



# Allometric relations between DBH and sapwood area for predicting stand transpiration: lessons learned from the *Quercus* genus

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## Abstract

Catchment-scale transpiration is commonly determined by the use of sap-flow sensors, and its quantification, which is critical for water and forest management, relies crucially on the total catchment's sapwood area ( $A_s$ ). Species-specific allometric relationships between the trees  $A_s$  and the trees diameter at breast height (DBH) are widely used for determining stand or catchment  $A_s$ . However, substantial differences between studies challenge the robustness of these relationships between sites displaying various topographical and environmental characteristics. Our objectives for this study are to compare the parameters of these relationships between species of the *Quercus* genus from different sites across the globe and to test the role of topographical factors on the  $A_s$ -DBH relationship in *Quercus petraea*. Using 145 trees sampled within a 0.455 km<sup>2</sup> catchment, we found that topography (slope, flow accumulation, aspect, curvature, and topographic wetness index) does not modulate the  $A_s$ -DBH relationship in *Q. petraea*, within our catchment. We compared our curve parameters with those from 16 studies on oak trees and found that the  $A_s$ -DBH relationship is not only species-specific, but depends on the site's conditions. The use of species-specific parameters from other sites may lead to more than 100% difference in the calculation of  $A_s$ , and therefore in forest transpiration. In the light of these results, we recommend building site- and species-specific  $A_s$ -DBH relationships for determining stand or catchment transpiration, using a minimum of nine, randomly sampled trees, and different methods and azimuthal directions for determining sapwood depth.

**Keywords** Sapwood area · Allometry · DBH · Topography · *Quercus* · Transpiration

## Introduction

The estimation of catchment-scale transpiration remains critical for forest and water management. To date, a widely applied method is based on the use of sap-flow sensors

(Hassler et al. 2018; Tsuruta et al. 2019; Mitra et al. 2020). Different types of sensors exist, but most rely on the measurement of sap-flux density in a subset of trees that is most commonly multiplied by the sapwood area of the trees to obtain catchment-scale transpiration (Granier et al. 1996; Flo et al. 2019). Sapwood area therefore plays a crucial role in estimating tree and catchment transpiration (Cermak and Nadezhdina 1998; Hölscher et al. 2005; Meinzer et al. 2005), which motivated numerous studies on sapwood allometric relations (e.g. Wang et al. 2010; Quiñonez-Piñón and Valeo 2017; Lubczynski et al. 2017; Mitra et al. 2020). Commonly, stand sapwood area is derived from empirical relationships with the DBH of the stand's trees, because sampling all the trees in a catchment/stand is too resource intense (e.g. Hassler et al. 2018; Tsuruta et al. 2019). Given the importance of these empirical relationships for determining forest water use, they have been studied in a wide range of forested ecosystems and on various tree species like temperate broad-leaved species (Gebauer et al. 2008), boreal tree species (Quiñonez-Piñón and Valeo 2017),

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snow-dependent tree species (Mitra et al. 2020), tropical rain forest species (Granier et al. 1996; Motzer et al. 2005; Horna et al. 2011; Aparecido et al. 2016; Kunert et al. 2015; Moore et al. 2018), Amazonian tree species (Parolin et al. 2008; Aparecido et al. 2019), desert tree species (Lubczynski et al. 2017), mountainous tree species (Vertessy et al. 1995; Tsuruta et al. 2019) or Australian tree species (Wang et al. 2016) among others. The relationships can take the form of different mathematical equations (e.g. linear, exponential, and hyperbolic). For most species from the Fagaceae family, including the *Quercus* genus, the relation commonly takes the form of a power-law function (Eq. 1),

$$A_s = B_0 * DBH^{B_1} \quad (1)$$

where  $A_s$  is the sapwood area of the tree (cm<sup>2</sup>), DBH is the diameter at breast height (cm), and  $B_0$  and  $B_1$  are curve parameters.

Methods for determining these empirical relationships can be destructive, like the use of a wood disc taken at breast height (Miranda et al. 2009), or invasive, such as core analysis (Gebauer et al. 2008; Horna et al. 2011), dye-immersed (Parolin et al. 2008; Aparecido et al. 2019) or thermo-imaged fallen trees (Granier et al. 1994). Non-destructive methods also exist and are commonly based on electromagnetic imaging techniques (Čermák et al. 2004; Bieker and Rust 2010a, b; Wang et al. 2016; Benson et al. 2019; Salomón et al. 2020). The allometric relations of trees from the *Quercus* genus have been extensively studied (Table 1), due to its high natural abundance (Rüther and Walentowski 2008; Petritan et al. 2012) and a broad range of suitable growing conditions (Mette et al. 2013; Pretzsch et al. 2013). Additionally, the sapwood-heartwood limit from most *Quercus* trees can be distinguished straightforwardly by the darker colour of the heartwood (Mosedale et al. 1996; Taylor et al. 2002), which facilitates the quantification of  $A_s$  within this genus by direct inspection after coring.

Many eco-hydrological studies aiming at quantifying tree or stand water uses rely on so-called species-specific relationships (e.g. Chiu et al. 2016; Hassler et al. 2018; Schoppach et al. 2021). However, different studies on the same species have shown contrasting values for the  $B_0$  and  $B_1$  parameters (e.g. Aranda et al. 2005; Schmidt 2007; Grossiord et al. 2014), questioning the robustness of these relationships between sites (Horna et al. 2011) and raising concern on the level of difference in sapwood area, when measurements are up-scaled to the stand or catchment level using these parameter values. In the past decades, studies showed that the  $A_s$ -DBH allometric relationships of Japanese cedar and Japanese cypress may be affected by topographical factors as they vary with the slope position of the trees (Kumagai et al. 2007; Kume et al. 2016). These topographical effects may explain the inconsistencies of  $B_0$  and

$B_1$  between studies. However, topographical effects on  $A_s$ -DBH relationships have never been explored in the *Quercus* genus, despite the wide use of this relationship for quantifying stand-scale transpiration, especially across Europe. To date, most forest transpiration studies at the catchment scale rely on  $B_0$  and  $B_1$  parameters from the literature. There is a need for testing the robustness of these parameters between sites, specific species of a given genus, and topographical factors, to provide guidance for researchers and practitioners to build strong  $A_s$ -DBH allometric relationships.

