree measurements using the robust and generally accepted sapflow methodologies (Cermak et al., 1973; Sakuratani, 1981; Granier, 1985). This approach has, however, been predominantly applied on homogenous lowland forest stands, which experience relatively uniform microclimatic conditions above the forest canopy (Oren et al., 1998; Ewers et al., 2002; Delzon et al., 2004; Delzon and Loustau, 2005; Gebauer et al., 2008; Kume et al., 2010).

In such cases, the estimation of water use by trees and forest stands using the sap flow methodology relies entirely on the accurate measurement of tree sap flux density (Js), accurate determination of sapwood area (SA) of the individual trees and the correct measurement of stand stem density (Granier et al., 2000; Wilson et al., 2001). In complex mountainous landscapes, however, both Js and SA/tree diameter relationships may vary spatially because of changing microclimate above the forest canopy, varying soil properties across the landscape and tree characteristics, due to the rugged topography (Kumagai et al., 2007), since mountains have some of the sharpest spatial and temporal gradients in climatic parameters (Beniston and Rebetez, 1996; Giorgi et al., 1997; Becker and Bugmann, 1997). Topography has a direct bearing on soil characteristics, runoff and soil moisture storage, with implications on soil moisture availability to trees, tree water use (TWU) and growth (Luizão et al., 2004; Tateno et al., 2004). Trees growing on mountain landscapes, therefore, adjust to the micro-habitat hydrology and micro-climate by modifying their water transport and water use characteristics (Kumagai et al., 2005a,b). Such modifications occur within short spatial scales, altering the functional allometric relationships such as tree size (DBH) vs. TWU, compromising the use of functional allometry in the up-scaling of stand-level transpiration in complex mountain terrains. For example, McJannet et al. (2007) observed that trees adjust to local edaphic conditions and microclimate, altering the magnitude of sap flux in the stem, as well as the relationships between DBH/SA and transpiration. Similarly, Jung et al. (2014) reported significant differences in tree transpiration rates and forest water use along topographic gradients that were independent of tree size.

In a complex mountain terrain where atmospheric conditions such as humidity, temperature and light change rapidly, canopy interaction with the external environment is likely to result in complex water use patterns on the landscape, dictated by the coordination between stomatal and hydraulic conductance and growth at the whole plant level. Thus, sensitivity of the stomata to changes in photosynthetic active radiation (PAR), vapor pressure deficit (VPD), soil moisture and atmospheric CO_2 concentration could lead to differences in TWU across the landscape (Jarvis, 1987). Where soil moisture and atmospheric CO_2 concentration remain invariable, canopy conductance to water vapor can be regarded as a function of PAR and VPD. Thus, integrated canopy conductance estimated from sap flow measurements could provide a basis to explore stomatal effects on transpiration with respect to tree species and stand position on mountain landscapes.

While a universal allometry between tree size and tree water use offers an easy solution for up-scaling from single trees to stand and catchment scales, structural and functional differentiation with elevation observed in mountains (Körner, 2003; Kumagai et al., 2008; Matyssek et al., 2009) may compromise the accuracy of such approaches. Analysis of the interaction between forest structure and canopy processes could provide a better insight into the patterns of water use on mountain landscapes and their determinants. Such approaches have received little attention, since water use by forests growing in complex mountainous landscapes has rarely been addressed in the past. In this study, we measured Js in trees, microclimate and tree characteristics (species composition, diameter distribution etc.) in two forest stands located at different elevations on the slope of the Dinghushan Mountain in south China to identify common functionalities. We hypothesized that complexity in landscape structure leads to variable water use patterns in complex mountain landscapes as a result of coordination between localized stand characteristics and canopy processes.

Table 1
Stand characteristics of the two forest stands where our measurements were conducted. Mean tree height, stem density and stand SA were estimated from 20 and 42 different tree species in the 50 and 330 m, respectively. Transpiration estimates are from the three dominant species *Castanopsis chinensis*, Hance (Fagaceae) *Machilus chinensis* (Benth.) Hemsl. (Lauraceae) and *Schima superba Gardner & Champ.* (Theaceae) common to both stands.

Elevation (m)	50	330
Exposition	South	West
Slope	6–8^0	8–9^0
Plot size (m^2)	600	600
Stand age (Years)	60–80	70–80
Mean tree height (m)	7.3	6.9
Stem density (stem/ha)	2400	4267
Stand SA (m^2/ha), DBH > 10 cm	12.8	16.2
Leaf Area Index (LAI)	4.0	3.7
Av. Transpiration rate (mm d^{-1})	1.8	1.7

2. Materials and methods

2.1. Description of the experimental sites

Dinghushan Biosphere Reserve (23°09′21″–23°11′30″N and 112°30′39″–112°33′41″E), located in Guangdong province in south China, covers an area of 1156 ha of an evergreen subtropical forest. The elevation ranges from 10 to 1000 m a.s.l., with an extremely complex terrain that leads to a fragmented landscape of rapidly changing aspects and slopes. The climate is typical south subtropical monsoon (Zhou et al., 2011, 2013). The mean annual rainfall is 1956 mm, with a distinct seasonality. About 85% of the rain falls in spring and summer (April–September) and only 15% in autumn and winter (October–March). The annual mean temperature and relative humidity are 22.3 °C and 77.7%, respectively. The lowest mean monthly temperature is 13.9 °C in January and the highest is 28.9 °C in August.

The bedrock is sandstone and shale. The soils have pH-values ranging from 4.0 to 4.9 and are classified as Utisol, according to the USDA soil classification system (Mo et al., 2008). The soil profile usually ranges from 50 to 80 cm in depth.

For this study, we selected two forest stands located at 50 and 330 m elevations, respectively, that were dominated by evergreen, broadleaf tree species. The two forest stands had similar slopes, but different aspects (Table 1).

The dominant broadleaf forest species common to the two monitored forest stands were species *Castanopsis chinensis*, Hance (Fagaceae) *Machilus chinensis* (Benth.) Hemsl. (Lauraceae) and *Schima superba Gardner & Champ.* (Theaceae). The biomass of several succession vegetation types has been monitored since 1980 (Zhou et al., 2007; Tang et al., 2011).

2.2. Measurements

2.2.1. Microclimate

Between October 2011 and May 2012, air temperature and relative humidity (Model HMP45C, Campbell Scientific, Logan, USA), Photosynthetic active radiation (PAR, LI-190, LI-COR USA) and rainfall at 30 m height (TB4MM, Campbell Scientific, Logan, USA) were measured every 30 s, averaged and logged every 30 min using data logger (CR5000, Campbell Scientific, Lincoln, USA). These microme-