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

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1 **Abstract**

2 Mountain landscapes have complex and rugged topographies, with abrupt spatial and
3 temporal changes in microclimate and soil properties, factors that directly affect tree
4 growth and canopy processes. These may alter functional relationships over short spatial
5 scales, rendering the use of allometry in scaling tree water use (TWU) from single trees
6 to stand level less accurate. On the other hand, canopy processes, especially stomatal
7 conductance are sensitive to the environmental conditions prevailing above the canopy.
8 Given that these also change rapidly in a mountain landscape, we speculate that patterns
9 of water use in a complex landscape are determined by the interaction between stand
10 structure and canopy conductance. We examined forest stand structure, microclimate and
11 sap flux density (Js) in two forest stands distributed at 50 m and 330 m elevations of the
12 Dinghushan Mountain in south China to determine how they influence tree functional
13 allometry for scaling up stand water use. Tree sapwood area (SA) was correlated with the
14 diameter at breast height (DBH) irrespective of species and location within the forest
15 catchment. The maximum sap flux density (Js) on a clear sunny day ranged from 18 ± 9 to
16 48 ± 12 and 25 ± 8 to 64 ± 11 $\text{g m}^{-2} \text{s}^{-1}$ in the 330 m and 50 m forest stands, respectively.
17 Differences among trees and between forest stands were significant ($p < 0.05$). Daily
18 maximum tree water use (TWU) ranged from 2 ± 4 to 36 ± 12 kg d^{-1} and 4 ± 3 to 42 ± 11 kg d^{-1}
19 in the 330 and 50 m, respectively. Differences between the stands were significant.
20 Within a stand, TWU was correlated with DBH irrespective of species. This functional
21 relationship was, however, different between the forest stands, resulting in different E
22 estimates for the respective stands. Cross-site variations were due to differences in vapor
23 pressure deficit (VPD), photosynthetic photon flux density (PPFD) and leaf specific

1 canopy conductance (g_t). While trees responded in a similar manner to the microclimatic
2 environment, between-site differences in stand characteristics shifted the functional
3 relationships. Thus, in this complex mountain terrain, using a universal, site-specific
4 allometric equation in scaling up sap flow from single trees to catchment-scale can lead
5 up to 30 % inaccuracy.

6

7 **Key words:** Functional allometry, Sap flux density, Microclimate, Mountain forests,
8 Stand structure, Tree water use

9

1.0. 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, 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 breast height - DBH) (Enquist et al. 1998, Wullschleger et al. 1998, Meinzer et al. 2001, Meinzer et al. 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, Sakurtani 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 (J_s), 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 J_s 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

1 gradients in climatic parameters (Beniston and Rebetez 1996, Giorgi et al. 1997, Becker
2 and Bugmann 1997, 2001). Topography has a direct bearing on soil characteristics,
3 runoff and soil moisture storage, with implications on soil moisture availability to trees,
4 tree water use (TWU) and growth (Luizão et al. 2004, Tateno et al. 2004). Trees growing
5 on mountain landscapes, therefore, adjust to the micro-habitat hydrology and micro-
6 climate by modifying their water transport and water use characteristics (Kumagai et al.
7 2005). Such modifications occur within short spatial scales, altering the functional
8 allometric relationships such as tree size (DBH) vs. TWU, compromising the use of
9 functional allometry in the up-scaling of stand-level transpiration in complex mountain
10 terrains. For example, McJannet et al. (2007) observed that trees adjust to local edaphic
11 conditions and microclimate, altering the magnitude of sap flux in the stem, as well as the
12 relationships between DBH/SA and transpiration. Similarly, Jung et al. (2014) reported
13 significant differences in tree transpiration rates and forest water use along topographic
14 gradients that were independent of tree size.

