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Tree-, stand- and site-specific controls on landscape-scale patterns of transpiration

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Abstract. Transpiration is a key process in the hydrological cycle and a sound understanding and quantification of transpiration and its spatial variability is essential for management decisions as well as for improving the parameterisation of hydrological and soil-vegetation-atmosphere transfer models. For individual trees, transpiration is commonly estimated by measuring sap flow. Besides evaporative demand and water availability, tree-specific characteristics such as species, size or social status control sap flow amounts of individual trees. Within forest stands, properties such as species composition, basal area or stand density additionally affect sap flow, for example via competition mechanisms. Finally, sap flow patterns might also be influenced by landscape-scale characteristics such as geology, slope position or aspect because they affect water and energy availability; however, little is known about the dynamic interplay of these controls.

We studied the relative importance of various tree-, stand- and site-specific characteristics with multiple linear regression models to explain the variability of sap velocity measurements in 61 beech and oak trees, located at 24 sites spread over a 290 km²-catchment in Luxembourg. For each of 132 consecutive days of the growing season of 2014 we modelled the daily sap velocities of these 61 trees and determined the importance of the different predictors. Results indicate that a combination of tree-, stand- and site-specific factors controls sap velocity patterns in the landscape, namely tree species, tree diameter, the stand density, geology and aspect. Compared to these predictors, spatial variability of atmospheric demand and soil moisture explains only a small fraction of the variability in the daily datasets. However, the temporal dynamics of the explanatory power of the tree-specific characteristics, especially species, are correlated to the temporal dynamics of potential evaporation. Thus, transpiration estimates at the landscape scale would benefit from not only considering hydro-meteorological drivers, but also including tree, stand and site characteristics in order to improve the spatial representation of transpiration for hydrological and soil-vegetation-atmosphere transfer models.

1 Introduction

Transpiration is a key process in the hydrological cycle. In vegetated ecosystems, plant-physiological and soil characteristics are the main controls of this water flux towards the atmosphere. The magnitude and dynamics of transpiration in turn affect the system's energy balance, soil water storage, groundwater recharge and stream flow (Barnard et al., 2010; Bond et al., 2002; Fahle and Dietrich, 2014; Moore et al., 2011; Pielke Sr, 2005). Hence, understanding and quantifying transpiration and its landscape-scale variability is essential for management decisions and can help to improve the parameterisation of hydrological and soil-vegetation-atmosphere transfer models.

Methods to measure transpiration span a wide range of scales, from water and CO2-exchange measurements on individual leaves to characterising the convective boundary layer which integrates transpiration at the landscape scale. At the plot and stand-level scale eddy-covariance techniques are applied, whereas at the tree scale measuring xylem sap flow is a common method. Determining transpiration of stands using sap flow entails the challenges of reliably estimating whole-tree water use and applying appropriate empirical relationships when upscaling to stands (Köstner et al., 1998). However, for the investigation of main controls for individual trees' water use sap flow measurements are a suitable tool.

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Atmospheric conditions and water availability are the main temporally variable abiotic controls for sap flow, influencing hourly, daily and yearly dynamics (Bovard et al., 2005; Clausnitzer et al., 2011; Ghimire et al., 2014; Granier et al., 2000; Oren et al., 1996; Schume et al., 2004). However, apart from the general boundary conditions, a set of tree-, stand- or site-specific characteristics also governs the magnitude of sap flow. At similar external conditions, different tree species show contrasts in sap flow due to their respective different hydraulic architecture and coping mechanisms with water stress (Bovard et al., 2005; Gebauer et al., 2012; Oren and Pataki, 2001; Traver et al., 2010). Tree diameter and thus tree size and crown area affects not only absolute sap flow rates, but differences in stem diameter might also entail different radial sap velocity patterns (Bosch et al., 2014; Hölscher et al., 2005; Lüttschwager and Remus, 2007; Vertessy et al., 1995). Within stands, variation in sap velocity can occur because of competition for light and water resources, depending on the species composition (Cienciala et al., 2002; Dalsgaard et al., 2011; Gebauer et al., 2012; Oren and Pataki, 2001; Vincke et al., 2005).

At the landscape scale, site-specific characteristics such as geology, soil type, soil depth or depth to groundwater, elevation, slope position and aspect could potentially control spatial sap flow patterns because of their influence on water and energy availability. Many of these characteristics can be derived from maps and digital elevation models and quantifying their importance is thus especially interesting for modelling purposes requiring landscape-scale transpiration. For instance, the geological setting and associated soil types determine soil water holding capacities, the location of the tree within the landscape's topography can influence its access to groundwater resources and the stand's microclimatic conditions, and differences of aspect also entail variation in energy input (Čermák and Prax, 2001; Vilhar et al., 2005). However, only few studies have focused on the relative strength and possible temporal dynamics of these controls. While the impact of differences in accessible soil volume and groundwater depth on sap flow dynamics has been well described (Angstmann et al., 2013; Čermák and Prax, 2001; Tromp-van Meerveld and McDonnell, 2006), there have been few attempts to empirically use geological or soil units as large-scale proxies for water availability or potentially also for rooting depth limitations (Boer-Euser et al., 2016). Slope position and elevation as site-specific controls of sap flow, which possibly influence soil characteristics and microclimate, have been investigated at a few sites. Bond et al. (2002) report no significant differences in sap flow with slope position for red alders and Douglas fir in Oregon, whereas Kumagai et al. (2007) found larger sap flux density values for cedars in a downslope stand compared to upslope trees, however, this was confounded by differences in tree sizes and stand structure, so that transpiration for the stands did not differ between the two slope positions. In a drought-prone eucalypt forest in Australia, Mitchell et al. (2012) also attribute lower sap flow values at their upslope plot compared to downslope positions to the differences in stand structure (lower basal area and sapwood area) and lower LAI. Otieno et al. (2014) compared two stands of subtropical evergreen forest in China at two different elevations and highlight the structural differences of the two stands, but also did not find differences in stand transpiration. However, differences were found among individual trees and were attributed to tree size as well as social position of the crown. Jung et al. (2014) studied the elevation aspect in deciduous forests on a mountain slope in South Korea at three different elevations, at 450 m, 650 m and 950 a.m.s.l, and found a decrease of total annual canopy transpiration with elevation as a consequence of decreasing length of the growing season, hence of differences in local climate. Sap flux density of individual trees, however, did not vary due to these effects.