In this study, we aim to fill these gaps by (i) comparing  $A_s$ -DBH allometric relationships between species of the *Quercus* genus growing in diverse site conditions from 17 field studies, (ii) investigating the role of topographical factors (i.e. slope, flow accumulation, aspect, curvature, and topographic wetness index) on  $A_s$ -DBH allometric relationships of *Q. petraea*, and (iii) determining the minimum number of samples required for a robust quantification of the  $A_s$ -DBH power-law function for *Q. petraea* in a temperate European forest.

## Material and methods

### Study site

The Weierbach is a forested catchment of 0.455 km<sup>2</sup> located in north-western Luxembourg (lat 49.827, long 5.795). The forest is a mix of European beech (*Fagus sylvatica* L.) and pedunculate (*Q. robur* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.) (Fabiani et al. 2021; Schoppach et al. 2021). Catchment's elevation ranges between 458 and 514 m asl, and the geology is composed of Devonian slate and phyllites covered by 60 cm of silt and rock fragments (Juilleret et al. 2011). Distributions of the catchment topographical characteristics can be found in Schoppach et al. (2021).

### Measurement of sapwood depth in oak trees and landscape characteristics analysis

During the 2019 and 2020 growing seasons, we measured sapwood depth of oak trees within 145 randomly selected trees in the catchment (Fig. 1b). Sapwood depth was determined by drilling one single core per tree directly coring horizontally, in a randomized azimuthal direction, at breast height. All sampled oak trees are mature trees in the co-dominant strata. Sapwood and heartwood were discriminated based on colour variation (Mosedale et al. 1996; Quiñonez-Piñón and Valeo 2018). Bark was removed from the cores before the sapwood depth was measured. Here, we assumed that the sapwood depth was constant on all azimuthal directions, and the tree trunks were considered as perfect cylinder for calculating  $A_s$  (Gebauer et al. 2008; Hassler et al. 2018).

**Table 1** Equation 1 parameters measured on oak trees (*Quercus* genus).

| Study                                                   | Binomial name                    | B <sub>0</sub>      | B <sub>1</sub> | R <sup>2</sup>                                             | RMSE  | Covered area (m <sup>2</sup> )                                                              | Trees | Data |
|---------------------------------------------------------|----------------------------------|---------------------|----------------|------------------------------------------------------------|-------|---------------------------------------------------------------------------------------------|-------|------|
| Our study                                               | <i>Quercus petraea</i>           | 0.3226              | 1.872          | 0.65                                                       | 149   | Within a 4.55 10 <sup>6</sup> m <sup>2</sup> catchment                                      | 145   | Raw  |
|                                                         | <i>Quercus prinus</i> L.         | 0.375               | 1.751          | 0.93                                                       | –     | Within a 1.92 10 <sup>4</sup> m <sup>2</sup> plot                                           | 46    | Eq   |
|                                                         | <i>Quercus alba</i> L.           | 0.979               | 1.514          | 0.81                                                       | –     | Within a 1.92 10 <sup>4</sup> m <sup>2</sup> plot                                           | 45    | Eq   |
|                                                         | <i>Quercus rubra</i> L.          | 1.122               | 1.440          | 0.75                                                       | –     | Within a 1.92 10 <sup>4</sup> m <sup>2</sup> plot                                           | 60    | Eq   |
| Wullschlegel and Hanson (2006)*                         | <i>Quercus alba</i> L.           | 0.1021              | 1.5483         | 0.89                                                       | –     | Within a 1.92 10 <sup>4</sup> m <sup>2</sup> plot                                           | 24    | Eq   |
|                                                         | <i>Quercus prinus</i> L.         | 0.1146              | 1.7154         | 0.92                                                       | –     | Within a 1.92 10 <sup>4</sup> m <sup>2</sup> plot                                           | 24    | Eq   |
|                                                         | <i>Quercus rubra</i> L.          | 0.0875              | 1.5075         | 0.77                                                       | –     | Within a 1.92 10 <sup>4</sup> m <sup>2</sup> plot                                           | 24    | Eq   |
|                                                         | <i>Quercus garryana</i>          | 0.37                | 1.42           | –                                                          | –     | –                                                                                           | 6     | Eq   |
| Poyatos et al. (2007)**                                 | <i>Quercus pubescens</i>         | 4.16                | 0.66           | –                                                          | –     | 78.5 m <sup>2</sup> (Within a 10 m circle)                                                  | 10    | Eq   |
| Limousin et al. (2009)                                  | <i>Quercus ilex</i>              | 0.363               | 2.149          | 0.97                                                       | –     | 4.2 10 <sup>2</sup> m <sup>2</sup> (Taken outside of the three 140 m <sup>2</sup> plots)    | 18    | Eq   |
| Grossiord et al. (2014)*                                | <i>Quercus cerris</i>            | 1.843               | 1.6351         | 0.90                                                       | –     | 2.7 10 <sup>3</sup> m <sup>2</sup> (Selected right outside the three 30 * 30 m study plots) | 21    | Eq   |
| Jung et al. (2011)                                      | <i>Quercus petraea</i>           | 0.3653              | 1.8483         | 0.94                                                       | –     | 2.7 10 <sup>3</sup> m <sup>2</sup> (idem)                                                   | 48    | Eq   |
|                                                         | <i>Quercus mongolica</i>         | 0.1846              | 2.1            | 0.94                                                       | –     | 2.0 10 <sup>3</sup> m <sup>2</sup> (Taken in the 40 m * 50 m plot)                          | 9     | Eq   |
| Aranda et al. (2005)                                    | <i>Quercus petraea</i>           | 0.90                | 1.7            | 0.92                                                       | –     | (In a plot near the experimental site)                                                      | –     | Eq   |
| Salomón et al. (2020)                                   | <i>Quercus ilex</i>              | 0.682               | 1.911          | –                                                          | –     | 3.0 10 <sup>2</sup> m <sup>2</sup> (Within three plots of 10×10 m)                          | 20    | Eq   |
| Benson et al. (2019)***                                 | <i>Quercus virginia</i> Mill     | 0.1808              | 0.4788         | 0.97                                                       | 5.99  | –                                                                                           | 19    | Raw  |
|                                                         | <i>Quercus nigra</i> L.          | 2.320               | 1.995          | 0.80                                                       | 20.59 | –                                                                                           | 7     | Raw  |
| Martin et al. (1998)                                    | <i>Quercus. coccinea</i> Muenchh | 0.2544              | 1.7            | 0.80                                                       | 21.66 | (Within the Coweeta Basin)                                                                  | 5     | Raw  |
| Schmidt (2007)                                          | <i>Quercus alba</i> L.           | 0.1148              | 1.973          | 0.88                                                       | 39.03 | (Idem)                                                                                      | 10    | Raw  |
|                                                         | <i>Quercus prinus</i> L.         | 1.496               | 1.372          | 0.95                                                       | 25.08 | (Idem)                                                                                      | 10    | Raw  |
|                                                         | <i>Quercus rubra</i> L.          | 0.1876              | 1.801          | 0.79                                                       | 41.63 | (Idem)                                                                                      | 9     | Raw  |
|                                                         | <i>Quercus petraea</i>           | 0.0627              | 2.25           | 0.97                                                       | 12.78 | 1.58 10 <sup>4</sup> m <sup>2</sup> (Within a 1.29 and a 0.23 ha plot)                      | 20    | Raw  |
| Study                                                   | Binomial name                    | Equation            | R <sup>2</sup> | Covered area (m <sup>2</sup> )                             | Trees | Data                                                                                        |       |      |
| Other relationship conformation than power-law function |                                  |                     |                |                                                            |       |                                                                                             |       |      |
| Bovard et al. (2005)                                    | <i>Quercus rubra</i> L.          | 3.24 * DBH—10.24    | 0.90           | 2.3 10 <sup>3</sup> m <sup>2</sup> (Within a 0.23 ha plot) | 11    | Eq                                                                                          |       |      |
| Jonard et al. (2011)                                    | <i>Quercus petraea</i>           | 9.442 * DBH –129.11 | 0.73           | 2.5 10 <sup>3</sup> m <sup>2</sup> (Within a 0.23 ha plot) | 16    | Eq                                                                                          |       |      |