15
16 In a complex mountain terrain where atmospheric conditions such as humidity,
17 temperature and light change rapidly, canopy interaction with the external environment is
18 likely to result in complex water use patterns on the landscape, dictated by the
19 coordination between stomatal and hydraulic conductance and growth at the whole plant
20 level. Thus, sensitivity of the stomata to changes in photosynthetic active radiation (PAR),
21 vapor pressure deficit (VPD), soil moisture and atmospheric CO₂ concentration could
22 lead to differences in TWU across the landscape (Jarvis 1976). Where soil moisture and
23 atmospheric CO₂ concentration remain invariable, canopy conductance to water vapor

1 can be regarded as a function of PAR and VPD. Thus, integrated canopy conductance
2 estimated from sap flow measurements could provide a basis to explore stomatal effects
3 on transpiration with respect to tree species and stand position on mountain landscapes.

4
5 While a universal allometry between tree size and tree water use offers an easy solution
6 for up-scaling from single trees to stand and catchment scales, structural and functional
7 differentiation with elevation observed in mountains (Körner 2003, Kumagai et al. 2008,
8 Matyssek et al. 2009) may compromise the accuracy of such approaches. Analysis of the
9 interaction between forest structure and canopy processes could provide a better insight
10 into the patterns of water use on mountain landscapes and their determinants. Such
11 approaches have received little attention, since water use by forests growing in complex
12 mountainous landscapes has rarely been addressed in the past. In this study, we measured
13 Js in trees, microclimate and tree characteristics (species composition, diameter
14 distribution etc) in two forest stands located at different elevations on the slope of the
15 Dinghushan Mountain in south China to identify common functionalities. We
16 hypothesized that complexity in landscape structure leads to variable water use patterns
17 in complex mountain landscapes as a result of coordination between localized stand
18 characteristics and canopy processes.

19 20 21 **2.0. Materials and methods**

22 23 *2.1. Description of the experimental sites*

24 Dinghushan Biosphere Reserve (23°09'21"–23°11'30"N and 112°30'39"–112°33'41" E),
25 located in Guangdong province in south China, covers an area of 1156 ha of an evergreen

1 subtropical forest. The elevation ranges from 10 to 1000 m a.s.l., with an extremely
2 complex terrain that leads to a fragmented landscape of rapidly changing aspects and
3 slopes. The climate is typical south subtropical monsoon (Zhou et al. 2011, 2013). The
4 mean annual rainfall is 1,956 mm, with a distinct seasonality. About 85% of the rain falls
5 in spring and summer (April-September) and only 15% in autumn and winter (October-
6 March). The annual mean temperature and relative humidity are 22.3°C and 77.7%,
7 respectively. The lowest mean monthly temperature is 13.9°C in January and the highest
8 is 28.9 °C in August.

9 The bedrock is sandstone and shale. The soils have pH-values ranging from 4.0 to 4.9 and
10 are classified as Udisol, according to the USDA soil classification system (Mo et al. 2008).

11 The soil profile usually ranges from 50 to 80 cm in depth.

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

15
16 The dominant broadleaf forest species common to the two monitored forest stands were
17 species *Castanopsis chinensis*, [Hance \(Fagaceae\)](#) *Machilus chinensis* ([Benth.](#)) [Hemsl.](#)
18 ([Lauraceae](#)) and *Schima superba* Gardner & Champ. ([Theaceae](#)). The biomass of several
19 succession vegetation types has been monitored since 1980 (Zhou et al. 2007, Tang et al.
20 2011).

21 **2.2. Measurements**

22 **2.2.1. Microclimate**

23
24
25 Between October 2011 and May 2012, air temperature and relative humidity (Model

1 HMP45C, Campbell Scientific, Logan, USA), Photosynthetic active radiation (PAR, LI-
2 190, LI-COR USA) and rainfall at 30 m height (TB4MM, Campbell Scientific, Logan,
3 USA) were measured every 30 seconds, averaged and logged every 30 minutes using data
4 logger (CR5000, Campbell Scientific, Lincoln, USA). These micrometeorological
5 sensors were installed on two different meteorological towers installed in both forest
6 stands.