While hillslope aspect at least partially controls radiation input, sap flow studies on the influence of aspect are scarce. In a simulation study, Holst et al. (2010) examined water balances for two beech stands on opposite slopes in Southwest Germany and found higher transpiration values for the south-west slope compared to the north-east slope, which the authors explained with the higher evaporative demand and higher precipitation input on that slope. Focusing on limits of atmospheric exchange, Renner et al. (2016) found that stand composition compensated differences in sensitivities of sap velocity to evaporative demand on the south- and north-facing slopes of a valley transect, which led to overall similar transpiration rates on both slopes.

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The reported studies have shown that in addition to the obvious atmospheric and tree-scale physiological controls, site-specific characteristics can influence landscape-scale sap flow patterns. So far this influence has mainly been studied as individual plot comparisons or on a seasonal basis, which does not provide information on the possible short-term, day-to-day changes in the importance of the different controls as a consequence of varying hydro-meteorological conditions. Yet estimating the dynamics of the various controls of sap flow is essential for understanding and predicting spatial patterns of transpiration at the landscape scale.

We wanted to know if we can explain daily landscape-scale patterns of transpiration based on tree-, stand- and site-specific characteristics and how the explanatory power of these characteristics is changing over time. We also wanted to explore if site characteristics become more relevant for landscape scale transpiration patterns under certain conditions and if the combination and strength of dominant controls can be related to hydro-meteorological conditions. Our analysis is based on daily multiple linear regression models for an extensive sap velocity dataset, measured on 61 beech and oak trees on 131 consecutive days in the growing season of 2014, spread over 24 locations in a 290 km²-catchment in Luxemburg.

2 Methods

2.1 Study site

The study site is located in the Attert catchment in western Luxemburg. The catchment covers three geological units (Fig. 1), predominantly Devonian schists of the Ardennes massif in the northwest, Triassic sandy marls, and a small area underlain by Luxemburg sandstone (Jurassic) on the southern catchment border (Martínez-Carreras et al., 2012). These different geological units gave rise to soils with different water retention properties. The soils on schists developed to haplic Cambisols, the soils on marls can be classified as different types of Stagnosols depending on their clay content of 20-60 % and the sandy textures on the Luxembourg sandstone gave rise to Arenosols. The soils were classified according to the WRB classification system (IUSS Working Group WRB, 2006) and described further by Sprenger et al. (2016). Plant available water was determined from mean water retention curves (using water tensions at 60hPa and $10^{4.2}$ hPa) based on 120 soil samples (Jackisch, 2015), amounting to 0.30 m³/m³ for Cambisols and Stagnosols and 0.25 m³/m³ for the Arenosols. However, the access to water is not only determined by the soil type. For example the Cambisols in the schist are very shallow and exhibit high rock content, however, there are cracks filled with soil material in the underlying schist which could provide water for tree roots. The Stagnosols in the marls area are very clayey in the subsurface, probably limiting plant-available water resources and root penetration in these layers. We observed maximum rooting depths, averaged for each soil type, of 68 cm for the Cambisols, 90 cm for the Stagnosols and 98 cm for the Arenosols (Sprenger et al., 2016). Mean annual precipitation of the study area is approximately 850 mm (Pfister et al., 2000). Land use varies from mainly pasture and agriculture in the marls area, mainly forests in the sandstone to a mixture of agriculture and pasture on the plateaus and forests on the steep slopes of the schist area.

The catchment is the focus area of the CAOS (Catchments As Organised Systems) research unit which investigates landscape-scale structures, patterns and interactions in hydrological processes for model development (Zehe et al., 2014). A monitoring network of 45 sensor clusters was installed in 2012/2013, covering the different geological units, the land use types deciduous forest and pasture, different slope positions and aspects. Measurements at the individual sites include meteorological parameters such as air temperature and humidity (Campbell CS215) and solar radiation (Apogee Pyranometer SP110) as well as soil moisture (Decagon 5TE) at three depths and three locations at each site. Sap flow is monitored with East30 Sap Flow Sensors at all 29 forest sites.

The forests covered by the monitoring network mainly consist of mixed deciduous stands with European beech (*Fagus sylvatica* L.), pedunculate and sessile oak (*Quercus robur* L. and *Q. petraea* (Mattuschka) Liebl., common hornbeam

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(*Carpinus betulus* L.) and a few maples (*Acer pseudoplatanus* L.) and alders (*Alnus glutinosa* (L.) Gaertn.). However, in this study only the most common species, beech and oaks are considered.

Figure 1: Map of the study site, the Attert catchment in Luxemburg.

2.2 Sap velocity measurements

The sites in the forest were characterised with a forest inventory on 20 x 20 m² plots, recording stem numbers, diameter at breast height (DBH) and basal area (BA) for all trees with a circumference of more than 4 cm, and tree height for a representative subset of the trees in the stand. Tree heights were measured for a representative subset of the trees in the stand; heights were gauged roughly as the canopy tops were not always clearly visible and probably reflect rather the social status of the trees than the precise height. Four trees per site were selected for sap flow sensor installation. The trees were chosen to roughly represent the stand structure at the site but also enable comparison to other sites where possible. Sap flow sensors were installed at breast height on the north-facing side of the stem and protected with a reflective cover to minimise the effects of radiation-induced changes in stem temperatures. After removing the bark, holes for the sensors were drilled using a drilling guide to ensure parallel installation of the sensor needles. The sensors, manufactured by East30Sensors in Washington, US, use the heat ratio method with a central heater needle and a thermistor needle upstream and downstream of the heater. Each thermistor needle contains three thermistors, at 5, 18 and 30 mm depth in the wood. Sap velocities (V_{sap} in m s^{-1}) at each of these locations are calculated from the temperatures measured at the corresponding thermistor pairs according to Eq. (1) (equations after Campbell et al., 1991):

$$V_{sap} = \frac{2k}{C_w(r_u+r_d)}\, ln\left(\frac{\Delta T_u}{\Delta T_d}\right) \quad (1),$$

where k is the thermal conductivity of the sapwood, set to 0.5 W m^{-1} K^{-1}, C_w is the specific heat capacity of water (J m^{-3} K^{-1}), r is the distance (m) from the heater needle to the thermistor needle (in our case 6 mm) and ΔT is the temperature difference (K) before heating and 60 seconds after the heat pulse. Subscripts u and d stand for location upstream and downstream of the heater.