Table 1 (continued)

| Study              | Binomial name                             | Equation                                            | R <sup>2</sup> | Covered area (m <sup>2</sup> )   | Trees | Data |
|--------------------|-------------------------------------------|-----------------------------------------------------|----------------|----------------------------------|-------|------|
| Wang et al. (2010) | <i>Quercus mongolica</i>                  | $\log_{10} A_s = -1.05(\log_{10} \text{DBH}) + 2.1$ | 0.95           | –                                | 8     | Eq   |
| Zhu et al. (2017)  | <i>Quercus variabilis</i><br><i>Blume</i> | $0.0083 * e^{0.0495 \text{DBH}}$                    | 0.95           | (Outside the experimental plots) | 10    | Eq   |

\*These studies used Eq. 1 with  $A_s$  in m<sup>2</sup> and DBH in m

\*\*This study used basal area instead of DBH in Eq. 1

\*\*\*Not measured at breast height but at various heights in each tree (2.2 different heights per tree, on average)

“ $B_0$ ” and “ $B_1$ ” parameters correspond to Eq. 1 parameters. “RMSE” = Root Mean Square Error. “Covered area (m<sup>2</sup>)” indicates the area in which trees have been sampled, using the original papers formulation for clarifying when it is ambiguously or vaguely described. “Trees” indicates the number of sampled trees within each study. “Data” indicates if the equations parameters are provided in the study (Eq.) or if only raw data are provided (Raw), so we calculated  $B_0$  and  $B_1$  parameters

We used a high-resolution (1 m) digital elevation model (Luxembourgish air navigation administration 2017) and the Spatial Analysis Toolbox of ArcGIS Desktop 10.5 to determine the topographical characteristics at each sampling location.

We smoothed our raster maps by averaging topographical values of each one-square-metre grid plot with the values of the plots encompassed within a 10 m circle around it, to avoid the influence of small differences from the tree actual position to the analysis. The topographical characteristics within those 10 m circles were extracted for each sampled tree. Two relationships between sapwood depth and DBH were established based on a value criterion for each topographical characteristic. We selected these criteria to obtain roughly balanced (Table 2) and normally distributed groups in terms of DBH (Fig. 2), without significant differences in the means and variances (Table 2). Criteria, number of trees composing each group, and mean  $\pm$  SE are displayed in Table 2. The slope values represent the steepness of the land surface. The flow accumulation represents the number of m<sup>2</sup> of converging area flowing into each downslope area. The aspect is the orientation of the down-hill slope. The curvature indicates if the surface is upwardly convex or concave. The topographic wetness index (TWI) was calculated as follows (Eq. 2):

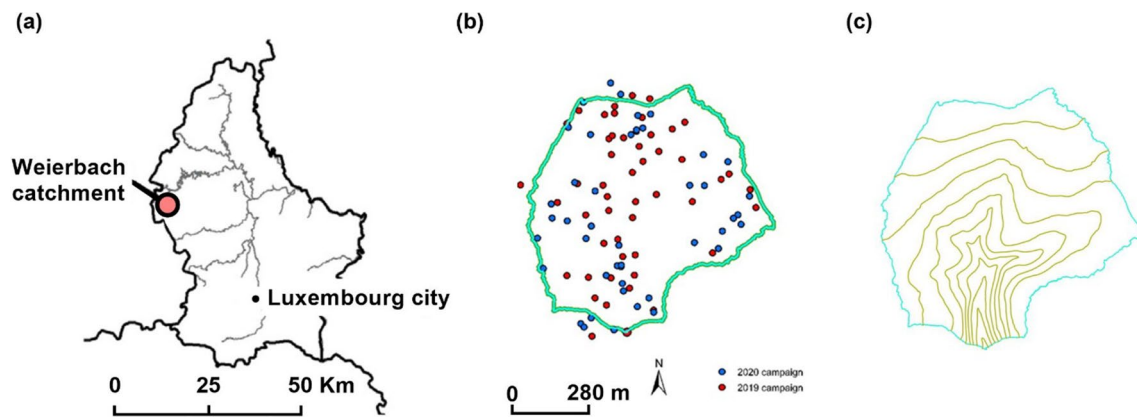
$$\text{TWI} = \ln \left( \frac{(\text{flow ac.} + 1) * a}{\tan \left( \text{slope} * \frac{\pi}{180} \right) + 0.001} \right) \quad (2)$$