7 2.2.2. *Soil water content*

8 Soil water content (SWC) in 30 cm depth was measured at each site using soil moisture
9 sensors (5TE, Decagon Devices, Washington, USA) randomly installed at 3 different
10 locations within the study plots in each forest stand and data were logged every 30
11 minutes (EM50 Data logger, Decagon Devices).

12

13 2.2.3. *Vegetation survey*

14 Vegetation survey was conducted in 2010 as described by Zhou et al. (2013). Six 10 m by
15 10 m plots were demarcated for survey in both forest stands. Tree height (inclinometer)
16 and diameter (diameter tape) at breast height (DBH) of all the individuals within the
17 study plots, with $DBH \geq 1$ cm were measured and recorded according to species.

18 Leaf area index (LAI) was measured with LAI-2200C Plant Canopy Analyzer (LICOR,
19 USA). In each of the 10 m by 10 m plots within a forest stand, LAI was measured at five
20 positions, which included the four corners and at the center. Poles were installed at these
21 locations so that follow-up measurements were conducted at the same points all the time.
22 Measurements were conducted early in the morning just before sunrise, or later in the day,
23 just after sunset. At every measurement, 10 data records were logged, before taking 5

reference logs in an open location within the forest canopy. During the growing season, from April to September, measurements were conducted once a month, otherwise, they were taken at 2 or 3-month intervals. A total of 7-8 campaigns were conducted each year. The LAI data were corrected using FV2200 software.

Also measured were the spatial coordinates (to 15 cm accuracy) of each individual tree.

2.2.4. Sap flow measurements

Sap flux density J_s ($\text{g m}^{-2} \text{s}^{-1}$) in the conducting sapwood was monitored in at least 5 individuals of the three dominant broadleaf tree species, *C. chinensis*, *M. chinensis*, and *S. superba* common to both forests. In both cases, the biomass of the three species account for 85% of the total stand biomass (see Table 2). The measurements were conducted between October 2011 and June 2012 using custom-made Granier-type sensors (Granier 1985, 1987). Details of sensor probes are provided by Otieno et al. (2014). The sensors were placed in the outer 20 mm of the sapwood, approx. 1.3 m from the ground (breast height). In cases where the tree trunk had sapwood radius greater than 20 mm, a second sensor was implanted 20 to 40 mm into the sapwood (see Table 2). This second sensor was spaced 10 cm circumferentially, away from the first sensor pair, but on the same side of the stem. All sensor installations were made on the north-facing side of the trees to avoid exposure to the sun and minimize direct short-wave radiation. In addition, the sensors were covered with a radiation shield (Styrofoam sheets with aluminum foil) to further minimize the direct thermal load. To examine azimuth-variations in sapflow, an extra set of sensors were installed on the east, west and south facing sides of the largest tree of each species for comparison. Temperature differences ($\Delta T^{\circ}\text{C}$) were measured every ten seconds and a 30-minute mean value was logged (DL2e

1 with LAC-1 in single ended mode, Delta-T Devices, England). J_s for each sensor was
 2 calculated from ΔT in accordance with Granier (1987), assuming zero J_s (i.e. $\Delta T_{\max}$) at
 3 night and VPD near zero:

$$4 \quad J_s = 119K^{1.231} \quad (1)$$

5 where,

$$6 \quad K = \frac{(\Delta T_{\max} - \Delta T)}{\Delta T} \quad (2)$$

7 Tree water use (TWU , kg h^{-1}) was obtained by multiplying J_s by the sapwood cross-
 8 sectional area (SA).

$$9 \quad TWU = J_{s_i} \cdot SA_i \quad (3)$$

10 where, J_{s_i} is J_s of the annulus i ($\text{g m}^{-2} \text{s}^{-1}$) and SA_i is sapwood area of the annulus i (m^2).