We correct these values to account for wounding of the xylem tissue caused by the drilling according to the numerical model solutions for the heat pulse velocity method suggested by Burgess et al. (2001):

$$V_c = bV_{sap} + cV_{sap}^2 + dV_{sap}^3 \quad (2),$$

where V_c is the corrected sap velocity (m s^{-1}) and b, c and d are correction coefficients; for our 2 mm-wounds we use b = 1.8558, c = -0.0018 s m^{-1}, d = 0.0003 s^2 m^{-2} (Burgess et al., 2001). Upscaling sap velocities to whole-tree water use is prone to uncertainty because of the azimuthal variation in sap velocities, differences in sap wood depth and sap wood conductivity with depth. We decided to avoid these additional uncertainties and use daytime sap velocity, averaged over a 12-hour window from 8am to 8pm, as comparable measurement among trees of different species, admitting that the tree water fluxes will differ from this value mainly due to size and species-specific sap wood characteristics. Our sensors provide measurements at three depths within the sapwood. Since radial sap velocity profiles differ between species and tree sizes, and because the sensors were not always ideally installed in the sapwood, we use the maximum value of these three depths as a reliable measure for our analyses.

2.3 Auxiliary variables: estimating potential evaporation and water availability

The main environmental limitations to sap flow are the atmospheric conditions as the driving gradient for transpiration and the water supply to the trees. We assess these influences by using a thermodynamically derived measure for potential

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evaporation E_{pot} which has been recently developed by Kleidon & Renner (2013) as well as the soil moisture observations at each sites as a measure of water availability.

Soil moisture was measured in three profiles per site at 10 cm, 30 cm and 50 cm depth. For our analyses we took the average across all depths and profiles to estimate the average soil moisture in the top 60 cm for each site.

E_{pot} was calculated as follows (Kleidon & Renner, 2013):

$$E_{pot} = \frac{1}{\lambda}\frac{s}{s+\gamma}\frac{R_{sn}}{2} \qquad (3)$$

where $\lambda = 2.5 \cdot 10^6$ Jkg^{-1} is the latent heat of vaporisation, s is an empirical approximation of the slope of the saturation vapour pressure curve, calculated as $s = s(T) = 6.11 \cdot 5417 \cdot T^{-2} \cdot e^{19.83-5417/T}$, with the temperature T (K). The psychrometric constant was approximated as $\gamma \approx 65$ PaK^{-1}, and R_{sn} (W/m²) is absorbed solar radiation. The air temperature was taken from the measurements within the stands at the forest sites. This gives room for some error, as the below-canopy temperature will differ from the above-canopy temperature. However, the temperature does not have very strong leverage in Eq. (3) and we would expect even larger errors if we were to use air temperature from nearby grassland sites because of the differences in microclimate and energy balance for the different land covers. Solar radiation features more prominently in the equation and therefore needs careful estimation. We use an approach deriving the above-canopy radiation from the digital elevation model of the catchment, using the GRASS GIS package r.sun. This method corrects for latitude, day of year and topography and corresponds well with the measured radiation at the pasture sites for cloudless days. Dividing the r.sun-estimated radiation values with the measured radiation values at each pasture site yields correction factors for actual cloud conditions for each day. We apply this cloud correction to the r.sun values for the forests, using the pasture site that is closest to the respective forest sites. These latitude-, topography- and cloud-corrected radiation estimates are then used for calculating E_{pot}.

We also use the radiation measurements within and outside the stands to determine the period when the canopy is fully developed and only use this period for our analyses. For the year 2014 this period lasted from the 11th of May to the 20th of September amounting to 132 days.

2.4 Data analysis

We selected a dataset of continuous sap flow measurements from 61 trees located at 24 of the altogether 29 forest sites in the CAOS dataset. Each of the monitored trees is associated with tree-, stand- and site-specific properties. Tree-specific properties are the species, diameter at breast height (DBH) and tree height, whereas the stands are characterised by the measurements undertaken in the forest inventory, namely basal area (BA) and median DBH of the stand as well as the number of stems recorded on the inventory plot. Additionally, there are several landscape attributes which can be associated with the monitored trees such as their position within one of the three geological units, their location on a slope and the aspect of that slope. These attributes can be considered as proxies for associated soil properties and energy availability influencing water availability and potential evaporation. The site characteristics and species enter the linear models as categorical variables. An overview of the dataset in relation to all tree-, stand- and site-specific characteristics is shown in Table 1, whereby the class “Plain” for slope position refer to the slopes with less than 5° slope angle, which are located in the marls area. The class “Flat” for aspect includes the same sites, however additionally less steep downslope parts of four slopes in the schist and sandstone areas. Both classes probably describe landscape positions with shallower depth to groundwater than the other sites.

Table 1: Overview of the properties of the sap flow tree dataset. Abbreviations are DBH for diameter at breast height, BA for basal area of the stand.

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Potential evaporation and water availability are usually considered as main external dynamic controls of sap flow, so we examined their importance for the temporal variability in sap velocity by correlating the time series of sap velocity with E_{pot} and soil moisture, using the Spearman rank correlation. However, we were interested primarily in the spatial variability of sap velocity as a way to determine influences on transpiration patterns at the landscape scale. We assessed this by examining the spatially distributed dataset of daily-averaged sap velocity of the 61 trees, for each of the 132 days of our study period.

In a first step, we examined the individual influence of the different tree-, stand- and site-specific controls listed in Table 1 and of the external controls soil moisture and E_{pot} at the respective forest sites, on sap velocity, averaged across the study period, separately for each tree. This first analysis ignored the multivariate interaction to get a simplified overview of the data, hence effects seen in these comparisons should not be over-interpreted because the controls are considered individually and in reality most likely have a combined effect. For the categorical variables (species, geology, slope position and aspect) we also looked at possible temporal changes of differences in sap velocity between the categories by testing daily datasets with the Mann-Whitney-U or the Kruskal-Wallis test, for variables consisting of three or two categories, respectively, to a significance level of $\alpha = 0.05$.

