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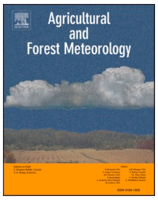

Species-specific control of DBH and landscape characteristics on tree-to-tree variability of sap velocity

R. Schoppach [a,*], K.P. Chun [b], Q. He [b], G. Fabiani [a], J. Klaus [a]

[a] Catchment and Eco-Hydrology Research Group, Environmental Research and Innovation department, Luxembourg Institute of Science and Technology, Belvaux, Luxembourg
[b] Department of Geography, Hong Kong Baptist University, Hong Kong, China

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ABSTRACT

The substantial tree-to-tree variability of transpiration poses a major challenge to a reliable stand-scale quantification of transpiration. The diameter at breast height (DBH) and landscape characteristics have been identified as drivers of tree-to-tree variability, but it remains unclear if their control on sap velocity varies between species-specific water-use and environmental conditions. We hypothesized that their controls are specie-specific, such as the temporal dynamic of their relative importance. To test our hypotheses, we used a multi-species stand that include 37 trees equipped with sap-flow sensors from four species representing the dominant species in central Europe. We analysed the daily relative importance of DBH, landscape slope, aspect, flow accumulation, and topographical position. We found that tree-to-tree variability of sap velocity was mainly dependent on DBH for oak (twice higher relative importance than other species) and on landscape characteristics for beech (36% higher relative importance than other species) and conifers. The temporal dynamics of the relative importance of most tested drivers was found to be species-specific and linked to root-related aspects in response to hydro-meteorological conditions. During dry summer months, the daily relative importance of oak's DBH increased to almost 60% to be three times higher than the value for beech. In contrast, the relative importance of flow accumulation was always two to three times higher for beech trees than oak and conifer trees. This indicated that larger oak trees accessed deeper water sources than smaller oaks. However, the shallower root architecture of beech trees involved a higher dependence on shallow soil water because a larger DBH is seemingly not enhancing the tree's capacity to explore deeper soils. These new insights emphasize the critical importance of accounting for DBH and landscape characteristics through a species-specific and temporally dynamic correction in further approaches for upscaling of sap-flow data from individual tree to stand-scale.

1. Introduction

A major challenge to a reliable stand-scale quantification of transpiration lies in the substantial tree-to-tree variability of transpiration induced by the diversity in landscape and vegetation characteristics (Bovard et al., 2005; Jiao et al., 2019; Tang et al., 2018; Chiu et al., 2016; Mitra et al., 2019). A reliable quantification and prediction of stand-scale transpiration remains nonetheless a crucial need for catchment hydrology, forest and water resource management, and land surface modelling especially in the context of climate change (Kumagai et al., 2007; Chiu et al., 2016). Recently, a series of studies (*e.g.* Kume et al., 2016; Renner et al., 2016; Hassler et al., 2018; Tsuruta et al., 2020) highlighted the key role of diameter at breast height (DBH) and landscape characteristics controlling the access to and the availability of water for sustaining transpiration and consequently in driving tree-to-tree variability. Despite agreeing on the importance of DBH and landscape characteristics, these studies resulted in contrasted effects from these drivers on transpiration. As these studies focused on different species under different conditions, and given that different species display different characteristics (e.g. iso- and aniso-hydricity, stomatal conductance, whole plant hydraulic conductance, rooting depth) leading to contrasted water-use (Moreno-Gutiérrez et al., 2012; Deans et al., 2019; Barbeta and Peñuelas, 2017; Looker et al., 2018); we argue the contrast in driver's effects arises from specie-specific responses to environmental conditions.

Stand-scale transpiration is commonly inferred by the measurement

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* Corresponding author.
E-mail address: remy.schoppach@list.lu (R. Schoppach).

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of sap velocity time series in a few trees (Granier et al., 1996; Tsuruta et al., 2019; Mitra et al., 2019) that are multiplied by the estimated total sapwood area of the stand (e.g. Crosbie et al., 2007; Loranty et al., 2008). Stand sapwood area is usually derived from empirical relationships with the DBH of the trees composing the stand (*e.g.* Hassler et al., 2018; Tsuruta et al., 2020). These relationships have been investigated for decades and are today established for a range of species (*e.g.* Hölscher et al., 2005; Hassler et al., 2018; Tsuruta et al., 2019, Mitra et al., 2019). However, our understanding of the relationship between DBH and sap velocity remains elusive. The DBH was found to be positively correlated to sap velocity of rain forest species (Granier et al., 1996; McJannet et al., 2007), bald cypress (Oren et al., 1999), multi-specific broadleaved trees (Chiu et al., 2016), and beech-oak stands (Hassler et al., 2018; Fabiani et al., unpublished data). In the meantime, the opposite was found on tropical forest species (Meinzer et al., 2001) and beech (Renner et al., 2016). Studies on tropical species (Phillips et al., 1999) and Japanese cypress (Tsuruta et al., 2019) also found no relation. Opposite effects on different temperate broadleaved species (Höschner et al., 2005) and tropical species (Otiento et al., 2014) was also found within the same stand. Overall, previous studies shown clear contrasts of the effect of DBH on sap velocity that we suspect to result from the different species or environmental conditions between studies.

The availability of water and energy are rarely homogeneous even at small scale, which adds additional complexity for predicting the tree-to-tree variability of sap velocity, even within a given species and DBH range (Bovard et al., 2005; Kume et al., 2016; Renner et al., 2016; Jiao et al., 2019; Tsuruta et al., 2020). Availability of water and energy are challenging to measure directly at stand-scale, but a strong relationship with landscape characteristics exists (Tromp-van Meerveld and McDonnell, 2006; Metzen et al., 2019; Percy et al., 2020). The landscape characteristics affecting sap velocity are usually topographical factors such as slope, aspect, curvature, flow accumulation, and topographic position, as they control water and energy availability through redistribution and exposure, respectively. Additionally, in areas with a pronounced heterogeneity of soil type and geology, those factors play a key role in setting the water availability (Hassler et al., 2018). VPD is known to control the temporal dynamic and the seasonality of sap velocity but over large areas, microclimatic conditions (VPD and radiation) may also induce tree-to-tree variability of sap velocity (Jung et al., 2014; Looker et al., 2018). Over relatively small areas, soil type, geology, and daily VPD can be considered as identical at all locations within the stand.

Among topographical drivers of sap velocity, slope and slope-position are the ones that attracted the most attention over the past decades. The effect of slope on sap velocity has shown contrasted results between different studies with no significant differences between aspen-dominated stands in up- and wetlands (Loranty et al., 2008), Japanese cedar growing in up- and low-slope positions (Kumagai et al., 2007), and cypress-dominated stands in different slope positions (Tsuruta et al., 2020). In contrast, substantial variations of in sap velocity was found along a slope forested by subalpine species (Adelman et al., 2008), in different slope positions of a mixed species eucalypt forest (Mitchell et al., 2012), at two different elevations of a sub-tropical evergreen forest (Otieno et al., 2014), along hillslopes transects dominated by European beech (Renner et al., 2016), between plateau, mid-slope, and hill-foot of a beech and oak stand (Fabiani et al. unpublished data), in upper and lower slope positions of a Japanese cypress plantation (Kume et al., 2016), or along Australian multi-species downslope transects (Metzen et al., 2019).