11 SA was determined as outlined in in 2.2.5 below.

12 We used the functional relationship between TWU and DBH for the measured trees
 13 within the respective plots to derive stand water use using inventory data (stand DBH
 14 data).

$$15 \quad \text{Stand transpiration } (E \text{ in mm}) \text{ was calculated as } \Sigma TWU / A_g, \quad (4)$$

16 where ΣTWU is total stand water use and A_g is area of the stand.

17 To identify possible sources of variation among individual trees, we calculated the total
 18 water vapor conductance of individual trees (g_t , mm s^{-1}) based on the approach by
 19 Köstner et al. (1992) from the ratio of tree transpiration E_t (mm h^{-1}) and vapor pressure
 20 deficit D measured above the tree canopies, with unit conversion factor $k=(6 \cdot G_v \cdot T_k)$.

$$21 \quad g_t = k \cdot E_t / D \quad (5)$$

1 where D is VPD, δ is the density of water (998 kg m^{-3}), G_v is gas constant for water vapor
2 ($0.462 \text{ m}^3 \text{ kPa kg}^{-1} \text{ K}^{-1}$), T_k is air temperature in Kelvin. E_t was calculated based on the
3 tree crown area.

4 5 2.2.5. *Sapwood area (SA) determination* 6

7 The depth of conducting sapwood was established using two methods. In the first case, an
8 increment corer ($D = 6 \text{ mm}$) was drilled into the centre of a tree stem of at least 5
9 individuals per species at 1.3 m height. A plastic pipette was then inserted into the drilled
10 hole (1-2 cm depth) and filled with water-soluble red dye (0.5% acid Fuchsin) early in the
11 morning (09:00-10:00). After 3-4 hours, wood samples were obtained with the same
12 increment corer, 3 cm above the initial hole to determine the depth of the water
13 conducting sapwood (stained wood). The second approach involved measurements on
14 several cores taken at breast height from different diameter classes of the measured tree
15 species, using an increment corer of 6 mm diameter. The extracted cores were oven-
16 dried at 80°C for 48 hours and stored in a desiccator for 1 week until a constant weight
17 was reached. Single dried cores were cut into 5 mm lengths, systematically from the
18 outermost part close to bark, to the innermost part, close to the pith and each length
19 weighed to determine the dry weight. Wood density (G/V) of each of the 5 mm sections
20 was calculated according to Valdez-Hernández et al. (2010) assuming a perfect cylinder,
21 where V is determined as:

$$22 \quad V = \pi D^2 * L / 4 \quad (6)$$

23 V is the core volume, D is the corer diameter; L is the length of the core (5 mm). Wood
24 density of the respective 5 mm sections were then plotted against depth (length from

bark) in order to determine the depth of the sapwood. In all the cases, the transition from sapwood to heartwood was marked by a drastic change in wood density.

Conducting sapwood area (SA) was calculated as:

$$SA = \pi[(r_T - d_B)^2 - (r_T - d_B - d_{sw})^2] \quad (7)$$

r_T is the radius of the tree trunk, d_B is the depth of the bark and d_{sw} is sapwood depth.

2.2.6. Quantifying variability

The initial assumption was that TWU universally scales with DBH for the entire mountain catchment and that spatial heterogeneity arising from site-specific differences are already registered in DBH. To prove this, we established stand specific allometry (DBH vs TWU) for the respective forest stands. These were then used to derive stand transpiration ($E \text{ mm d}^{-1}$), using stand inventory data. Each site-specific equation was then employed to determine E for the respective stands (assuming a universal allometric relationship) and data compared.

2.2.7. Statistical analysis

Comparison between forest stands was performed using t-test, while trees were compared using One-Way ANOVA. Post-Hoc tests were performed using Tukey-LSD. Factor influence was assessed using regression analysis. All statistical tests were performed using SPSS 15 standard statistical package (SPSS, USA).

3.0. Results

3.1. Microclimate and soil water content

Weather conditions and soil water content at the two forest stands during the measurement period are shown in Fig. 1.