with *flow ac.* being the flow accumulation of a m<sup>2</sup>, *a* being the size (1 m<sup>2</sup>), and slope being the *slope* value in degrees.

We tested the statistical differences between the  $A_s$ -DBH relationships derived from all pairs of datasets (two groups per topographical characteristic) using extra-sum-of-squares *F* tests and Akaike’s information criterions. For both approaches, we tested the probability that one model with identical  $B_0$  and  $B_1$  parameters fits the data as well as two models with different  $B_0$  and  $B_1$  values.

### Comparison between $A_s$ -DBH allometric relationships from the literature

For determining the significance of the difference in  $A_s$  produced by the application of the various  $B_1$  and  $B_0$  parameters from the literature, we applied Eq. 1 to our dataset of 145 DBH and compared the resulting  $A_s$ . We used one-way analysis of variance (ANOVA) to determine the significance ( $p < 0.05$ ) of the species and site effect on the produced  $A_s$ . Given the obvious differences between relationships of different species, we focused our analysis on *Q. Petraea* datasets, which present



**Fig. 1** Location of the study site within Luxembourg (a), location of the wood core samplings within the catchment (b), and 5 m contour lines (c). Panel B: Red circles represent the location of the trees sam-

pled in 2019, and blue circles represent the location of the trees sampled in 2020. Light green line delineates the catchment boundaries. (Color figure online)

**Table 2** Groups characteristics for topographical investigation.

| Criteria                              | Sample size | Mean DBH ( $\pm$ SE) | $p$ value $t$ test <sup>a</sup> | $p$ value $F$ test <sup>b</sup> |
|---------------------------------------|-------------|----------------------|---------------------------------|---------------------------------|
| Slope $< 5^\circ$                     | 66          | 52.90 $\pm$ 1.34     | 0.83                            | 0.36                            |
| Slope $> 5^\circ$                     | 79          | 52.54 $\pm$ 1.10     |                                 |                                 |
| Aspect $< 160^\circ$                  | 72          | 52.43 $\pm$ 1.29     | 0.75                            | 0.22                            |
| Aspect $> 160^\circ$                  | 73          | 52.97 $\pm$ 1.11     |                                 |                                 |
| Curvature $< 0^\circ$                 | 60          | 53.77 $\pm$ 1.49     | 0.29                            | 0.05                            |
| Curvature $> 0^\circ$                 | 85          | 51.95 $\pm$ 1.00     |                                 |                                 |
| Flow accumulation $< 100 \text{ m}^b$ | 70          | 53.29 $\pm$ 1.31     | 0.51                            | 0.25                            |
| Flow accumulation $> 100 \text{ m}^2$ | 75          | 52.16 $\pm$ 1.10     |                                 |                                 |
| TWI <sup>c</sup>                      | 68          | 52.57 $\pm$ 1.22     | 0.88                            | 0.77                            |
| TWI                                   | 77          | 52.82 $\pm$ 1.19     |                                 |                                 |

<sup>a</sup> $p$  value of the unpaired  $t$  test between both groups

<sup>b</sup> $p$  value of the  $F$  test for comparing variances between both groups

<sup>c</sup>TWI topographic wetness index

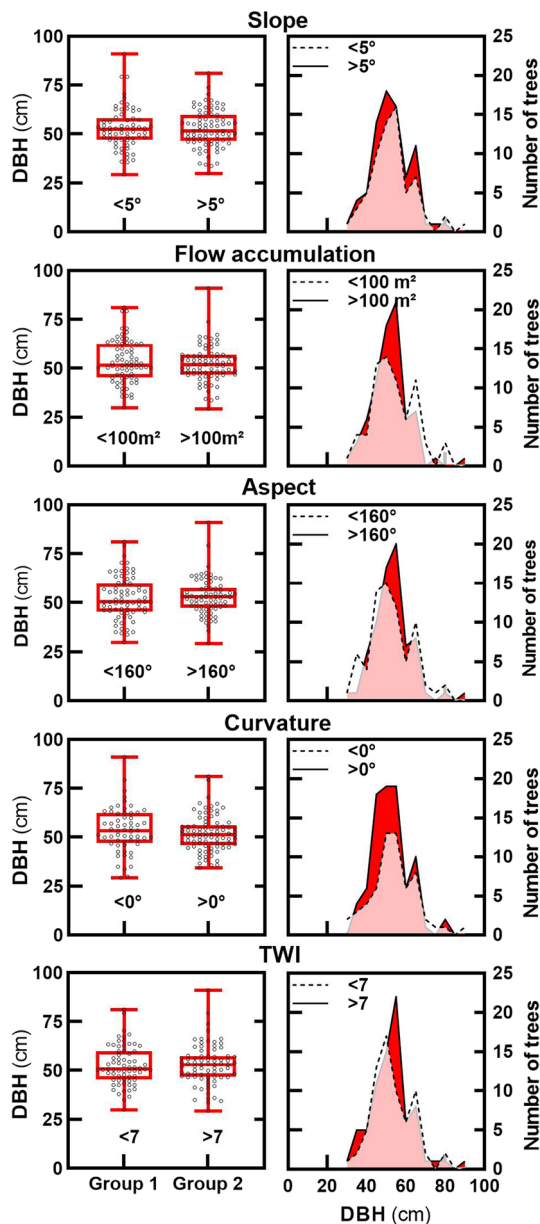
relatively similar curves, and ran a Tukey's multiple comparison test in order to test the significance of the site effect alone.