At this point, there is still a disagreement on the effect of DBH and landscape characteristics on the tree-to-tree variability of sap velocity. Especially, it remains unclear if the effects of DBH and landscape characteristics vary owing to species-specific characteristics and environmental conditions, because we lack studies that jointly evaluate the importance of these drivers and their temporal dynamics on different species composing a multi-species stand. In this paper, we address this pressing need through a first species-specific analysis of the relative importance of the DBH and landscape characteristics and their temporal dynamics on the tree-to-tree variability of sap velocity. We use an experimental set-up in a multi-species stand in Luxembourg that include 37 trees equipped with sap-flow sensors from four species representing the dominant species in central Europe (*i.e. Fagus sylvatica; Quercus robur L./ petraea (Matt.) Liebl.; Piceas abies* (L.) Karst.; *Pseudotsuga menziesii* (Mirb.) Franco). We hypothesized that (i) both DBH and landscape characteristics are jointly responsible for tree-to-tree variability of sap velocity, (ii) the controls of DBH and landscape characteristics on sap velocity are specie-specific, and (iii) the temporal dynamic of their relative importance throughout the growing season vary between species. We tackle these hypotheses by exploring the following research questions:

1- Does the tree-to-tree variability of sap velocity within a stand stem from the variability of DBH within each species?
2- Does the landscape characteristics explain a substantial part of tree-to-tree variability of sap velocity within each species of the stand?
3- Does the relative importance of sap velocity drivers and its temporal dynamic vary between species in link with their specific water-use?

Here, we go beyond previous work by providing a first specie-specific analysis of the relative importance of DBH and landscape characteristics, concurrently on different species from the same stand. This allows revealing the different temporal dynamics of the relative importance between species. Understanding the species-specificity and the temporal variability of the different controls of sap velocity is critical for implementing further reliable prediction of stand-scale transpiration that account for tree-to-tree variability. Moreover, the novelty of the approach applying a relative importance analysis on each species is applicable on any other multi-species stand in order to determine the drivers of tree-to-tree variability within any other tree species.

2. Methods

2.1. Study site

The Weierbach is a fully forested catchment (Fig. 1a) covering 0.45 km^2 in the Ardennes in North-West Luxembourg (49°49'38'' N, 5°47'44''E) (Fig. 1c) (Glaser et al., 2020; Hissler et al., 2020; Rodriguez et al., 2021). The catchment is dominated by a plateau with deeply incised V-shape valleys. The slope varies between 0.6° to 31° with a mean of 5.86° and the large majority (86.5%) of the catchment has slopes of less than 10° (Fig. 4b). Elevation in the catchment ranges from 458 to 514 m asl (Martinez-Carreras et al., 2016). Hydro-meteorological data (Fig. 2) were recorded at the Roodt weather station 3.5 km southeast of Weierbach catchment (Fig. 1c). The area has a semi-oceanic climate with mean annual precipitation of 815 mm and monthly precipitation ranging from 39 mm in April to 103 mm in December (2007-2019). The mean annual temperature over the 2007-2019 period was 8.9°C and ranged from 0.8°C (January) to 17°C (July). The time series of precipitation and evapotranspiration are out of phase and higher evapotranspiration rates in summer result in pronounced seasonality of streamflow, with lowest values between July and October. The soil type and the geology are homogeneous with Devonian slate and phyllites that are covered by deposits from the periglacial Pleistocene (Juilleret et al., 2011). These deposits mainly consist of silt and few rock fragments (± 0.6 m) on a lower layer dominated by rock fragment oriented parallel to the slopes (Juilleret et al., 2011). According to the WRB classification (FAO-ISRIC-IUSS, 2006), the soil is a Leptic Cambisol (Humic, Ruptic, Dystric, Endosketelic, Siltic - Juilleret et al., 2011). Eighty-nine percent of the catchment is covered by a mixed forest (Fig. 1b) consisting of European beech (*Fagus sylvatica*) and pedunculate and sessile oak (*Quercus robur L. and Q. petraea* (Matt.) Liebl.). The remaining eleven percent of vegetation (Fig. 1b) are monospecific

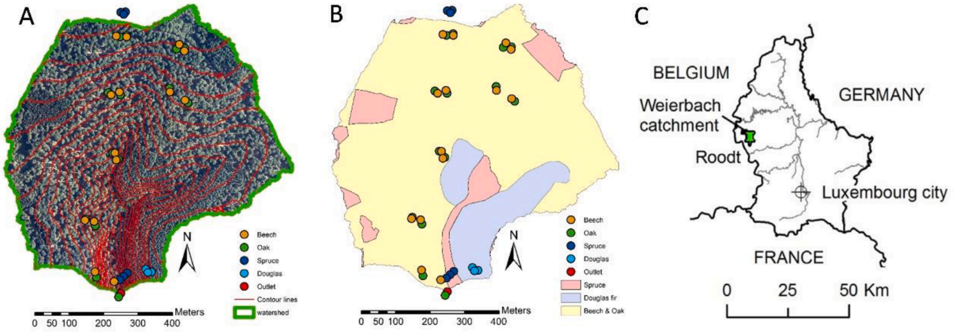

Fig. 1. Catchment study site. Panel A displays the catchment and the aerial picture of vegetation. Contour lines delineate 2.5 m of elevation step. Red, yellow, dark blue, green, and light blue circles represent respectively the location of beech, oak, spruce, and douglas fir trees equipped with SFM1 sap-flow sensors and the catchment's outlet. Panel B represents areas covered by different vegetation types, with yellow, pink, and light blue representing beech and oak mixed-stands, spruce, and douglas fir, respectively. Panel C shows the location of the catchment in Luxembourg country. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article)

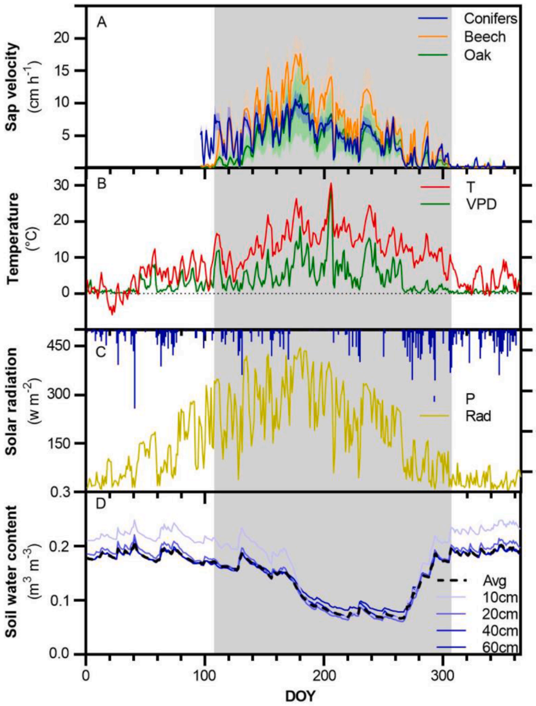

Fig. 2. Time series of sap velocity and environmental conditions during the 2019 growing season. Panels A displays sap velocity time series from 9 conifers (blue lines), 14 beech (orange lines) and 14 oak trees (green lines). Translucent coloured areas around the lines represent standard deviation of the mean. Panels B and C display environmental data measured in Roodt weather station. T= Temperature (°C), VPD= Vapor pressure deficit (kPa), P=precipitation (mm), Rad= Solar radiation (Wm^{-2}). Panel D display the average soil moisture of the catchment. Avg= Average soil volumetric water content (m^3 m^{-3}), VWC10, VWC20, VWC40 and VWC60= soil volumetric water content at 10, 20, 40 and 60 cm deep respectively, DOY= Day of the year. Light grey area throughout all panels represents the growing season from doy= 109 to doy=306. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article)