FIG. 1

1
2 We recorded a mean daily temperature difference of about 1.5°C between the two forest
3 stands. At the 50 m elevation stand, the lowest and highest mean air temperatures were 7
4 $\pm 2^{\circ}\text{C}$ and $29 \pm 3^{\circ}\text{C}$ between December and January and in May, respectively. Due to
5 frequent fog formation, the 330 m elevation stand recorded, on average, lower light
6 intensities compared to the 50 m elevation stand (Fig 1b). At the 50 m stand, the daily
7 maximum PAR reached $30 \text{ mol m}^{-2} \text{ d}^{-1}$, while the daily maximum PAR at the 30 m stand
8 was around $9.5 \text{ mol m}^{-2} \text{ d}^{-1}$. The highest daily VPD ranged between 1.5 – 4.0 kPa at the
9 50 m and 0.5 and 2.5 kPa at the 330 m elevation stands (Fig 1c). Rainfall amounts and
10 patterns were similar (not shown), leading to similar soil moisture content within the 30
11 cm depth (Fig 1d). Measurement of SWC in the 300 m plot was regularly interrupted
12 from January due to sensor failure until it was replaced in May. The lowest soil moisture
13 contents of $0.2 \text{ m}^3 \text{ m}^{-3}$ were recorded between October and December while the highest
14 values of $0.3 \text{ m}^3 \text{ m}^{-3}$ were recorded between May and June.

15 16 3.2. Stand structure and tree species composition

17
18 There was a strong representation of trees with DBH of 1-10 cm but the number of
19 individuals decreased with increasing tree size (Table 2). The 330 m forest stand had
20 significantly higher representation of individuals in the 1-10, 11-20 and 31-40 cm DBH
21 ranges compared to the 50 m stand. In terms of species composition, *S. superba* was the
22 most dominant within DBH > 10 cm range.

23 24 3.3. Sapwood area characteristics of tree species and forest stands

To identify variations in SA distribution among tree species and between forest stands, the DBH vs. SA plots were fitted with power functions ($SA=kDBH^x$) (Fig 2) as: $SA = 0.156*DBH^{1.98}$ ($R^2=0.95$) for the 50 m stand and $SA = 0.237*DBH^{1.83}$ ($R^2=0.76$) for the 330 m stand. There were no significant differences ($P>0.05$) among tree species and also between forest stands, hence a common function $SA=0.05*DBH^{2.32}$ ($R^2=0.91$) was established for both forests. The total estimated stand SA (DBH>10 cm) was 7.29 and 12.25 m² in the 50 and 330 m stands, respectively (Table 1).

FIG. 2

3.4. Sap flux density (*J_s*) and tree water use (TWU)

On the morning to a maximum during the day but the patterns and peak rates were variable among trees, with peak rates occurring at different times (10:00 to 15:00) of the day (Fig 3). Similar patterns were observed both in the 50 and 330 m forest stands.

The mean maximum *J_s* rates during the day ranged between 15-30 g m⁻² s⁻¹ at the 50 m and 5-20 g m⁻² s⁻¹ at the 330 m elevation stands. Within a stand, the differences among individual trees were significant ($P<0.001$). On average, trees in the 50 m elevation stand had higher ($P<0.01$) *J_s* rates compared to the 330 m stand (Fig 4).

FIG. 4

The observed differences in *J_s* among trees could not be explained by differences in tree size (DBH), tree height (*T_h*), crown size (*C_a*) nor species. On the other hand, TWU was

1 correlated with DBH in a power function, $TWU = aDBH^b$ (Fig. 5) both in the 50 m (R^2
2 $=0.86$) and in the 330 m ($R^2=0.72$) elevation stands. Within stand differences in daily
3 water use among trees were significant ($P=0.006$ and 0.001 , in the 50 and 330 m plots,
4 respectively).