The multidimensional effect of all tree-, stand- and site-specific influences was then analysed with multiple linear regression models separately for each day. The response variable for each of the 132 daily models was the log-transformed daily sap velocity of each tree, because the logarithmic values corresponded better to a normal distribution. The linear regression model can be expressed as

$$\ln(V_{sap}) = \beta_0 + \sum_{i=1}^{n} \beta_i x_i, \qquad (4)$$

with n predictors ($x_0, \ldots x_i$), and the regression coefficients ($\beta_0, \ldots \beta_i$) estimated to obtain an optimum fit.

Before applying the regression models we checked the predictors for collinearity by determining the correlation matrix. There was only one combination of predictors with a Spearman rank correlation coefficient above the widely employed critical value of collinearity, $|\rho| > 0.7$ (Dormann et al., 2008; Tannenberger et al., 2010), the number of stems and median diameter of the stand, at $\rho = -0.73$. The effects of this correlation on the linear models was tested by running the models for both the original set of predictors and again, leaving out number of stems. As the results did not differ with respect to the variance contributions of the different predictors, we kept all predictors in the final analysis. We also did not include interaction terms in the final models because after testing with various interactions, these did not contribute much to the explained variance.

Although a step-wise simplification of the models using the Akaike information criterion led to a higher percentage of explained variance by the models, we refrained from using this simplification in order to keep the model structures similar for each day to allow comparability of the temporal, day-to-day changes in predictor importance. This relative importance of the predictors for explaining the observed sap flow variance was assessed using the approach of Grömping (2007) which is based on a proportional marginal variance decomposition that is more stable and robust than calculating the partial correlation coefficient. To check for overfitting, we performed a comparison between the residual standard error (RSE) of the original models and the root mean square error (RMSE) of a 10-fold cross validation (Fig. 2). Both error measures differ only marginally and are largest when sap velocities are small. These are the days when the linear model generally fails to explain the variance in the datasets. For days with high sap velocities, the small errors as well as the small difference between RSE and RSME show that the models are not overfitted. Additionally, Figure 2 shows that limiting the analysis to the period of fully developed canopy excludes periods of larger errors at the beginning and end of the season.

Figure 2: Comparison of residual standard error of the original linear models (LM-RSE) and the root mean square error of a 10-fold cross validation (CV-RMSE), in relation to mean and standard deviation of daily sap velocities (Vsap). The dashed lines depict the analysis period with a fully developed canopy which we determined from radiation analyses as described in section 2.3.

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We analysed the temporal dynamics of the variance contributions of the individual predictors and the category sums for tree-, stand- and site-specific characteristics. We also correlated these time series to catchment-averaged time series of soil moisture and E_{pot} as indicators for general atmospheric demand and water availability, using the Spearman rank correlation. All statistical analyses were carried out in the language and environment R (R Development Core Team, 2014).

3 Results

3.1 Controls of temporal dynamics of sap velocity

Correlations of time series of sap velocity for each tree with E_{pot} and soil moisture yielded high positive and significant (α= 0.05) Spearman rank correlations for E_{pot}, but correlations to soil moisture were slightly negative and very weak (Fig. 3).

Figure 3: Histograms of temporal correlations between (a) E_{pot} and (b) soil moisture at each site with sap velocity for the 61 trees in the dataset. The small numbers in grey on top of the bars indicate how many of the correlations in the specific group are significant.

3.2 Controls of daily spatial patterns of sap velocity

A first simplified overview of the influence of the various factors on sap velocity patterns was derived from plotting sap velocity, averaged over the entire study period for each tree, against the factors or their respective categories (Fig. 4). Obviously, this graph neglects the combined influence of the interplay of all these factors, but yields a first overview of the data and possible relations. For example, the difference between higher sap velocities in beech trees compared to oaks can be seen as well as a possible positive relation between sap velocity and DBH or tree height. In the category Aspect, the boxplots show a difference between higher sap velocities on north-facing slopes compared to south-facing ones, with trees located in plains having somewhat intermediate velocities.

Figure 4: Individual influence of each factor on sap velocity means for each tree over the entire study period.

The categorical factors were assessed in more detail looking at temporal changes in sap velocity differences. Statistical tests (Mann-Whitney-U for two and Kruskal-Wallis for three categories, α= 0.05) applied to the sap velocity datasets for each day for the example of the categorical factors geology, species, slope position and aspect showed significant differences (Fig..5). There is in particular a significant difference between south- and north-facing slopes and between beech and oak trees for most days of the dataset (Fig. 5), providing a first indication of the importance of both tree- and site-specific influences. In contrast, there were only few days with differences in geology or slope positions.

Figure 5: Influence of (a) geology, (b) species, (c) slope position and (d) aspect on daily sap velocity patterns. Lines show average dynamics of each category. Asterisks at the bottom of the panels indicate significant differences for each day according to Mann-Whitney-U or Kruskal-Wallis tests at α= 0.05, for differences between the two or three categories, respectively.

In a more comprehensive approach we assessed the combined effect of the various tree-, stand- and site-specific influences on sap velocity with the help of multiple linear regression generating 132 daily models describing the spatial patterns. The total explained variance for the models ranged from 20%, on days when the models fail to explain the spatial variability in the dataset, to 72%, which constitutes fairly good explanatory power (Fig. 6). The total explained variance correlated

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strongly with catchment averages of sap velocity (Pearson's r = 0.84, p < 0.001), especially at sap velocities > 7 cm h^{-1} (Fig. 7). Spatial variability of sap velocity in the catchment, expressed as standard deviation of the daily values for the 61 trees, also increased with increasing mean sap velocity (Pearson's r = 0.98, p < 0.001; Fig. 7). The consistent model structure showed that the change in the proportion of explained variance over time was different for the various predictors (Fig. 6). Mean values for the tree-specific predictors across the 132 daily models were 9% of the explained variance for species, 9% for DBH, 4% for tree height. Characteristics of the stand yielded 1% for BA, 1% for median DBH, 4% for number of stems, and the site-specific predictors amounted to 2% for slope position, 4% for geology and 6% for aspect. The external dynamic controls of sap flow, E_{pot} and soil moisture, explained 7% and 3% of the variance in daily sap velocity patterns, respectively. The contribution of the different predictors to the overall explained variance of the linear models varied strongly from day to day. On days when average and spatial variability of sap velocity was low the models performed badly. There were some predictors which showed larger fluctuations, for example species, compared to more constant contributions from predictors like the number of stems or DBH (Fig. 6).