conifer stands with 5% of Norway spruce (*Piceas abies* (L.) Karst.) and 6% of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). In this paper, we lumped spruce and douglas fir data into one conifer category, because of a limited number of replicates for each species. We are aware that conifer species might differ in their water-use strategies and root architecture, but the physiological contrast to broadleaved trees likely surpasses these differences.

2.2. Hydro-meteorological monitoring

Precipitation was measured with a tipping bucket rain gauge following the World Meteorological Organization standards (Sevruk et al., 2009). Temperature (T), relative humidity (RH), and solar radiation were measured hourly. Hourly vapour pressure deficit (VPD) was calculated using Eq. (1):

$$VPD = 0.61375 \times e^{(17.502\times T/(240.97+T))\times(1-RH/100)} \tag{1}$$

Volumetric soil water content was derived every 30 min at seven locations across the catchment with CS650 reflectometers (Campbell Scientific Ltd, Logan, UT, USA). At each location, eight probes were installed parallel to the surface at 10, 20, 40, and 60 cm depth. Each depth contained two probes separated by 1 m. For each depth, we calculated the mean value across locations (14 sensors per depth). Then, we determined the catchment average soil moisture as the mean value of all depths.

2.3. Determination of landscape characteristics

We used a high-resolution (1 m) digital elevation model (DEM) (Luxembourgish air navigation administration, 2017) to calculate aspect, slope, curvature, and flow accumulation through the Spatial Analysis Toolbox of ArcGIS Desktop 10.5. The aspect represents the direction the downhill slope faces. The values of each of each squared meter indicate the compass direction the surface faces at that location. It is measured clockwise in degrees from 0 (due north) to 360 (again due north), coming full circle. Flat areas having no downslope direction are given a value of -1. The slope values represent the steepness of each squared meter. The lower the slope value, the flatter the terrain; the higher the slope value, the steeper the terrain. A positive and negative curvature value indicates the surface at that squared meter is upwardly convex or concave, respectively. A value of 0 indicates the surface is flat. The flow accumulation is determined by accumulating the weight for all squared meter that flow into each downslope squared meter. Each raster map of landscape characteristics has been smoothed by averaging values in 10 m circle using the focal statistic tool from Spatial Analysis Toolbox of ArcGIS in order to avoid the influence of small misplacements of the tree position on the analysis. To quantify the topographic position of each tree, a topographical position index (TPI- Wilson and Gallant, 2000; Weiss, 2001) was defined as follows:

$$TPI = E - E_{avg50} \tag{2}$$

where E is the elevation at the tree location and E_{avg50} is the average elevation in a 50 m circle around the tree. Positive values mean that the tree is above the area around, while negative values denotes the opposite. Zero represents either a constant slope or a flat area on the 50 m circle. The higher and lower values represent therefore the ridge and the valley areas respectively (Weiss, 2001).

2.4. Distributions of DBH and landscape characteristics

An inventory transect (20 m x 360 m) was realized in spring 2019 (Fig. 2a) in a beech-oak populated area of the catchment. All trees with circumference at breast height higher than 10 cm located inside this band were recorded and tree were classified within 15 equal-interval (5 cm) DBH classes (*i.e.* 2.5-7.5 cm / 7.5 -12.5 cm /… / 72.5 -77.5 cm) in order to characterize the catchment composition in terms of species and DBH. The landscape characteristics of each square meter were derived to characterize the distribution of each factor across the catchment and the extent of the coverage of our sap velocity monitoring setup. Classification was based on 100 equal intervals from the lower to the higher value for each landscape characteristic. DBH and landscape characteristics of our sampled trees are displayed in supplementary Table 1.

2.5. Deriving sap velocity from measurements

In this study, we focused our analysis on sap velocity rather than sap-flow, because the latter depends strongly on DBH through the relation of DBH to sapwood area (e.g. Gebauer et al., 2008; Meinzer et al., 2005; Hassler et al., 2018). Therefore, the use of sap-flow would have excluded the possibility of including DBH as a driver of variability in sap-flow, because of the dependence between the variables. Tough, the outer part of the sapwood is known to display a higher conductivity compare to inner sapwood (e.g. Poyatos et al., 2007; Lüttschwager and Remus, 2007). As the sapwood depth is not constant across DBH but needle length remains the same for all the trees, one can suppose that the inner thermistor was located in “less conductive” part of the sapwood in the smaller trees compared to larger trees.

We determined sap velocity based on heat ratio method (HRM, Burgess et al., 2001; Bleby et al., 2004) at 37 trees (Fig. 1a and b) using SFM1 sap-flow sensors (ICT International, Armidale, NSW, Australia) over the 2019 growing season and beyond (April-December). The SFM1 sensors are composed of four thermistors placed on two needles enclosing a third heating needle. All needles were spaced by 0.5 cm and inserted horizontally in the tree along a vertical straight line. The sap-flow sensors were installed at breast-height and on the east-facing side of the trees and were protected with metal shield in order to avoid direct sunlight exposure.

In the HRM, the ratio of temperature increase between downstream and upstream thermistor is determined after the release of a heat pulse. Heat pulse velocity is then calculated following Eq. (3):

$$V_h = \frac{k}{x}\ln(v_1/v_2)3600 \tag{3}$$

where k is thermal diffusivity of fresh wood set to 0.0025 $\text{cm}^2\ \text{s}^{-1}$ (Marshall, 1958), x is the distance between the needles (0.5 cm), and v_1 and v_2 are the increases in temperature in the downstream and upstream thermistor, respectively. Next, V_h was automatically corrected to V_c (corrected heat pulse velocity) in order to account for wounding using a wound coefficient of 0.13 cm; see Burgess et al. (2001) for details. V_c is then converted into sap velocity according to Eq. (4).

$$V_s = \frac{V_c\rho_b(c_w + m_c c_s\ )}{\rho_s c_s} \tag{4}$$

where ρ_b is the basic density of wood set constant to 0.5 g cm^{-3} for all species (Burgess and Downey, 2014), c_w and c_s are the specific heat capacity of the wood matrix and sap (1200 and 4182 J $\text{kg}^{-1}{}^{\circ}\text{C}^{-1}$ (Becker and Edwards, 1999; Lide, 1992)), m_c is the water content of sapwood (set constant to 0.5 g cm^{-3}; Burgess and Downey, 2014) and ρs is the density of water (set constant to 1 g cm^{-3}).