5
6 Differences in TWU between the two stands were significant ($P=0.001$). The mean daily
7 TWU for the measured trees ranged from 4.1 ± 1.5 to 46.0 ± 10.3 $kg\ d^{-1}$ in the 50 m and
8 2.5 ± 1.3 to 34.4 ± 15.2 $kg\ d^{-1}$ in the 330 m forest stands. Stand transpiration (E) derived
9 from the functions in Fig. 5 and stand structure data were varied. E estimate for the 50 m
10 stand was $1.24\ mm\ d^{-1}$, using the 50 m-site specific model. When we employed the
11 function derived from the 330 m plot to estimate E in the 50 m plot, the resultant E was
12 $0.84\ mm\ d^{-1}$, an underestimation by 33%. E derived from the 330 m plot using site-
13 specific model was $0.98\ mm\ d^{-1}$ but using the 50 m function in the 330 m stand resulted
14 in 33% overestimation.

16 *3.5. Sources of variation in water use among individual trees and between forest stands*

17
18 There were significant ($p<0.05$) correlation between Js and PAR and between Js and
19 VPD ($R^2 = 0.54$ and 0.85 , respectively). About 72-78% of daily Js fluctuations were due
20 to PAR, while VPD explained 55-57% (Fig 6). Higher sensitivity to PAR in the 330 m
21 plot was observed, although due to low light intensity at this site, Js never attained
22 saturation (Fig 6a).

23 FIG. 6
24

1 Since J_s response to microclimate is manifest through stomatal conductance, we
2 examined canopy conductance (g_t) of the respective trees in the two forest stands. Fig 7
3 shows daily trends of g_t in selected trees of *S. superba* in both plots on 01.11.2011. There
4 were distinct differences in patterns of g_t between the two plots. Trees in the 50 m plot
5 showed a rapid decline in g_t just before midday. This was not the case in the 330 m stand
6 where g_t remained high during midday.

7 FIG. 7

8 Differences in g_t among trees were also significant. To identify possible causes of the
9 observed variability, we examined the influence of tree characteristics on g_t for the 50 m
10 plot, given that in this plot, g_t reached saturation for most trees given the high levels of
11 PAR and high VPD (non-limiting). A strong ($R^2=0.73$) correlation between g_t and C_a/T_h
12 ratio (Fig 8) suggested a functional link between canopy g_t , tree height and canopy size.

13 FIG. 8

14 Generally, VPD explained patterns of g_t in both forest stands (Fig 9), even though values
15 in the 330 m plot were lower.

16 FIG. 9

17 **4.0. Discussions**

18 Water transport in trees is confined to the sapwood, thus SA is a potential predictor of a
19 tree's water transport capacity (Meinzer et al. 2001). The observed positive correlation
20 ($R^2=0.92$ and 0.95) between DBH and SA, irrespective of species or stand (Fig. 2)
21 demonstrated that trees on this mountain landscape share common wood properties and
22 hence water transport characteristics. This was contrary to our initial hypothesis, since we
23 anticipated stand-specific shifts in tree growth characteristics related to water transport.

Correlation between SA and DBH has been previously reported for lowland tropical forests (Vertessy et al. 1995, Enquist et al. 1998, Meinzer et al. 2001), in subtropical forests (Horna et al. 2011) with relatively homogeneous terrains and in mountain conifer forests (Kumagai et al. 2005, 2007).

Trees with narrow SA can improve water supply to their crowns through higher Js rates. As SA gets larger, however, down-regulation of Js is necessary in order to lower the demand on roots and minimize cavitation chances (Meinzer et al. 2001). Crown exposure to higher radiation and VPD also leads to higher Js irrespective of tree size (Horna et al. 2010, Meinzer et al. 2013). This may be the case with smaller trees that grow at forest edge or at the edge of a depression. Thus lack of relationship between Js and DBH, as in our case was not surprising. We attributed this to a combination of factors linked to canopy position within the crown (exposure) and traits influencing water consumption. Similar observations have been reported by several studies elsewhere (Oren et al. 1999, Kumagai et al. 2007, Horna et al. 2010, Meinzer et al. 2013).