Figure 6: Explained variance of daily linear models of spatial sap velocity patterns: 132 daily models from 61 trees at 24 sites.

Figure 7: (a) Explained variance of the linear models in relation to mean sap velocities for all 132 days of the study period and (b) standard deviation of sap velocity depending on mean sap velocities for those 132 days.

3.3 Temporal dynamics of predictor importance for daily spatial sap velocity patterns

Comparing the dynamics of the cumulated variance contributions for the groups of tree-, stand- and site-specific predictors to the catchment-average dynamics of E_{pot} and soil moisture (Fig. 8) shows that the stand- and site-specific predictors' contributions stayed relatively constant apart from the days when the model failed, whereas the tree-specific predictors varied to a greater extent. Already visual comparison hints at a link between fluctuations of tree-specific influences and potential evaporation (E_{pot}), but not soil moisture.

Figure 8: (a) Explained variance of the daily linear models, separated according to tree-, stand- and site-specific predictors. (b) Catchment average of soil moisture and potential evaporation E_{pot}.

The Spearman rank correlations of the predictors' explained variance with E_{pot} and soil moisture, listed in Table 2, also confirm that changes in species influence were strongly linked to changes in E_{pot}, with a significant correlation (at α= 0.05) of r = 0.81. Further weaker but significant correlations were detected between E_{pot} and number of stems at r = 0.50, aspect at r = 0.67 and soil moisture at 0.55, respectively. Summarised into categories, the influence of tree-specific predictors strongly correlated with E_{pot} (r = 0.86); similarly, there was a strong correlation of the overall explained variance with E_{pot} (r = 0.84). Some of the correlations with soil moisture were significant, however, they were mostly weak at |r| <= 0.37.

Table 2: Spearman rank correlation between the time series of the different predictors' explained variance and the time series of potential evaporation (E_{pot}) and soil moisture. Values in bold italics are significant correlations (at α= 0.05).

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4 Discussion

4.1 Controls of temporal dynamics of sap velocity

The strong positive temporal correlation of sap velocity and E_{pot} confirms the well-known role of E_{pot} as a main external driver for transpiration (Bovard et al., 2005; Clausnitzer et al., 2011; Granier et al., 2000; Jonard et al., 2011). Soil moisture on the other hand did not affect the temporal dynamics of sap velocity in a similar way. One reason for this weak relation could be that water is not a limiting factor for transpiration in this landscape, or at least not during the observed time period. For example, in the schist area of the catchment, anecdotal evidence given by forest wardens suggests that beech trees on south-facing slopes are indeed water-stressed during dry, hot summer months, although in our data we did not see a limitation of sap velocity for the beech trees. A different explanation for the lack of correlation is that soil moisture in the top 60 cm of the soil profile is simply not a sufficiently good proxy for water availability. In the soils of the schist there might be additional water resources stored in the weathered bedrock or the schist fractures which could be accessible to roots, as these can exceed the average maximum rooting depth in the soil (only 68 cm, estimated from power drill cores; Sprenger et al., 2016). In the deep sandstone soils with average maximum observed rooting depths of 98 cm (Sprenger et al., 2016) roots could also reach deeper, exploiting larger soil volumes or possibly tapping groundwater. The mostly flat marl areas exhibit shallow groundwater tables, so water limitation is unlikely for longer periods during the year. Thus, although water availability is an important boundary condition for transpiration, soil moisture measurements for the top 60 cm might not be an appropriate proxy, and including available information on groundwater levels or also soil moisture in deeper layers could be useful in that regard. However, successful explanation of temporal transpiration dynamics at individual points is only one necessary aspect for estimating and modelling transpiration. If the goal is to represent hydrological processes at the landscape scale, the spatial representation of transpiration and the identification of the main controls of spatial transpiration patterns are similarly important.

4.2 Controls on daily spatial patterns of sap velocity

Even from the simplified univariate assessment the relation of characteristics such as species, DBH and aspect to spatial sap velocity patterns is visible. In the more comprehensive approach applying multiple linear regression models to the daily sap velocity datasets, the combined effect of tree-, stand- and site-specific predictors surpasses by far the explanatory power of the boundary conditions, as E_{pot} and soil moisture (Fig. 6) together explained only around 10% of the variance in sap flow patterns. The explained variance of the tree-specific characteristics amounted to 22 % averaged over the 132 models. Mechanisms underlying the differences in sap flow related to species, tree diameter and height have been studied in great detail in the field of tree physiology. The species contrast in our case consists of higher sap velocities for beech, as beech shows physiological advantages in transpiration efficiency and outperforms the oaks in sufficiently moist conditions (Hölscher et al., 2005). Tree height contrasts probably reflect the differences in social status, larger, dominant trees reaching higher transpiration values than understorey trees. That larger trees, both higher and with larger DBH, exhibit higher sap velocities is likely due to their associated larger canopy and root volume, ensuring on the one hand the exposure of the leaves to the atmospheric gradient, on the other hand having access to a larger soil volume and potential water supply (Bolte et al., 2004; Nadezhdina and Čermák, 2003).

The stand density, expressed by the number of stems, explained on average 4% of the variance in the daily models. Decreasing sap velocities with increasing stand density hints at the competition for light and resources among individual trees (Cienciala et al., 2002; Dalsgaard et al., 2011; Gebauer et al., 2012; Oren and Pataki, 2001; Vincke et al., 2005). However, in our study, the site-specific predictors we included because they might be deduced from readily available distributed datasets, were more important than stand characteristics to explain daily sap velocity patterns. The average

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combined explained variance of these predictors of 12% showed that considering these predictors can help to improve estimates of landscape-scale transpiration variability.

