Göttingen Centre for Biodiversity
and Ecology

Biodiversity and Ecology Series B
Volume 4

Tobias Gebauer

Water turnover in species-rich and species-poor deciduous forests: xylem sap flow and canopy transpiration

GEORG-AUGUST-UNIVERSITÄT
GÖTTINGEN

Published as volume 4 in the Series B as part of the
„Biodiversity and Ecology Series“
Göttingen Centre for Biodiversity and Ecology 2010

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Georg-August-Universität Göttingen
2010

Bibliographische Information der Deutschen Nationalbibliothek

Die Deutsche Nationalbibliothek verzeichnet diese Publikation in der Deutschen Nationalbibliographie; detaillierte bibliographische Daten sind im Internet über <http://dnb.ddb.de> abrufbar.

Editor Dr. Dirk Gansert
Göttingen Centre for Biodiversity and Ecology,
Georg-August-Universität Göttingen, www.biodiversitaet.gwdg.de

Dissertation zur Erlangung des Doktorgrades der
Naturwissenschaftlichen Fakultäten der
Georg-August-Universität Göttingen
vorgelegt von Tobias Gebauer

Referent: Prof. Dr. Christoph Leuschner
Korreferent: Prof. Dr. Dirk Hölscher

Anschrift des Autors
Tobias Gebauer
e-mail: tgebaue@gwdg.de

Typesetting and layout: Tobias Gebauer
Cover image: Tobias Gebauer

DOI: http://dx.doi.org/10.3249/webdoc-2324
urn:nbn:de:gbv:7-webdoc-2324-4

GÖTTINGER ZENTRUM
FÜR BIODIVERSITÄTSFORSCHUNG UND ÖKOLOGIE

– GÖTTINGEN CENTRE FOR BIODIVERSITY AND ECOLOGY –

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Diplom-Agraringenieur

Tobias Gebauer

aus
Walsrode

Göttingen, Dezember, 2008

Referent: Prof. Dr. Christoph Leuschner

Korreferent: Prof. Dr. Dirk Hölscher

Tag der mündlichen Prüfung: 20.02.2009

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Summary

The importance of plant diversity for ecosystem functioning has been one of the central research topics in ecology during the past 15 years. While much research has focused on the role of species diversity for plant biomass and plant productivity in grasslands, much less is known how tree species diversity and tree identity influence ecosystem processes. The amount of water consumed by forest stands through transpiration is an important ecosystem function which determines the water loss through deep seepage and groundwater yields. Until recently, the dependence of canopy transpiration on tree species diversity or functional diversity and tree species identity has not systematically been investigated.

Starting in 2005, stem xylem sap flux measurements using the constant-heating method after Granier were conducted synchronously in the Hainich National Park in six temperate broad-leaved forest stands differing in tree diversity (1 to > 5 tree species). Hydraulic architecture characterization such as radial sap flux density patterns and the extent of the hydro-active xylem was investigated to reduce the bias during up-scaling procedures and to characterize different functional groups and their influence in water consumption performance. Therefore, xylem flux sensors were installed in various depths of the xylem. Additional dye injection into the transpiration stream and wood coring gave a picture of the extent of the sapwood. The response of leaf conductance, stem xylem sap flux, leaf water potentials and hydraulic conductance of the tree species to changing vapor pressure deficits and soil water contents were used to classify the tree species in order of their drought stress response.

In all investigated species except the diffuse-porous beech (*Fagus sylvatica* L.) and ring-porous ash (*Fraxinus excelsior* L.), sap flux density peaked at a depth of 1 to 4 cm beneath the cambium, revealing a hump-shaped curve with species-specific slopes. Beech and ash reached maximum sap flux densities immediately beneath the cambium in the youngest annual growth rings. Experiments with dyes showed that the hydro-active sapwood occupied 70 to 90% of the stem cross-sectional area in mature trees of diffuse-porous species, whereas it occupied only about 21% in ring-porous ash. Dendrochronological analyses indicated that vessels in the older sapwood may remain functional for 100 years or more in diffuse-porous species, and for up to 27 years in ring-porous ash.