TWU however, integrates SA and Js and hence is a preferred parameter for the up-scaling of water use from single trees to stand level. A positive correlation between DBH/TWU (Fig 5) was a reminiscent of increased water use in larger trees, likely due to larger crowns that are better exposed to higher light and VPD environment above the crowns and a larger transpiring surface. We adopted this functional relationship to derive stand level TWU, and then E determined according to Eq.4. While this relationship was true within a stand, the difference between the stands was significant ($P>0.05$). This had

1 implications on the scaling of catchment water use from individual trees. As
2 demonstrated in our results, employing the different functional relationships resulted in
3 varying E estimates. We attributed these differences to site-variations in microclimate
4 (Figs. 1 and 6).

5 Microclimatic variables influence TWU through their effects on stomatal conductance
6 (g_t). In both forests, g_t was quite variable among trees (Fig 7). We examined g_t data at
7 saturating PAR and VPD in the 50 m elevation plot. The results showed that a part from
8 microclimate, the regulation of g_t is a balance between crown size and tree height. Taller
9 trees with smaller crown area tend to exhibit higher g_t . Taller trees have better crown
10 exposure to the prevailing PAR and VPD above the canopy. A smaller crown for tall
11 trees is a strategy to lower the transpiring surface thus, allowing higher g_t , with low
12 cavitation risks. Otieno et al. (2014) reported a positive correlation between height and
13 DBH for this forest, which is in line with the results shown in Fig 8. A lower g_t at low
14 VPD values in the 330 m plot were likely due to wet leaves and also low PAR since this
15 site was regularly characterized by fog formation, which could depress g_t during the early
16 part of the day, especially in the sub-canopy trees (Fig 9). In general g_t response to VPD
17 was similar in both plots.

18 Given that J_s is determined by stomatal conductance, we conclude that within stand
19 variability in J_s is a function of tree height and crown size (Fig 8). According to Zeppel
20 (2013), regulation of hydraulic architecture through shifting sapwood area vs. leaf area
21 ratio vary the patterns of stomatal conductance and the regulation of J_s according to tree
22 size are some of the strategies that trees employ in order to achieve converging patterns
23 of water use among species growing together in a stand. As in our case, Vertessy et al.

(1995) observed that while DBH and J_s were not related, single-tree transpiration was strongly related to DBH for all the trees growing together in a forest stand. Considering the allometric relationship shown in Fig. 2, it is logical that TWU is higher in larger trees, since they have a larger capacity for water transport. In larger trees, water transport is spread over a larger SA, compensating for the need to increase J_s to meet canopy water demand. In this case, a negative J_s vs. DBH correlation is expected (Meinzer et al. (2001), assuming that the flux driving force remains the same. In a closed forest canopy however, tree crowns are exposed to light differently, and those with short crowns (smaller DBH) are likely to experience lower VPD too (Granier et al. 2000, Horna et al. 2010). A combination of these factors is likely to distort any relationship between J_s and DBH.

Sensitivity of J_s to microclimate demonstrated in Fig. 8 and microclimatic differences among the forest stands shown in Fig. 1 potentially lead to varying TWU between the stands, since the interaction between microclimate and tree characteristics determines E. Despite significantly lower VPD and PAR at the 330 m compared to the 50 m stand (Fig. 2), the respective daily E rates were 1.24 and 0.98 mm d⁻¹ and were not significantly different, due to higher SA at the 330 m stand. Thus, even though J_s was low because of lower VPD and PAR, higher SA and crown area contributes to higher TWU and stand E. The interaction between microclimate and tree size therefore calls for caution in catchment upscaling of water use using isolated single tree sapflow measurements. In our case, we observed that this could result in up to 30% error in E. Although the use of generalized allometric equations is appealing, since it simplifies the process of estimating

of E at landscape levels, caution is called for when dealing with heterogeneous landscapes, such as complex mountain terrains.