### Power analysis to determine the minimum number of samples required

We used a power analysis to estimate the minimum sample size required to reasonably detect an effect of a given size (Maxwell 2000). The effect size is a number measuring the strength of the relationship between two variables in a sampling panel. In our case, the relationship links  $A_s$  to DBH. Our effect size estimation is based on Lehr's rule of thumb which states that the sample size  $n$  for a two-sided two-sample  $t$  test with power 80% ( $\beta=0.2$ ) and significance level ( $\alpha=0.05$ ) should be (Lehr 1992; Van Belle 2011):

$$n = \frac{16}{\Delta^2} \quad (3)$$

where  $\Delta$  is the treatment difference to be detected in units of the standard deviation—the standardized difference. We used “*pwr*” R package (Champely et al. 2018) to calculate the number of samples needed to get at least the same level of coefficient of determination that we obtained with our 145 samples. As Eq. 1 is not linear, *pwr* was applied on the relation between  $A_s$  and  $pA_s$  (the predicted  $A_s$  based on Eq. 1). The coefficient of determination is based on a linear assumption which is not technically appropriate for our nonlinear study, but we use them for a rough performance reference.



**Fig. 2** Topographical characteristics associated with each group of trees. Left panels display boxplots of the topographical characteristics with horizontal lines representing the minimum, mean and maximum values of DBH. Right panels display the DBH distribution within each group of trees. Solid line filled with red and dashed line not filled delineate the distribution of the different groups. Threshold values defining each group are displayed on each pane. (Color figure online)

## Results

### Effect of topographical characteristics on $A_s$ -DBH relationships

According to the extra-sum-of-squares  $F$  test, among all tested topographical characteristics (i.e. slope, flow

accumulation, aspect, curvature, and TWI), none produced a significant effect on the  $A_s$ -DBH relationship (Fig. 3). The strongest effect of topographical factor in our dataset was the aspect, but with only a  $p$  value of 0.1 between the two models. Results are similar using the Akaike's information criterion. Except for the aspect, none of the topographical characteristics produced a likely effect.

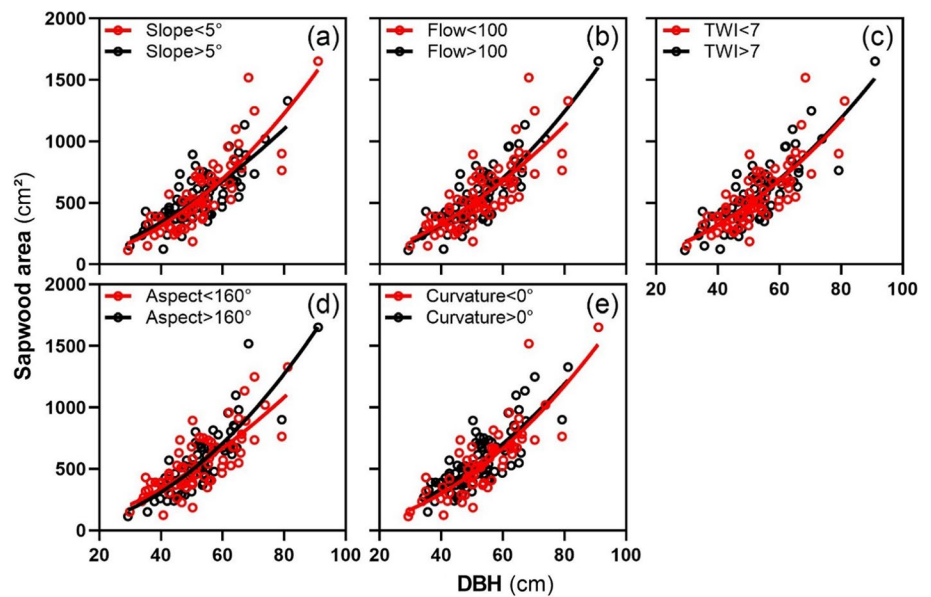
### Variations of the $B_1$ and $B_0$ coefficients between species of the *Quercus* genus and sites

We identified 16 studies in the literature in which the allometric  $A_s$ -DBH relationship was determined for oak trees (Table 1). Within these studies and our additional study, 14 relationships have the shape of a power-law function (Fig. 4), while two others were linear and one exponential (Table 1). The  $A_s$ -DBH relationship was established for 13 different species from the *Quercus* genus (Fig. 4a, Table 1). We found a highly significant ( $p$  value < 0.0001) effect of the studies, which includes species and sites effects, on the different  $A_s$  datasets calculated using  $B_1$  and  $B_0$  coefficients from the literature and our DBH dataset. The mean  $A_s$  calculated varies by two orders of magnitude (between 56.7 and 6592 cm<sup>2</sup>) using the most extreme study-specific parameters. Beside our study, four other studies determined the  $A_s$ -DBH relationship on *Q. petraea* (Aranda et al. 2005; Schmidt 2007; Jonard et al. 2011; Grossiord et al. 2014). Our study has, on average, seven times more samples than the previous studies (145 vs. an average of 20). Our  $A_s$ -DBH relationship presents a  $R^2$  36% lower (0.65 vs an average of 0.88). The area covered by the sampling is almost a thousand time larger (904) than the mean area of all the other studies (Table 1). We found a highly significant site effect ( $p$  value < 0.0001—Fig. 5) on the calculated  $A_s$  of *Q. Petraea*. The mean  $A_s$  ranged from  $368.5 \pm 8.03$  cm<sup>2</sup> when applying Jonard's  $B_0$  and  $B_1$  parameters to  $1151 \pm 35.0$  cm<sup>2</sup> when applying Grossiord's parameters (Table 3).