We corrected potential misalignment of needle via the zero velocity method (Burgess et al., 2001; Pearsall et al., 2014) assuming a zero velocity period from December 8 to December 19. During this period, evaporative demand was the lowest of the observation period and no diurnal cycle was apparent in sap velocity.

Finally, we averaged sap velocities values measured at the outer and inner thermistors (1.25 cm and 2.75 cm below bark respectively) for generating the final sap velocity time series of each tree.

2.6. Relative importance of sap velocity drivers

A linear regression model (Eq. (5)) is used to link sap velocity (y) and p drivers, denoted here as regressors ($x_1,\ldots,x_{(p)}$). In our analysis, we accounted for six (p=6) drivers, namely DBH, slope, flow accumulation, aspect, curvature, and TPI.

$$y = \beta_0 + \beta_1 x_1 + \ldots + \beta_p x_p \tag{5}$$

where $\beta_1,\ldots,\beta_p$ are unknown regression coefficients. Coefficients values $(\widehat{\beta}_1,\ldots,\widehat{\beta}_p)$ are obtained through an iteration process and fitted sap velocity $(\widehat{y})$ can be written as:

$$\widehat{y} = \widehat{\beta}_0 + \widehat{\beta}_1 x_1 + \ldots + \widehat{\beta}_p x_p \tag{6}$$

We use the coefficient of determination R^2 to evaluate the goodness of fit of the regression model. In our case, R^2 represents the proportion of variation in y explained by the p regressors and can be written as:

$$R^2 = \frac{Model\ SS}{Total\ SS} = \frac{\sum_{i=1}^{n}\left(\widehat{y}_i - \bar{y}\right)^2}{\sum_{i=1}^{n}(y_i - \bar{y})^2} \tag{7}$$

where n is the number of observed trees per species. Different drivers are conjectured to have different degrees of contribution to the sap velocity at a given time. These contributions are determined through a relative importance analysis. The most common method for assessing relative importance is the Lindeman Merenda and Gold (LMG) method (Lindeman et al., 1980). The LMG method consists in decomposing R^2 and quantifying the contributions of each regressor to the total R^2. The LMG measurement for k^{th} regressor x_k is based on sequential R^2. This means that the regressors are entered into the model in the order they are listed, and its relative importance is therefore dependent on that order. This ordering effect is subsequently eliminated in Eq. (8) by averaging all possible orderings ($p!$) for p regressors (Grömping, 2006).

$$LMG(x_k) = \frac{1}{p!}\sum_{r permutation} seqR^2(\{x_k\}S^r) \tag{8}$$

where r denotes r-permutation (i.e. $r = 1,\ 2,\ldots,p!$) and

$$seqR^2(\{x_k\}S^r) = R^2(\{x_k\} \cup S^r) - R^2(S^r) \tag{9}$$

where $R^2(S^r)$ indicates the R^2 of regressors (called set S^r) entered into the model before x_k, and $R^2(\{x_k\} \cup S^r)$ is the R^2 of regressors in set S^r and x_k, on the order in the r^{th} permutation. Therefore, $seqR^2(\{x_k\}r)$ denotes sequential R^2 for the regressor x_k in the ordering of the regressors in the r^{th} permutation. For example, if p=3, there are six different orderings (3!=6), and then six different sequential R^2 estimations for each regressor. In this case, the relative importance of each regressor calculated by LMG is the average of six estimations.

The link between the growing season dynamic of relative importance and water or energy limitations was investigated through Spearman correlations between daily relative importance of each factor and daily soil water content and radiation.

A correlation matrix presenting the bivariate Pearson index between each topographical driver within the catchment is displayed in the supplementary material (sup. Table 2). Only one combination of topographical factors are above the widely employed critical value of collinearity (Spearman> 0.7) (Dormann et al., 2008; Hassler et al., 2018). This is the combination of TPI and curvature (Spearman=0.71). Consequently, the relative importance analysis may not accurately partition the variance in daily sap velocity due two these two factors.

2.7. Data analysis

Data analysis (relative importance, frequency distribution, correlations) was carried out using R 3.5.0 software (Team R-C, 2013).

3. Results

3.1. Hydro-meteorological conditions

The 2019 growing season in the Weierbach lasted from April 19 (DOY=109) to November 2 (DOY=306) derived from sap velocity observations (Fig. 2a). Outside this period, transpiration was negligible due to the very low evaporative demand and the absence of evaporative surface for the deciduous trees. Sap velocity data outside this period was therefore excluded from the analysis.

Daily meteorological data showed clear seasonality (Fig. 2) with higher temperature, VPD, and solar radiation during summer months reaching a maximum of 30.6°C, 3.0 kPa, and 445 W m^{-2} (Fig. 2b and c). The total annual precipitation in 2019 was 1030 mm, the highest precipitation sum since 2007, and thus above the long-term (2007-2019) average of 815 mm (Fig. 3b). However, over the summer months reduced precipitation occurred (Fig. 2c). The mean annual T was 9.59°C and VPD was 0.37 kPa, respectively. These make 2019 the second (after 2018) warmest and water demanding year since 2007, when recording of meteorological data in Roodt was initiated (Fig. 3a). The average T, VPD, and the total precipitation over the growing season were 14.4°C, 0.56 kPa, and 510 mm while average over 2007-2019 was 13.6°C, 0.41 kPa and 434 mm, respectively (Fig. 3).

Average daily soil water content (θ) ranged from 0.066 to 0.210 m^3 m^{-3} over the year with a mean of 0.150 m^3 m^{-3}. Soil moisture was lower during the growing season (range: 0.066 to 0.187 m^3 m^{-3}; average 0.120 m^3 m^{-3}). Top-soil moisture showed higher variability compared to the measurement of deeper soil layers. Soil moisture was spatially consistent. The Spearman correlation coefficients between all eight available time series measured at different locations within the catchment were from 0.9 to 0.99 (data not shown).