Landscape characteristics such as topography and geology will control sap velocity patterns of otherwise homogeneous forests because they influence spatial patterns of either water or energy availability. Topography is primarily controlling radiation input, and to some extent water availability through depth to groundwater and also soil characteristics, while geology is mainly controlling root distribution and water availability because it determines the depth to bedrock and depth to groundwater as well as soil type and soil depth. The effect of soil depth on transpiration for example has been shown by Tromp-van Meerveld and McDonnell (2006) for soils of the same soil type on the Panola hillslope, and the contrasts between different geological units in the Attert basin are likely to be even more pronounced. The soils in the schist area are very shallow, restricting rooting depth to an average of 68 cm and together with moderate plant-available water (Jackisch, 2015) even lessened by the high rock content possibly leading to smaller sap velocities in the schist compared to the sandstone or marls. These differences in soil depth and water retention characteristics on different geological units affect landscape-scale hydrological processes which can be seen in the differences in runoff generation between schist, marls and sandstone areas in the Attert catchment (van den Bos et al., 2006; Wrede et al., 2015). Depth to groundwater and the geological setting of the storage control tree access to these storage systems and favour species with adapted rooting systems (Dalsgaard et al., 2011), thus introducing a landscape-scale effect on sap flow.

The variation in aspect was mainly due to the south-facing slopes having smaller sap velocities compared to north-facing slopes. As energy input is larger on south-facing slopes, these slopes might be more prone to water limitation (Holst et al., 2010), especially when combined with other limiting factors such as the shallow soils in the schist area which holds a large proportion of the south-facing slopes in our dataset. Additionally there might be a sampling effect because the south-facing slopes in our dataset support more oak-dominated forests which have generally lower sap velocities compared to beech trees. Slope position did not play a major role in explaining spatial sap velocity patterns. A reason for this lack of explanatory power could be that the information within this variable is partly also included in aspect because both the aspect category "flat" and the slope position categories "plain" and "downslope" suggest sites which are close to groundwater resources.

In a way, the site-specific influences of geology, aspect and slope position can be regarded as proxies for underlying characteristics of water availability and thus affect landscape-scale transpiration patterns.

4.3 Temporal dynamics of predictor importance for explaining the daily spatial sap velocity patterns

Understanding the feedback of these patterns with hydrological processes requires assessing the temporal dynamics of site- and tree-specific controls on transpiration at characteristic time scales, for example on a seasonal or daily basis. Our analyses indicate that landscape-scale sap velocity patterns are governed by tree-, stand- and site-specific characteristics, but temporal shifts in these controls depend on hydro-meteorological conditions, especially potential evaporation. And whereas the direct influence of variability in hydro-meteorological conditions on sap flow has been highlighted in many studies (Bovard et al., 2005; Clausnitzer et al., 2011; Granier et al., 2000; Jonard et al., 2011), the link between these conditions and spatial patterns of sap flow and their controls is still not well understood. Additionally, most studies which include site-specific controls focus on a seasonal basis or undertake plot comparisons.

The temporal dynamics of the different predictor categories showed contrasting dependency on potential evaporation. While the stand- and site-specific predictors remained fairly constant in their total explained variance, the tree-specific predictors, and here predominantly species, were temporally variable and their explained variance strongly correlated to the dynamics of E_{pot}. The species effect in this context is the contrast between oaks which can only respond to increasing E_{pot} up to a certain threshold (Fig. 5) and beech trees, when not water limited, can reach higher sap velocities.

A second predictor with considerable positive correlation with E_{pot} is aspect. As the south-facing slopes seem to be water-limited for some amount of time the differences in sap velocities between north- and south-facing slopes will increase with

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increasing E_{pot}. Lastly, the overall explained variance of our linear models also correlates with E_{pot}. Obviously the predictors we consider in our study are useful to describe large differences in sap velocity patterns, when high potential evaporation entails contrasts in for example species or aspect. At lower values of potential evaporation, the spatial variability of sap velocity is less pronounced and not primarily determined by the predictors included in our models. .

Finally, it is important to note that we are focusing on sap velocities in this study because of precautions in sensor installation in 2014, leading to non-ideal sensor depths preventing the reliable calculation of sap flow volumes. Additionally, scaling up from sap velocities to tree and stand transpiration entails uncertainties in the representativeness of sap velocity estimation due to circumferential variability, wounding effects and the challenge of determining sap velocity depth profiles and sapwood area. For some of the abovementioned predictor effects the contrasts will be even more pronounced when considering actual sap flow instead of sap velocities. For example, the species effect shows higher velocities for beech compared to oaks. As the active sapwood of oaks is limited to the outermost annuli whereas for larger beeches it can easily reach a depth of 7 cm (Gebauer et al., 2008), the difference in actual transported water and hence transpiration would be even more pronounced. On the other hand, the aspect effect might be not as strong as seen in the sap velocities. Renner et al. (2016) showed in a recent study considering only a few of the sites that differences in sap velocity due to aspect might be countered by variation in the relative sap wood area for the respective stands. The effects we see in our sap velocity analyses should be studied further and compared to patterns in up-scaled stand transpiration estimates to comprehensively understand the dynamics of landscape-scale patterns of transpiration and their effect on hydrological processes.

5 Conclusions

A combination of tree-, stand- and site-specific characteristics influenced the observed daily spatial sap velocity patterns. The temporal dynamics of the relative importance of especially the tree-specific controls were closely linked to the dynamics of potential evaporation.

Our results suggest that landscape-scale transpiration estimates for management or modelling purposes could benefit from including not only the obvious influence of the potential evaporation and water availability but also the spatial patterns of sap flow resulting from the interplay of tree-, stand- and site-specific controls at the landscape scale. Similar to resolving agricultural areas according to crops at the field scale, one could represent the spatial structure in forest transpiration resulting from patterns in water and energy availability due to site characteristics such as geology or topography, in forests that appear homogenous in terms of species and stand structure. Additionally, identifying phases of varying importance of the different predictors, and their dependence on E_{pot}, could help modellers decide when to best include site-specific characteristics to describe spatial patterns of transpiration in models and when a classification according to species and stands might be more appropriate. Thus the spatial representation of transpiration in hydrological models could be attempted in a temporally dynamic way.

The way forward from these findings should be to address the well-known challenge of analysing whole-tree water use instead of sap velocities and to attempt the upscaling from trees to stands to obtain a dataset of actual stand transpiration with optimised sensor installation. This data could then be used as a reference for soil-vegetation-atmosphere transfer and hydrological models. Furthermore, including information from forest inventories and digital elevation models in the multiple regression of sap flow datasets and identifying the dominant controls and temporal dynamics could consequently enable the regionalisation and prediction of transpiration processes at the landscape scale using these readily available distributed datasets.