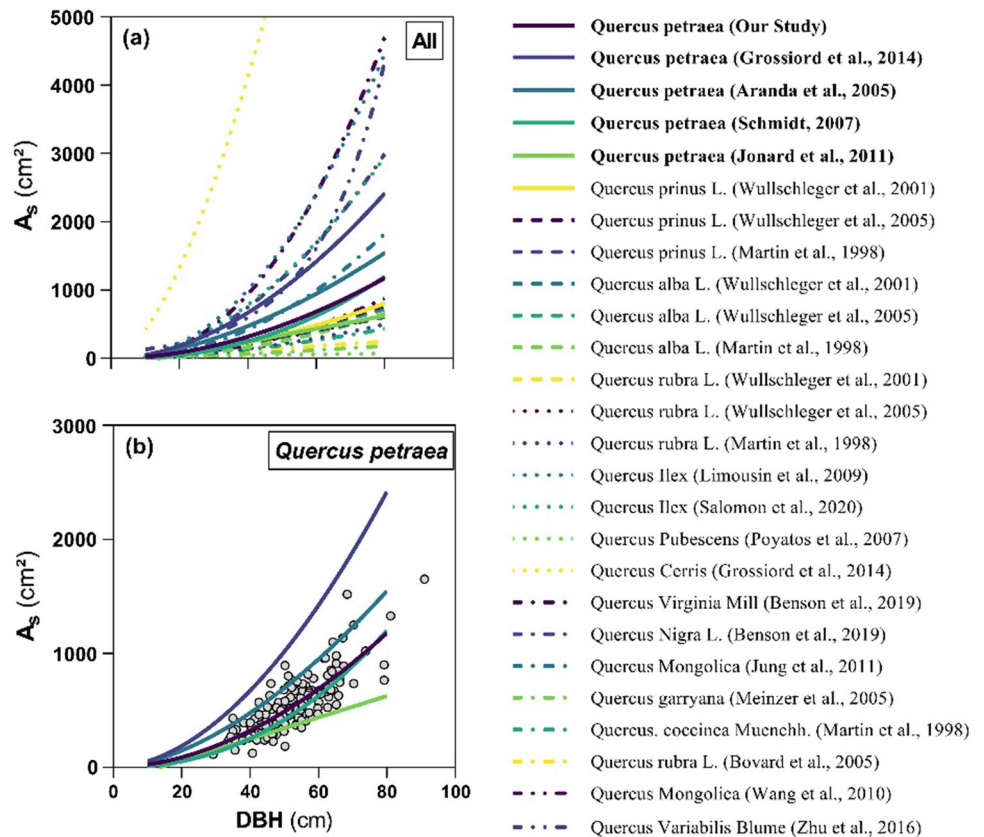
### Number of samples required for a reliable quantification of $A_s$ -DBH relationship

The power tests indicated that at least nine samples are needed to reach the same level of correlation, or even better, than what we obtained with our 145 samples ( $n = 8.7$ ,  $r = 0.81$ ).

**Fig. 3** Effect of the topographical characteristics on the  $A_s$ -DBH allometric relationship. Each circle represents one tree and the colours denote their group within each topographical characteristic. Black and red curves represent the  $A_s$ -DBH allometric relationship (Eq. 1) fitted to each group of data. (Color figure online)



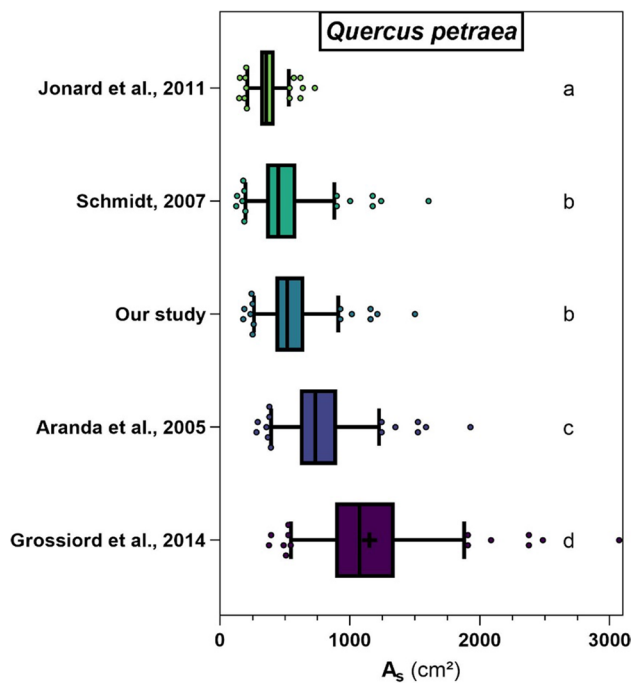
**Fig. 4**  $A_s$ -DBH allometric curves determined on *Quercus* trees. Panel **a** displays the  $A_s$ -DBH relationships of all *Quercus* species from literature, while panel **b** displays the  $A_s$ -DBH relationship on *Quercus petraea* only. Different colours represent different studies and species (see legend). In panel **b**, each grey circle represents one of our core measurements. (Color figure online)



## Discussion

### Topography does not modulate the allometric relation between DBH and sapwood area in *Q. petraea* at our study site

Topography does not influence the  $A_s$ -DBH allometric relationship in *Q. petraea* at the Weierbach study site. This contrasts with the results of Kumagai et al. (2007) and Kume et al. (2016) in Japanese cedar and Japanese cypress who found different relationships at different slope positions. Based on our analysis, we can argue that  $A_s$ -DBH



**Fig. 5** Sapwood areas ( $A_s$ ) calculated via Eq. 1 using different  $B_0$  and  $B_1$  parameters from *Q. petraea* and our 145 DBH dataset. The box extends from the 25th to 75th percentiles. The line in the middle of the box is plotted at the median. Whiskers represent 5th and 95th percentiles. Dots represent data outside of the 5–95 percentiles. Letters denote significant differences between groups

relationship in *Q. petraea* is robust, independent of the topographical position of the sampled trees at the study site. This is a major finding for the robustness of future upscaling analysis relying on this allometric relation. Further research on different species and in different topographical settings is undoubtedly needed as a way forward.