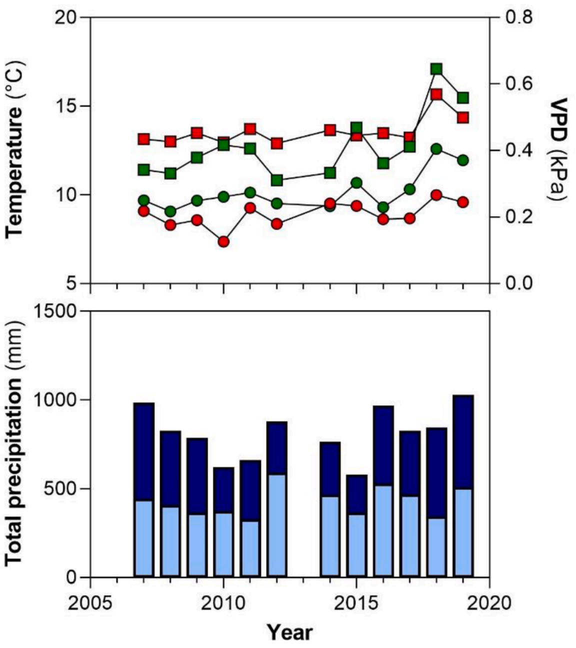

Fig. 3. Historical data of temperature, VPD and precipitation measured at the Roodt climate station. Panel A displays the yearly average (circle) and growing season average (square) temperature (red) and VPD (green). Panel B displays the total yearly (dark blue) and growing season (light blue) precipitation. Eighty percent of the data form 2013 are missing and therefore the entire year is not presented. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article)

3.2. Distributions of DBH and landscape characteristics

DBH at the inventory transect ranged from 3.2 cm to 74.5 cm. Trees

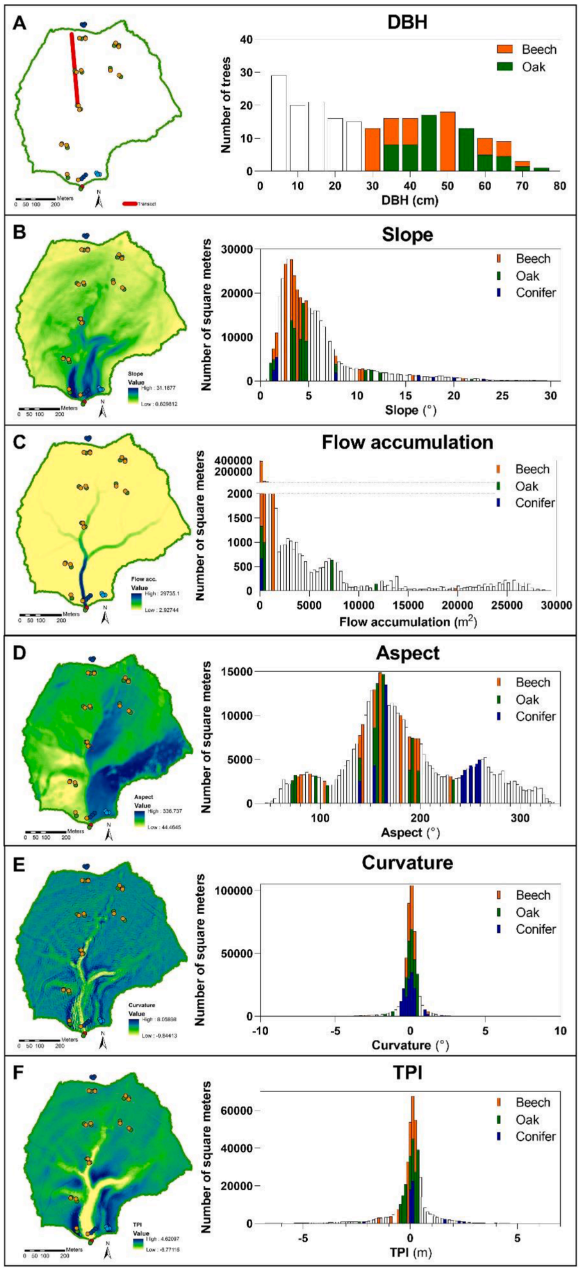

Fig. 4. Distribution of DBH and landscape characteristics within the Weierbach catchment. DBH data was acquired through the 360m x20m inventory transect located in the beech-oak stand and represented by the red line in panel A map. Distribution is based on 15 equal intervals (5cm). Panel B to F represent landscape characteristics (i.e. slope, flow accumulation, aspect, curvature, and TPI). Distributions are based on 100 equal intervals between the smallest and the largest value of each characteristic. Orange, green and blue colours in the bars indicate classes covered by at least one tree equipped with sap-flow sensor from beech, oak or conifer species, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article)

equipped with sap-flow sensors covered all diameter classes higher than 30 cm with at least one replicate (Fig. 4a). No data on the distribution of DBH among a representative sample of conifers within the catchment were available.

Slope and flow accumulation were log normal distributed in the catchment. Aspect, curvature, and TPI approximated a normal (Gaussian) distribution (Fig. 4b–f). Values of slope were from 0.6° to 31°; flow accumulation were from 151 m^2 to 29586 m^2; aspect were from 45.9° to 335.3°; curvature were from -9.75 to 7.97; and the TPI were from -6.71 m to 4.56 m.

3.3. *Sap velocity time series*

Sap velocities were recorded hourly from April 6 to December 19 (Fig. 2a). Due to technical problems linked to power supply and data logging, 14% of the time series data are missing. During the growing season, average daily sap velocity and standard deviation was 7.13 ± 2.3, 3.94 ± 2.2 and 4.76 ± 2.2 cm h^{-1} for beech, oak, and conifers, respectively.

Substantial tree-to-tree variability occurred within each species. Average sap velocity throughout the growing season, calculated only from days with complete datasets (days with no missing data), varied up to 390%, 520%, and 430% between the trees displaying highest and lowest velocities for beech, oak and conifers, respectively.

Daily sap velocity showed a clear temporal variability for each species (Fig. 2a) but was significantly correlated to daily soil water content only in the case of deciduous trees (p-value < 0.05 and Spearman r $=$ -0.17 for beech; p-value < 0.0001 and Spearman r $=$ -0.36 for oak). High transpiration and evaporation rates in summer led to low soil water content when VPD was the highest. Therefore, sap velocity and soil water content were negatively correlated.

For each species, Spearman correlation coefficients between average sap velocity during the growing season, DBH and landscape characteristics were computed (Table 1). The only significant correlation was found between DBH and sap velocity of oak trees (Table 1).

3.4. *Relative importance of DBH and landscape characteristics for explaining tree-to-tree variability in sap velocity*

Some missing sap velocity data led to gaps in the temporal pattern of relative importance (Fig. 5- 2.5%, 8.5%, and 34.4 % for beech, oak, and conifers, respectively). Nevertheless, the DBH was the main driver of tree-to-tree variability in sap velocity for each studied species. The DBH explained in average 24%, 43%, and 20 % of the tree-to-tree variability for beech, oak, and conifers, respectively over the growing season (Table 2). Individually, landscape characteristics (*i.e.* slope, flow accumulation, aspect, curvature, and TPI) displayed a lower relative importance compared to DBH. However, all landscape characteristics together explained 49%, 35%, and 37% of the tree-to-tree variability in sap velocity for beech, oak, and conifers, respectively. In average throughout the entire growing season, the relative importance of each landscape characteristics varied with species. Flow accumulation displayed the highest value with 18% of tree-to-tree variability explained for beech trees, followed by aspect with 12% of tree-to-tree variability explained for conifers (Table 2). The main landscape characteristic controlling tree-to-tree variability in oak trees is curvature with 11% explained (Table 2).