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Table 1: Overview of the properties of the sap flow tree dataset. Abbreviations are DBH for diameter at breast height, BA for basal area of the stand.

Property	Group	Class (and # of trees in each class)	Value (25/50/75 percentile)
Species	Tree-specific	Beech (39), Oak (22)	
DBH (cm)	Tree-specific		34/ 46/ 63
Height (m)	Tree-specific		24/29/ 34
BA (m^2 ha^{-1})	Stand-specific		27/40/54
Median DBH (cm)	Stand-specific		5/14/28
# of stems	Stand-specific		20/24/43
Geology	Site-specific	Marls (13), Sandstone (22), Schist (26)	
Slope position	Site-specific	Upslope (41), Downslope (9), Plain (11)	
Aspect	Site-specific	North (17), South(29), Flat (15)	

Table 2: Spearman rank correlation between the time series of the different predictors' explained variance and the time series of potential evaporation (E_{pot}) and soil moisture. Values in bold italics are significant correlations (at α= 0.05).

Predictor	E_{pot}	Soil moisture
Species	***0.81***	***-0.30***
DBH	***0.32***	-0.14
Height	0.11	-0.05
BA	-0.15	-0.05
Median DBH	***0.44***	-0.16
# of stems	***0.50***	***-0.35***
Slope	***-0.32***	***0.21***
Geology	0.04	***0.18***
Aspect	***0.67***	***-0.37***
E_{pot}	***0.34***	***-0.18***
Soil moisture	***0.55***	***-0.30***
Tree-specific	***0.86***	***-0.34***
Stand-specific	***0.28***	***-0.33***
Site-specific	***0.35***	-0.14
Total exp. var.	***0.84***	***-0.38***

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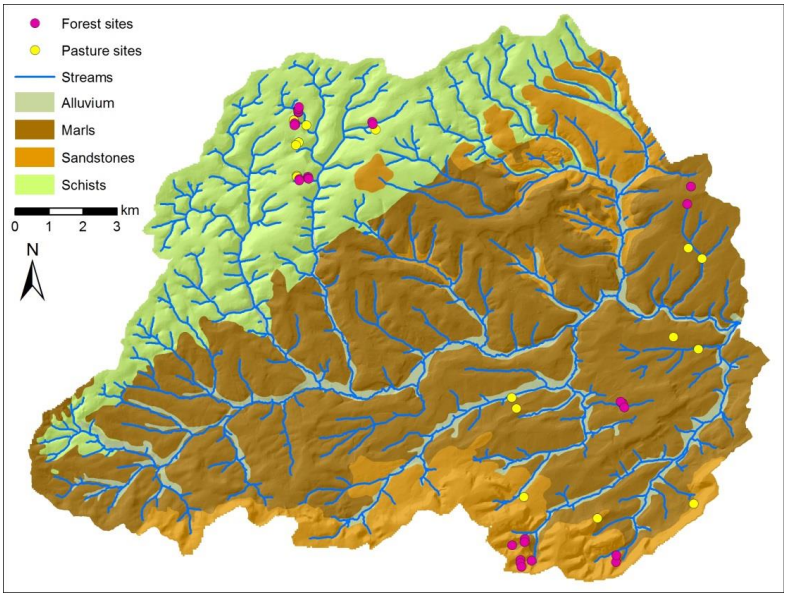

Figure 1: Map of the study site, the Attert catchment in Luxembourg.

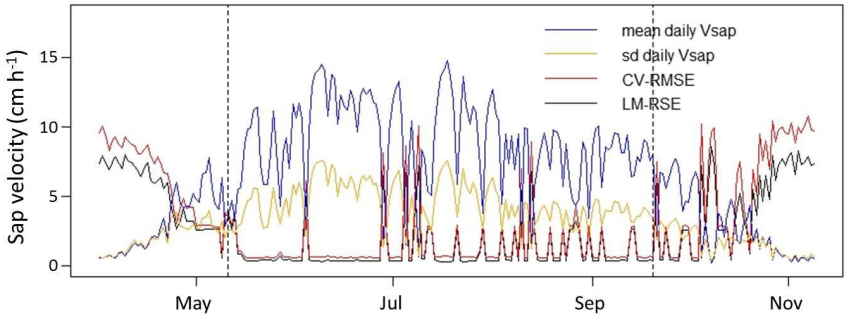

Figure 2: Comparison of residual standard error of the original linear models (LM-RSE) and the root mean square error of a 10-fold cross validation (CV-RMSE), in relation to mean and standard deviation of daily sap velocities (Vsap). The dashed lines depict the analysis period with a fully developed canopy which we determined from radiation analyses as described in section 2.3.

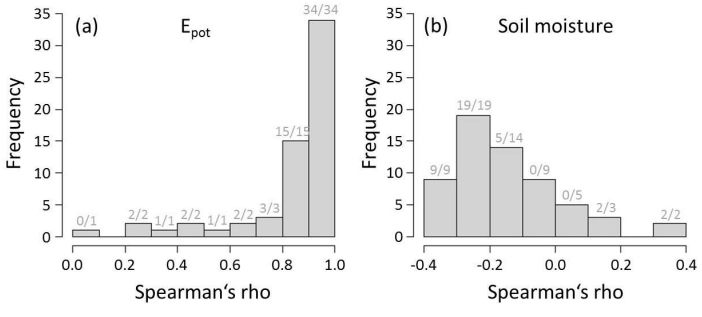

Figure 3: Histograms of temporal correlations between (a) E_{pot} and (b) soil moisture at each site with sap velocity for the 61 trees in the dataset. The small numbers in grey on top of the bars indicate how many of the correlations in the specific group are significant.