### Allometric curves vary between species of the *Quercus* genus

The allometric  $A_s$ -DBH relationships are commonly described as “species-specific”. In our study, we show that

determining  $A_s$  using different *Quercus*’s  $B_0$  and  $B_1$  parameters from the literature produce highly significant differences. This site and species specificity of parameters led to a difference of two orders of magnitude in the calculated mean  $A_s$ . Tropical forests typically display a wide variety of species which commonly imposes the use of a single pair of parameters for determining  $A_s$  of a stand (e.g. Moore et al. 2018) with Eq. 1. For the species from the *Quercus* genus in temperate forests, we demonstrated that this method leads to under- or over-estimate  $A_s$  by up to hundred times. This massive difference confirms and reinforces the requirement of species-specific relationships when upscaling sap-flux density data from a subset of trees to stand or catchment scale.

### *Quercus petraea*’s $B_0$ and $B_1$ parameters vary between sites

Our analysis showed that applying  $B_0$  and  $B_1$  parameters determined in different studies and at different sites on pedunculate oaks resulted in significantly different values of  $A_s$  (Table 3, Fig. 5). Using the parameters from other studies would induce a difference ranging from an overestimation of 107% (Grossiord et al. 2014) to an underestimation of 44% (Jonard et al. 2011) compared to the  $A_s$  determined with our own  $B_0$  and  $B_1$ . These major differences highlight the need for, not only species-specific, but also site-specific allometric relations when estimating sap-flow at stand or catchment level. Similar investigations on larger catchments would help evaluating how far  $B_0$  and  $B_1$  remain valid.

Interestingly, the use of  $B_0$  and  $B_1$  parameters from our study and Schmidt (2007) did not result in significant differences in  $A_s$  (Fig. 5). In Jonard et al. (2011), authors found a linear relationship, probably because of the too low DBH range of the sample trees (29–48 cm). Schmidt’s study was carried out in northern Bavaria, less than 300 km from Weierbach. Jonard’s study was carried out in the Belgian Ardennes, the northern site among the five, located within less than 100 km from Weierbach. Aranda’s study was carried out in Spain, and Grossiord’s study took place in Tuscany, both being much further south and in a clearly

**Table 3** Meteorological and stand characteristics of the studies on *Quercus petraea*

| Study                   | Mean annual temperature (°C) | Total annual precipitation (mm) | Tree density (Tree/ha) | Mean $A_s$ ( $\pm$ SE)** |
|-------------------------|------------------------------|---------------------------------|------------------------|--------------------------|
| Our study               | 8.9                          | 815                             | 301                    | 555.9 $\pm$ 17.1         |
| Aranda et al. (2005)    | 8.1                          | 1105                            | 867                    | 777.8 $\pm$ 21.7         |
| Schmidt (2007)          | 7.7                          | 800                             | 350 and 636*           | 494.0 $\pm$ 18.6         |
| Jonard et al. (2011)    | 9.8                          | 1044                            | 468                    | 368.5 $\pm$ 8.03         |
| Grossiord et al. (2014) | 13.5                         | 950                             | 867                    | 1151 $\pm$ 35.0          |

\*Two plots with two densities mentioned

\*\*Mean  $A_s$  determined by applying  $B_0$  and  $B_1$  parameters from each study to our database of 145 DBH values

different climate than the two first cited. One explanation for the significantly different curve parameters within the same species could therefore be the growing conditions effect on the trees allometry. Indeed, higher water demand and lower water availability have been pointed out as a driver of defoliation, which subsequently affects the proportion of sapwood area (e.g. Bréda et al. 2006; Limousin et al. 2012). In Scots pine, summer vapour pressure deficit and maximum temperature have been shown to be negatively correlated with the leaf area/sapwood area ratio across Europe (Mencuccini and Bonosi 2001). Sapwood proportion is suspected to depend on the availability of light (Sellin 1994; Thurner et al. 2019) and the water demand (Gebauer et al. 2008; Horna et al. 2011). Trees exposed to higher level of light and potential evapotranspiration require to maximize sapwood area for sustaining the higher evaporative demand and thus preventing leaf overheating and dehydration (Aparecio et al. 2019). Importantly, the hydraulic conductivity of sapwood is also influenced by growth rate which depends on resources availability and demand (Medhurst and Beadle 2002). The total annual precipitation amount, the mean annual temperature, and the tree densities varies between the five above-mentioned studies on *Q. petraea* (Table 2). Total radiation received by each site and the associated potential evapotranspiration are not available in the original papers. However, Spanish and Tuscan sites are likely to receive higher level of annual radiation and are exposed to higher evaporative demands due to their southern locations compared with Luxembourgish, Belgian, and German sites (Cornes et al. 2018). Sites with lower tree densities present lower sapwood area for a given DBH, which contrasts with the findings of Benyon et al. (2015) in eucalypt forests, showing a decrease in sapwood thickness with an increase in forest density. Higher forest density is supposed to reduce the exposition to high radiation and VPD conditions, which influences the development of sapwood. Here, we cannot decipher the various effects of the growing conditions on the  $A_s$ -DBH relationship based on these annual data. Further research is certainly needed to unravel the role of temperature, radiation, water demand, water availability, and forest density on the  $A_s$ -DBH allometric relationship on *Q. petraea*.

### Number of samples required for a reliable quantification of $A_s$ -DBH relationship

For upscaling purposes, a reliable quantification of the  $A_s$ -DBH allometric relationship remains crucial as it appeared that Eq. 1 parameters are constrained not only by species, but also by sites/stand characteristics. We thus recommend to experimentally determine Eq. 1 parameters for each site rather than using values from literature. According to our power test, at least nine samples are needed for building a robust  $A_s$ -DBH relationship. Importantly, the sampled trees

should cover a range of DBH that is as wide as possible to avoid misinterpretation of the curve shape (e.g. Jonard et al. 2011). This number of samples is close to or lower than the number of samples most studies on *Quercus* genus used (Table 1). Therefore, Eq. 1 parameters extracted from these studies can be considered as robust for the species and sites concerned. However, the  $A_s$ -DBH allometric relation calculated in this study displays a substantially lower  $R^2$  compared to previous studies, which potentially pools down the required number of samples.