Table 1
Spearman correlations between average sap velocity throughout the entire growing season and drivers of tree-to-tree variability.

[a]ρ / [b]p-val.	DBH	TPI	[c]Flow ac.	Curvature	Slope	Aspect
Beech	0.48/0.08	-0.26/ 0.37	0.52/ 0.06	-0.26/ 0.36	0.44/ 0.11	-0.37/ 0.20
Oak	0.88/ <0.0001	0.37/ 0.20	-0.33/ 0.25	0.42/0.14	-0.13/ 0.66	-0.12/ 0.69
Conifers	-0.63/ 0.08	0.26/ 0.50	-0.13/ 0.74	0.10/0.81	-0.18/ 0.64	-0.28/ 0.46

[a] ρ = Spearman correlation coefficient.
[b] p-val = p-value of the correlation
[c] Flow ac. = Flow accumulation.

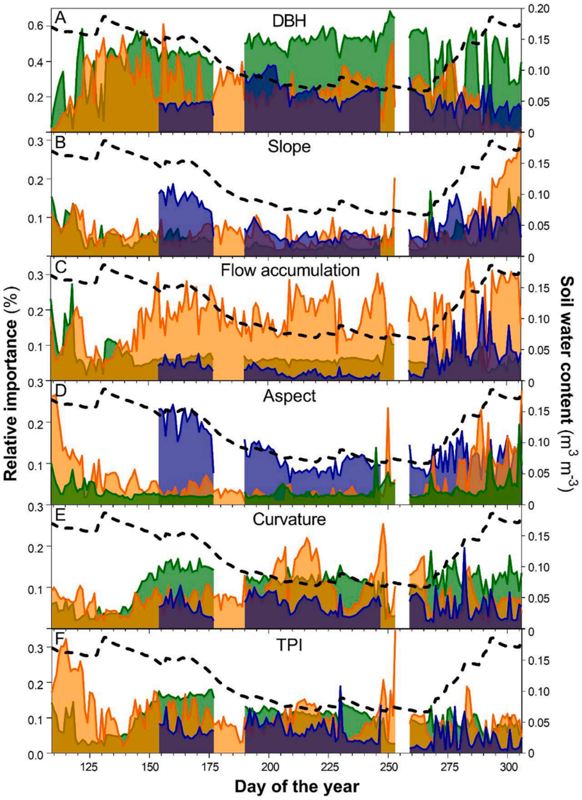

Fig. 5. Daily relative importance of the drivers of tree-to-tree variability of sap velocity. Values are presented for the entire growing season (from April 19 [DOY=109] to November 2 [DOY=306]). Solid lines and filled areas below represent the daily relative importance of each tested driver with orange, green, and blue colours representing beech, oak and conifers, respectively. Dashed black lines represent the soil water content on right Y-axis. TPI= Topographical position index.

We observed a clear temporal variability in the relative importance of each driver (Fig. 5) and the seasonal dynamic of each driver's relative importance displayed species-specificity (Fig. 5). Highest relative importance of DBH of oak and conifers for explaining tree-to-tree variability in sap velocity occurred during summer months, when soil water content is the lowest (Fig. 5a). For beech trees, the maximum relative importance of DBH was reached at the beginning of the season (Fig. 5a). The relative importance of DBH of oak and conifers showed strong correlations with soil water content, while this correlation does not exist for beech (Table 2).

For both deciduous species, the relative importance of slope was highest at the beginning and the end of the growing season, while the relative importance of slope followed the dynamic of soil water content for conifers (Fig. 5b). The relative importance of flow accumulation tended to increase throughout the growing season for beech, stayed constantly low for oak, and increased only at the end of the growing season for conifers (Fig. 5c). The relative importance of aspect remained low for both deciduous species, with short lasting increases at the beginning and the end of the growing season. For conifers, aspect's relative importance followed the dynamic of soil water content (Fig. 5d). The relative importance of curvature steeply increased around DOY 150 for oak, before it remained rather constant until the end of the growing season. For beech trees, curvature's relative importance reached its

Table 2

Relative importance average throughout the growing season for all sap velocity drivers and spearman correlation between driver's relative importance and soil water content and radiation.

	Beech			Oak			Conifers		
Drivers	Var[a] [%]	ρ[b] SWC[c]	ρ Rad[d]	Var [%]	ρ SWC	ρ Rad	Var [%]	ρ SWC	ρ Rad
DBH	24	-0.08	0.20**	43	-0.56***	0.17*	20	-0.53***	0.43***
Slope	7	0.45***	-0.16*	5	0.65***	-0.33***	8	0.70***	0.02
Flow ac.[e]	18	-0.22**	-0.07	7	0.10	0.33***	5	0.73***	-0.50***
Aspect	6	0.62***	-0.24***	3	0.23**	-0.34***	12	0.50**	0.21*
Curvature	9	-0.54***	0.25***	11	-0.16*	-0.09	6	-0.15	0.12
TPI	10	0.06	0.23**	10	-0.24***	0.42***	6	-0.01	0.26**

[a] Var = average variance explained over the growing season.

[b] ρ = Spearman correlation coefficient.

[c] SWC= Soil water content.

[d] Rad= Solar radiation.

[e] Flow ac.=Flow accumulation. Superscript stars denote significant correlation with ***= p-val≤0.001; **=p-val≤0.01; *=p-val≤0.05. Main results are displayed in bold.

maximum during summer months while it stayed mainly constant for conifers (Fig. 5e). The relative importance of TPI displayed similar trends as curvature for oak and conifer trees, for beach however, it reached its maximum at the beginning of the growing season (Fig. 5f).

4. Discussion

4.1. Relative importance of DBH for explaining tree-to-tree variability of sap velocity

We observed a substantial tree-to-tree variability of sap velocity, both between and within species. Throughout the growing season, beech trees presented on average a sap velocity 1.8 and 1.5 times higher than oak and conifers, respectively. This can be explained by the physiological characteristics (i.e. high stomatal conductance, efficient root water uptake) displayed by beech under non-limiting water conditions (Hölscher et al., 2005; Köcher et al., 2009; Hassler et al., 2018). Importantly, we found a substantial tree-to-tree variability resulting in sap velocity varying by four (beech) to almost seven times (oak) within a given species. Our relative importance analysis revealed that, individually, DBH was the main driver of tree-to-tree variability for each species, which is consistent with previous studies (Hölscher et al., 2005; Chiu et al., 2016; Hassler et al., 2018). However, DBH has a substantially stronger influence on sap velocities for oak than for other species. This might be explained by the differences in root architecture between oak and the other species. For oak, larger trees can access deeper water sources than smaller oaks due to an increase of root depth with tree size. Beech and conifer trees are known to develop preferentially a shallow root system (Leuschner et al., 2001; Coners and Leuschner, 2005; Pretzsch et al., 2013; Matheny et al., 2017; Lanning et al., 2020), this eventually means that increasing DBH is not enhancing the tree's capacity to explore deeper soils. Until today, only few studies have investigated the relationship between above-ground biomass or DBH and maximum rooting depth and these studies compared different vegetation types and not tree species (Schenk and Jackson, 2002; Smith-Martin et al., 2020). Recently, Fan et al., (2017) reviewed the mean rooting depth of a large range of tree's genus and indicated a commonly deeper root system for the Oaks (5.23 m) than the beeches (0.83 m). To our knowledge, no study determining the relationship between DBH and rooting depth of our two tested species is available. Such a study could help to confirm the specie-specific role of DBH in accessing water.