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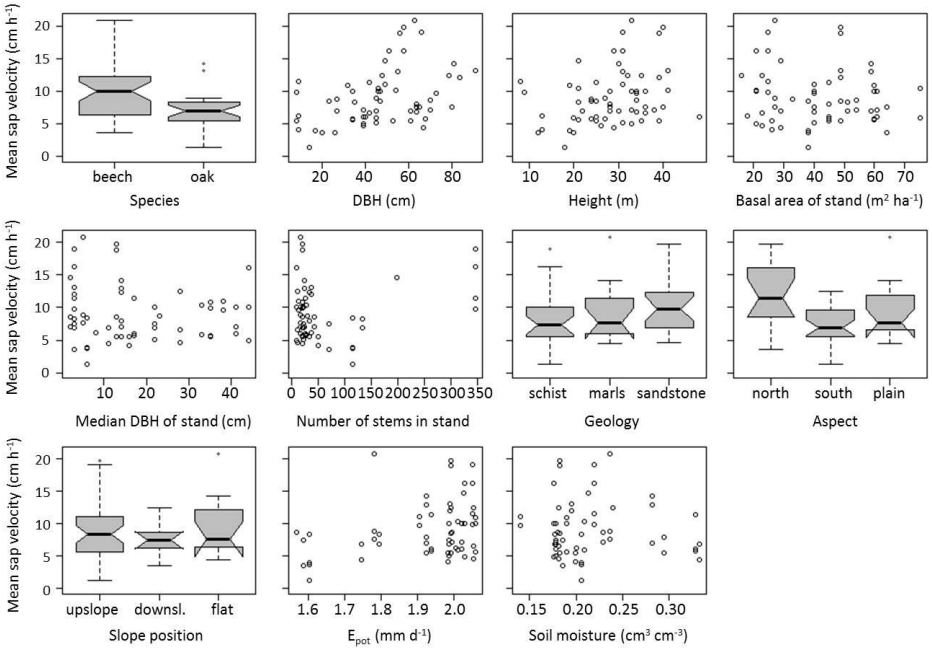

Figure 4: Individual influence of each factor on sap velocity means for each tree over the entire study period.

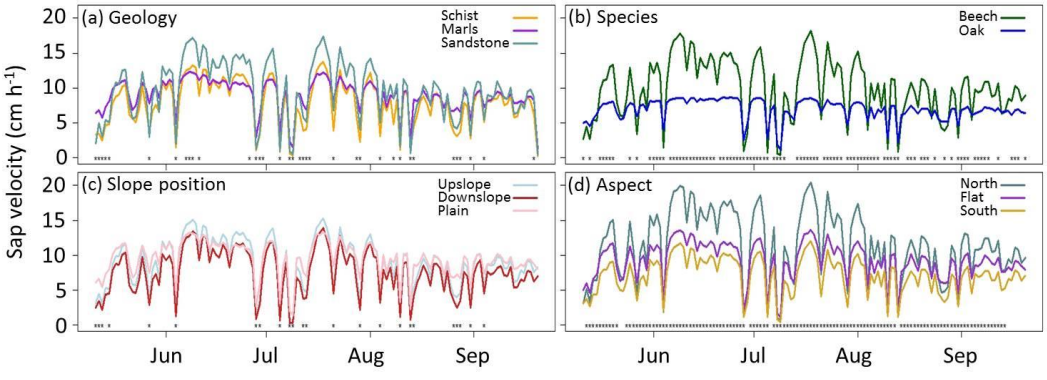

Figure 5: Influence of (a) geology, (b) species, (c) slope position and (d) aspect on daily sap velocity patterns. Lines show average dynamics of each category. Asterisks at the bottom of the panels indicate significant differences for each day according to Mann-Whitney-U or Kruskal-Wallis tests at α= 0.05, for differences between the two or three categories, respectively.

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Figure 6: Explained variance of daily linear models of spatial sap velocity patterns: 132 daily models from 61 trees at 24 sites.

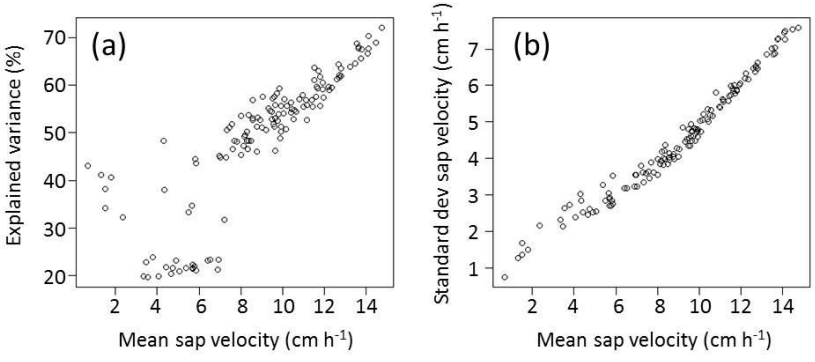

Figure 7: (a) Explained variance of the linear models in relation to mean sap velocities for all 132 days of the study period and (b) standard deviation of sap velocity depending on mean sap velocities for those 132 days.

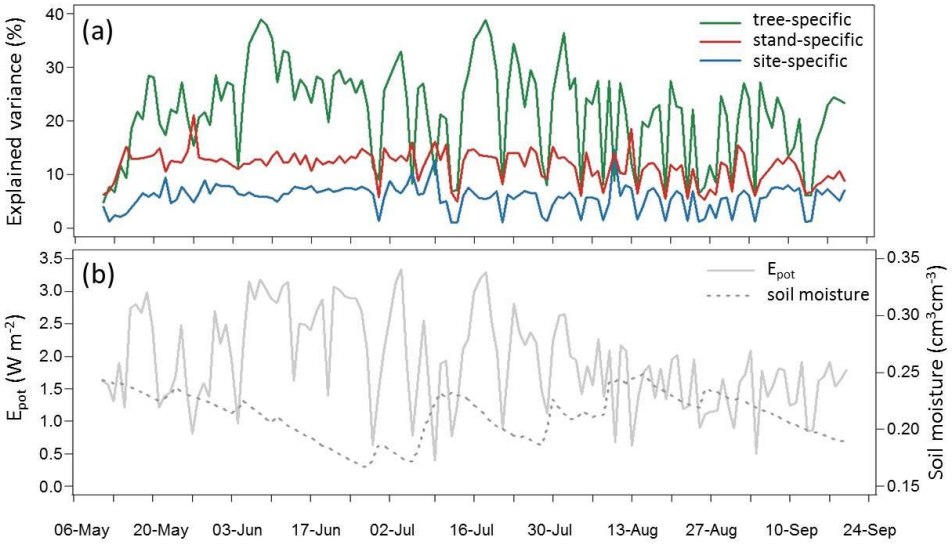

Figure 8: (a) Explained variance of the daily linear models, separated according to tree-, stand- and site-specific predictors. (b) Catchment average of soil moisture and potential evaporation E_{pot}.