### Confounding effects and methodological caveats

In this study, we were not able to highlight significant topographical effects on the  $A_s$ -DBH relationship of *Q. petraea*. Also, we determined an  $A_s$ -DBH relationship displaying a substantially lower  $R^2$  compared to literature. Confounding effects may be responsible for the lack of significance of the topographical effects and the lower  $R^2$ . Confounding effects may include a much larger sampling area than other studies with higher unexplained variances and random errors, a higher number of sampled trees, a wider range of tree's DBH, or methodological limitations.

A methodological limitation that may introduce some deviation of the measurement from the  $A_s$ -DBH curve is that  $A_s$  of each tree was inferred from a single core sampled at a random azimuth. We assumed the sapwood depth to be constant on all azimuths (Čermák et al. 2004; Tsuruta et al. 2010; Benson et al. 2019). Sapwood area was indeed inferred from a single core taken at random azimuth because we had no authorization from the forest owner to core each tree more than once during the experiment. However, the radial profile of sapwood thickness is suspected to be variable (e.g. Looker et al. 2016), especially in regard to slope (Pilate et al. 2004). Indeed, trees growing on a slope will produce tension wood to counteract the forces of gravity (Scurfield 1973; Pilate et al. 2004). This alters the production of wood, and presumably the sapwood thickness around the circumference of the tree, which could be a substantial confounding effect. The variability in radial sap-flux densities was found to be considerable in temperate broad-leaved species (Gebauer et al. 2008). For boreal trees, radial profile of sapwood thickness was shown to be dependent on the species; some species displaying constant sapwood depth, while others are growing thicker on the North-East side (Quiñonez-Piñón and Valeo 2017). For trembling aspen and white spruce, the influence of azimuthal direction on sapwood depth had a low impact (Merlin et al. 2020). In oak trees, the xylem vessel size was found to be larger on the northern side of *Quercus suber*, compared with the southern side (Barij et al. 2011), but, to our knowledge, the influence of azimuthal direction on sapwood depth itself remains unexplored in *Q. petraea*.

Topographical effect may also be confounded by the threshold values selected for comparing groups, which was imposed by catchment characteristics and done in such a way to force similar sample sizes, but was not necessarily tied to meaningful physical attributes. Further research on catchments displaying larger ranges of topographical characteristics could help untangling these effects.

Within studies on *Q. petraea* displaying power-law functions, Aranda et al. (2005), Schmidt (2007), and Grossiord et al. (2014) had a difference between their smaller and larger DBH of 14, 20, and 36 cm, respectively. Our dataset displayed a difference of 61 cm and our number of sampled trees was substantially higher. Also, our panel encompassed many trees with large DBH, while both Schmidt (2007) and Grossiord et al. (2014) had no trees larger than 50 cm. This value falls at 19 cm for Aranda et al. (2005). However, excluding the 85 trees larger than 50 cm in DBH from our dataset led to a substantially lower  $R^2$  (0.28) of the  $A_s$ -DBH relationship. Larger range of DBH within the sampled trees therefore did not explain the low  $R^2$  value displayed by our relationship.

Our dataset presents sapwood depth values varying between 10 and 86 mm with a mean of 42 mm. If we consider a deviation of 1 mm due to a recurrent measurement error, this one mm deviation would result in a deviation of 2.17% (14 cm<sup>2</sup>) of the  $A_s$  of a tree with average DBH (53 cm). For our smallest tree (DBH = 29.3 cm), the deviation increases to 9% (8.5 cm<sup>2</sup>). However, the potential effect of a systematic measurement mistake remains far too weak for explaining the observed spread of the points around the allometric curve (Fig. 3b). Dyeing experiments suggest that  $A_s$  is likely susceptible to be overestimated by the determination solely on heartwood coloration (Aparecido et al. 2019), despite other studies contradicting this suggestion (e.g. Githiomi and Dougal 2012). Experiments using dye are able to differentiate between observable sapwood and the functional conducting sapwood, the latter being typically lower. For this reason, we recommend the use of variable methods to validate the delimitation of sapwood.

The influence of the sampling area cannot be ignored. Most studies presented in Table 1 aimed at quantifying stand transpiration, and their main objectives was not to determine the  $A_s$ -DBH allometric relationship, which is commonly done only on few trees outside the field setup. In our experiment, we sampled within a catchment of 0.455 km<sup>2</sup>, which is by far wider than all previous studies on oak trees. Therefore, our  $A_s$ -DBH curve is likely to be influenced by non-accounted micro-climatic conditions, influencing the resources availability (i.e. water and radiation) and the evaporative demand.

## Conclusion

Sapwood area plays a key role for determining sap-flow of a tree and upscaling sap-flow measurements from tree to stand or catchment level. A reliable quantification of sapwood area is therefore crucial for water and forest management. In this study, we confirmed that the  $A_s$ -DBH allometric relationship of the *Quercus* genus is not only species-specific, but depends on the site conditions. We showed that topography does not modulate the  $A_s$ -DBH relationship in *Q. petraea*, within our catchment. In the light of these results, we emphasize that each upscaling study should rely on its own site- and species-specific relationship and recommend a minimum of nine, randomly sampled trees, in order to build a robust  $A_s$ -DBH relationship. Due to the potentially high variability in radial profile of sapwood thickness and the caveats related to colour distinction, we recommend coring at different azimuthal locations in the trees and validating the delimitation of sapwood via different methods. Further research is certainly needed for evaluation on how far  $B_0$  and  $B_1$  parameters remain valid.

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**Data availability** The data used in this study are the property of the Luxembourg Institute of Science and Technology (LIST) and can be obtained upon request to the corresponding author, after approval by LIST.

**Code availability** Not applicable

## Declarations

**Competing interests** The authors declare no competing interests.

**Conflict of interest** The authors declare that they have no known competing financial interests or personal relationships that could appear to influence the work reported in this paper.

**Consent for publication** Not applicable

**Ethical approval** Not applicable

**Consent to participate** Not applicable

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