4.1.1. Temporal dynamic of the relative importance of DBH

The temporal dynamic of the DBH relative importance for explaining tree-to-tree variability was found to be species-specific. It has been shown previously that these dynamics depend on hydro-meteorological conditions throughout the growing season (Hassler et al., 2018). As 2019 was both among the most water demanding and rainy years since 2007, a large variation in the hydro-climatic conditions and their consequent controls on sap velocity drivers was expected. We observed a clear contrast between the dynamic of the relative importance of DBH for beech and oak. While the relative importance of DBH was similar at the beginning of the season, the values for oak became twice as high as the values for beech during summer months when the soil water content was the lowest. This is confirmed by the correlation analysis displayed in Table 2. The concomitance of high relative importance of oak's DBH and dry soil conditions supports that different dynamics are due to the variable root architectures between species. The importance of accessing deeper water sources can be reasonably expected to be higher in drier periods. In contrary, Hassler et al. (2018) found that DBH control on sap velocity of a beech-oak stand remained fairly constant over the 2014 growing season. It is likely explained by the fact that the relative importance was not determined in a specie-specific way; so contrasted effects from DBH on beech and oak sap velocities could have compensated each other.

4.1.2. Likely mechanisms of DBH control on sap velocity

We observed a substantial effect of DBH on sap velocity that is even apparent for oak trees via the correlation analysis with yearly mean sap velocities. However, this effect was opposite in broadleaved trees and conifers. Larger DBH induced larger yearly average sap velocity in broadleaved trees (i.e. beech and oak), but smaller velocities in conifers. These decreases and increases in sap velocity associated with higher DBH were already reported before (e.g. Höschner et al., 2005; Otiento et al., 2014). Larger velocities associated with larger DBH are likely due to the associated size of the canopy and soil volume colonized by the root system. Indeed, being larger ensure the exposure of the canopy to the to direct radiation and a larger atmospheric gradient through a better social status of the tree such as an access to a larger soil volume and potential water supply (Nadezhdina and Cěrmák, 2003; Bolte et al., 2004; Hassler et al., 2018). In our stand, broadleaved trees grow in relatively low density of mixed-species while conifers grow in mono-specific, densely planted areas. We suspect this density to create a competition for resources and especially radiation (Sobachkin et al., 2005). In these conditions, larger trees involve denser canopy within the stand that can lead to a higher shading effect and consequently a decrease in sap velocity (Coates et al., 2009). This explanation is supported by the positive and significant correlation between the relative importance of DBH for explaining tree-to-tree variability of conifers and radiation (Table 2).

While we emphasised the key role of species-specific root architectures and management practices for explaining the DBH's control on the tree-to-tree variability of sap velocity, our approach included some limitations. On one hand, further studies on the role of DBH on sap velocity should consider forest density as the effect of DBH was found to be different in dense plantation and natural stands. Future studies should also include a larger amount of conifer trees from various aged stands and planting densities in order to unravel the interplay between the shading effects resulting from larger trees and a larger water reservoir from a larger root system. On the other hand, DBH was the only variable related to tree size that we considered. Therefore, it combined tree characteristics such as tree height, leaf area, social status, or volume explored by the root system. This potentially provided an excessive explanatory power to this driver as it encompasses the effect of all these variables. A step further for supporting our explanation of the mechanism driving tree-to-tree variability in relation to tree size would be to include other size-related variables into the analysis. This would help dissociating the roles of belowground and aboveground processes in the accessibility of water and energy. Root-related characteristics would be particularly relevant considering that geology was previously identified as one of the main drivers of spatial variability in transpiration of beech and oak, especially because of its control on root distribution (Hassler et al., 2018).

4.2. *Relative importance of landscape characteristics for explaining tree-to-tree variability in sap velocity*

Tree-to-tree variability was mainly determined by landscape characteristics for beech and conifers but not for oak. For beech trees, the cumulated relative importance of all five tested landscape characteristics explained, in average over time, half of the tree-to-tree variability of sap velocity. The larger relative importance of landscape characteristics for beech trees was mainly driven by flow accumulation and TPI. Convergent areas, characterized by high flow accumulation and low TPI, commonly display higher soil water content during drying periods due to the water redistribution from upslope contributing areas (Hawthorne and Miniat, 2018; Lin et al., 2019) and capillary rises from shallower groundwater (Miller et al., 2010; David et al., 2013; Brooks et al., 2015). For oak trees, most landscape characteristics displayed lower relative importance than beech, seemingly because of its lower dependence on shallow soil water. The highest relative importance of flow accumulation for beech is consistent with its specific root system relying in a higher proportion than oak on shallow soil water (Leuschner et al., 2001; Fabiani et al., unpublished data). This result contrasts with studies from Loranty et al. (2008), Kumagai et al. (2007) and Tsuruta et al. (2020) who found no difference in sap velocity of trees located at different slope positions; but is in line with Kume et al. (2016) who found a sap velocity significantly higher in lower slope position. However, it is important to notice that these studies focused only on conifer species and that lower slope position does not necessarily correspond to convergent areas. For the conifers, the aspect was the most important driver among landscape characteristics in terms of relative importance. The high relative importance of aspect for conifers is consistent with the above-mentioned competition for light in dense stands, as aspect is known to influence the canopy light interception (Renner et al., 2016). However, these results have to be taken cautiously as we found a significant correlation between the DBH of conifers and aspect. The Spearman correlation coefficient was 0.75, which is above the critical value of collinearity, Spearman $>$ 0.7 (Dormann et al., 2008; Hassler et al., 2018). This is due to the low number of sampled conifer trees and their location within the catchment (Fig. 4a and d).

4.2.1. *Temporal dynamic of the relative importance of the landscape characteristics*

Relative importance of slope and aspect presented a contrasted temporal dynamic between deciduous trees and conifers. For the formers, relative importance displayed higher influence of landscape characteristics at the beginning and the end of the growing season. These periods coincide with the transition active-dormant and dormant-active for deciduous trees. Therefore, we believe that slope and aspect, via their influence on light exposure, affect the timing of leaf flush and fall. Consequently, slope and aspect influence the tree-to-tree variability in sap-velocity during these transition periods via their lever on leaf area. In their study, Hassler et al. (2018) did not to observe this effect of slope and aspect during transition periods because their dataset was selected for fully developed canopy only (*i.e.* started one month later and stopped one and half month earlier in the growing season compare to our dataset). In the case of conifers, the daily relative importance of slope, aspect, and flow accumulation presented a strong positive correlation with soil water content (Table 2). This may indicate a substantial dependence on soil water (top 60 cm) for sustaining conifer sap velocities. Under wet soil conditions that are not constraining the sap velocity, tree-to-tree variability arises from a variable radiation exposure. However, under dry conditions, water limitation impedes the most exposed trees to take advantage from the higher radiation input. Further investigations including a larger number of conifer trees spread on a larger range of slope and aspect values would definitely help our understanding of tree-to-tree variability in sap velocity. For the other landscape characteristics (i.e. flow accumulation for deciduous species, curvature, and TPI) no clear temporal pattern was identified for any species.