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List of Tables

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

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3 **Table 2:** Size distribution of all the trees in the plots. Sixty four tree species were sampled
 4 both in the understory and the canopy. The three dominant species sampled for sap flux
 5 densities and their representative numbers per DBH class and in each forest stand are
 6 indicated. Five trees with DBH>30 cm were installed with two sap flow probes in order
 7 to take care of the inner sapwood beyond the first outer 20 mm. The rest (21 trees) were
 8 only installed with one sensor.

Elevation	No of stems (All species) in each DBH class /ha				
	1-10 cm	11-20 cm	21-30 cm	31-40 cm	41-50 cm
All trees on the plots					
50 m	1650	467	250	17	17
330 m	3300	533	233	183	17
Stem distribution (within stand) of species sampled for sap flow					
50 m plot					
<i>C. chinensis</i>	133	33	50		
<i>S. superba</i>	350	217	67		
<i>M. chinensis</i>	33	33	50	17	
330 m plot					
<i>C. chinensis</i>	17	83	33		
<i>S. superba</i>	33	83	67	67	17
<i>M. chinensis</i>	83	100	33		

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Figure caption

Fig.1 Microclimatic conditions, mainly A) air temperature (T_{air}), B) photosynthetic active radiation (PAR), C) vapor pressure deficit (VPD) and D) soil water content (SWC) at 30 cm depth in the two forest stands at 50 m and 330 m elevations between October 2011 and June 2012 during the period when sap flow measurements were carried out.

Fig 2 Relationship between tree diameter at breast height (DBH) and sapwood area (SA) of trees in the two forest stands. Tree species from both 50 m and 300 m stands are represented by similar symbols. Closed and open symbols represent data from the 50 m and 300 m forest stands, respectively. Relationship between DBH (cm) and SA (cm²) are described by the same function.

Fig. 3 Diurnal patterns of sap flux density (J_s) within the outer 20 mm sapwood on a typical sunny day (1st Nov. 2011) for all the measured trees. The figures are grouped according to tree species. The left and right panels represent forest stands at 330 and 50 m elevations, respectively. Stem diameters at breast height (DBH) of the respective trees are shown. Also, the diurnal magnitudes of photosynthetic active radiation (PAR) and vapor pressure deficit (VPD) at the A) 330 m and B) 50 m elevations, respectively, are shown.

1 **Fig. 4** Mean daily peak J_s ($J_{s_{max}}$) for the respective 25 trees belonging to *C. chinensis*, *M.*
2 *chinensis* and *S. superba* in the 330 and 50 m forest stands. Data are daily maximum J_s
3 for the respective trees averaged for the entire measurement period. Data for one tree in
4 the 50 m stand has been excluded due to rampant sensor failure.

5 **Fig. 5** Relationship between DBH and mean daily tree water use (TWU) in the respective
6 forest stands at 50 and 330 m elevations.

7 **Fig. 6** Relationship between the mean daily maximum sap flux density (averaged for all
8 measured trees) and A) photosynthetic active radiation (PAR) and B) mean daytime VPD
9 for the respective forest stands located at 330 m and 50 m elevations.

10 **Fig. 7** Daily patterns of the total canopy conductance (g_t) of trees of *S. superba*
11 individuals measured on 01.11.2010 (same as Fig 3) in the (A) 50 m and (B) 330 m forest
12 stands. Given that the response patterns among species were similar, *S. superba* from
13 both stands have been presented here for demonstration.

14 **Fig. 8** Relationship between tree canopy conductance (g_t) and the ratio between crown
15 area (C_a) and tree height (T_h) for the trees growing in the 50 m plot. In this case, the rate
16 of water loss from the canopy was regarded as a function of C_a and T_h . Data presented
17 here were from same day as in Fig 7.

18 **Fig. 9** Response of tree canopy conductance (g_t) to changing VPD during the season. The
19 data presented are the maximum g_t during the day for the respective trees for the entire
20 measurement period.

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3 List of Figures

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1 **Fig. 3**

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4 **Fig. 5**

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5 **Fig. 6**

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Fig. 7

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4 **Fig. 9**