4.2.2. *Likely processes of landscape characteristics controls on sap velocity*

Except for aspect, the correlation analysis revealed opposite effects in controlling sap velocities for the studied landscape characteristics between beech and oak. This striking contrast is the result of the different water-use strategies displayed by the two species. Oak trees located on top of the slopes or on flat areas displayed higher average sap velocities due to a sufficient access to deep water and a greater light canopy interception than oak trees growing in convergent areas. In contrast, beech trees located in convergent areas benefit from the likely higher water availability in shallow soil than the ones growing on the plateau or top slope positions. While soil moisture was measured in different positions within the catchment, we only suspect higher soil moisture in convergent areas compared to higher slope positions, but our limited distribution of sensors does not allow confirming this. Nevertheless, we can conclude, when compared to each other, that sap velocity of oak trees was more light-limited and sap velocity of beech trees was more water-limited.

The control of conifer sap velocities from the landscape characteristics remains highly elusive because of the limited distribution of the studied trees within the catchment. The role of curvature and TPI on the studied species remains unclear because of a narrow distribution of these driver's values within our experimental area. Another possible explanation comes from the correlation between these variables (sup. Table 2) and the inability of the relative importance analysis to partition variance between correlated variables (cf. Section 4.4).

4.3. *Implications for determining stand transpiration while accounting for DBH and landscape characteristics in upscaling*

Our results have critical implications for upscaling individual sap-flow data to stand transpiration. Here, we demonstrated the key specie-specific and temporally dynamic influence of DBH and landscape characteristics on the sap velocity of a given tree. While the common upscaling procedure account for temporal variability in sap velocity (e.g. Granier et al., 1996; Wilson et al., 2001; Wullschleger et al., 2001; Cermák et al., 2004), new approaches should be developed that consider tree-to-tree variability in sap velocity through species-specific relationships with DBH and landscape characteristics. This could take the form of a correction factor depending on the species, the DBH and the landscape to be apply on the average time series of sap velocity. Additionally, in lights of the temporally dynamic aspect of the DBH and landscape controls, one should consider a temporal aspect in the correction factor. This correction factor could be calculated for each day and each species based on the relationships between daily sap velocities and the values of the drivers (*i.e.* DBH and landscape characteristics).

Both relationships would have a different weight in setting the value of the correction factor. The weight of each relationship could be derived from the daily relative importance of each driver. As an example, the correction factor to be apply on daily sap velocity of a given oak tree on a dry summer day would be mainly determined by the DBH-sap velocity relationship. The weight of this relationship on the correction would be lower on a spring day because the relative importance of DBH is lower during this period. On the same summer day, the correction factor to be apply to the daily sap velocity of beech would be mainly determined by the relationship between flow accumulation and sap velocity. The potential improvement in the prediction of stand transpiration resulting from including this correction factor remains to be quantified but could have substantial implications on forest management, climate modelling, or catchment hydrology. Further research on the prediction uncertainty in stand-scale transpiration is pressingly needed to pave the way for novel and robust approach for upscaling sap-flow data.

4.4. *Overall value of the relative importance analysis*

The information provided by the relative importance analysis is particularly useful for identifying the contribution of a predictor or driver, in combination with other drivers to the total predictable variance of a criterion (Johnson and LeBreton, 2004). However, to our knowledge, only one study (Hassler et al., 2018) applied this method before in order to identify the drivers of tree-to-tree variability in sap velocity. The main advantage from the relative importance analysis is it allows revealing the temporal dynamic of each driver control on sap velocity. As we determined the part of variance explained by each driver on a daily basis, it allows investigating the link between the dynamic of daily relative importance of a driver and the daily hydro-meteorological conditions. The novelty of our work lies in the application of this method on each species separately. This allowed the identification of variations in the temporal dynamics of driver's relative importance between different species. These new findings open the way for a novel approach to account for tree-to-tree variability in upscaling of sap-flow data, based on species-specific and temporally dynamic relationships.

Despite the valuable results from the relative importance analysis, two important limitations of the method must be acknowledged. Firstly, previous studies showed that relative importance analysis generally failed to appropriately partition variance between drivers when they are correlated to each other (Tonidandel and LeBreton, 2011), which could be the case for landscape characteristics. Secondly, the relative importance analysis makes no assumptions about the statistical significance of a driver, no matter of the part of the variance that is explained. In the case of the first limitation, alternative methods like dominance analysis (Budescu, 1993; Kleinbauer et al., 2020) and relative weight analysis (Fabbris, 1980; Johnson, 2000; Kleinbauer et al., 2020), have been developed within the framework of other disciplines and for more accurate variance partitioning among correlated drivers. However, it is beyond the scope of this study to apply these alternative methods.

5. Conclusion

In this study, we identified DBH and landscape characteristics as drivers of tree-to-tree variability of sap velocity, the temporal dynamic of their daily relative importance and, for the first time, their species-specificity. Through the relative importance analysis, we confirmed our three hypotheses and concluded that tree-to-tree variability of sap velocity was mainly dependent on DBH for oak and on landscape characteristics for beech and conifers. The temporal dynamics of the relative importance of the drivers was also found to be species-specific and linked to root-related aspects in response to hydro-meteorological conditions. The control of DBH on tree-to-tree variability of sap velocity was twice as important for oak as for beech and conifers trees. In contrast, the relative importance of landscape characteristics on tree-to-tree variability of sap velocity of beech trees was 36% higher than the other tested species. During dry summer months, the daily relative importance of oak's DBH increased to almost 60% to be three times higher than the beech value. This indicates that larger oak trees can access deeper water sources than smaller oaks while the shallower root architecture of beech trees involves that increasing DBH is not enhancing the tree's capacity to explore deeper soils. Higher sap velocities were displayed by beech trees growing in convergent areas probably taking advantage of higher soil moisture sustained from upland converging areas and capillary rises from shallower groundwater. One should remain cautious when interpreting the conifer data, as they were narrowly distributed in the catchment and the variability of our used drivers for tree-to-tree variability in sap velocity were thus narrow too. Nevertheless, our results indicate that the drivers of tree-to-tree variability of sap velocity and the temporal dynamics of their controls are related to the specie-specific characteristics and the hydro-meteorological conditions. These new insights emphasize the critical importance of accounting for DBH and landscape characteristics through a species-specific and temporally dynamic correction factor in further approaches for upscaling of sap velocity data from individual tree to stand-scale.

Declaration of Competing Interest

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

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Supplementary materials

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