In summer 2005 with average rainfall, canopy transpiration was by 50 % higher in DL3 than in DL1 and DL2 stands (158 vs. 97 and 101 mm). In contrast, in the relative dry summer 2006, all stands had similar canopy transpiration rates (128 to 139 mm). Water consumption

per crown projection area differed up to 5-fold among the 5 species, which was probably due to contrasting sapwood/crown area ratios. However, species differences in canopy transpiration were similarly large on a sapwood area basis, mostly reflecting species differences in hydraulic architecture and leaf conductance regulation. Single-factor and multiple regression analyses were used to identify key factors controlling canopy transpiration of individual species and of the stands differing in diversity. The five co-occurring tree species of the mixed stands differed considerably. The four diffuse-porous species exhibited higher leaf area-related transpiration rates ($E_{\mathrm{L})}$ than ring-porous *Fraxinus excelsior*. Vapor pressure deficit (vpd) was the most influential variable explaining 75-87 % of the variation in E_{L} on the stand level, while the influence of soil moisture (θ) was small (mostly < 5 %) or absent. Stands with low or high tree species diversity were not different with respect to its environmental control of canopy transpiration. On the species level, *F. excelsior* differed from the other species in being less vpd controlled, while θ had a larger influence on E_{L}. Species diversity (Shannon diversity index *H*') had a negligible effect on canopy transpiration at the species and stand levels with the exception of *F. excelsior*. The sizes of sapwood area and leaf area as morphological attributes, and the hydraulic conductance in the root-to-leaf pathway and leaf conductance as physiological traits were identified to be main factors determining different water consumption rates of the tree species.

The five analyzed species can be arranged with regard to their drought sensitivity at the leaf or canopy level in the sequence *Fraxinus excelsior* < *Carpinus betulus* < *Tilia cordata* < *Acer pseudoplatanus* < *Fagus sylvatica*, if the following tree responses are used as criteria of a low sensitivity: (i) maintenance of predawn leaf water potentials (Ψ_{pd}) at a high level during drought periods, (ii) high leaf conductances in periods with not too dry soils, and (iii) reduction of sap flux only moderately upon soil drought. With an increase in the frequency and intensity of summer heat waves, as predicted for parts of Central Europe, species like ash and hornbeam will have an advantage over beech, which dominates many forests today. Species with high water consumption (e.g. *Tilia*) may exhaust soil water reserves early in summer, thereby increasing drought stress in dry years, and possibly reducing ecosystem stability in mixed forests.

Canopy transpiration may increase or decrease with increased tree species diversity, but a universal trend is unlikely to exist, because complementarity in root water uptake in mixed stands is not generally observed. Tree species identity and the related specific functional traits are more important for forest water consumption than is tree diversity as such.

Chapter

1

General Introduction

1.1 Biodiversity, productivity, and ecosystem functioning

Biodiversity is the variety of live on earth. It includes all genes, species, ecosystems, and the ecological processes of which they are part (Gaston 2001). The Millennium Ecosystem Assessment (2005) clearly stated that changes in biodiversity due to human activities were more rapid in the past 50 years than at any time in human history, and is predicted to continue, or to accelerate. Depending on the scenario and regions used in the models, the drivers of global change causing biodiversity loss and changes in ecosystem services are either steady and show no evidence of declining over time, or are increasing in intensity (Pimm et al. 1995). The most important direct drivers of biodiversity loss and changes in ecosystem services are habitat fragmentation, climate change, invasive alien species, overexploitation, pollution, and loss of resilience against calamities, pests, and sudden dramatic weather events (e.g. storms, blizzards, heavy rainfall, flooding) (Millennium Ecosystem Assessment 2005).

Biodiversity affects key processes and functions of terrestrial ecosystems such as biomass production, nutrient and water cycling, and soil formation and retention (Hooper et al. 2005, Loreau et al. 2001, 2002) - all of which regulate and guarantee supporting services and goods. In experimental ecosystems that have reduced levels of biodiversity, plant productivity, nutrient retention, and resistance to invasions and diseases are sometimes related to increasing species richness. However, this is in contrast to natural ecosystems, where these direct effects of increasing species richness are usually overridden by the effects of climate, resource availability, or disturbance regime (Millennium Ecosystem Assessment 2005).

Ecosystem functioning, and hence, ecosystem services, is at any given moment in time strongly influenced by the ecological characteristics of the most abundant species. Several studies have demonstrated that not only a high species richness is of importance, but also how species are joined in functional groups (e.g. Körner 1994, Tilman et al. 2007a, Naeem and Wright 2003) and whether keystone species are present (e.g. Bond 1994, Hooper et al. 2005). Thus, conserving or restoring the composition of biological communities, rather than simply maximizing species numbers, could be essential to maintain ecosystem services.

Experimental studies on diversity-ecosystem functioning relationships are a hot topic since some years. Whereas most research on the role of species diversity for plant biomass and plant productivity has focused on grasslands and old-field communities (Cardinale et al. 2007, Flombaum and Sala 2008, Hector et al. 1999, Loreau et al. 2001, 2002, Tilman et al. 2001, van Ruijven 2005), less is known about the functional role of tree diversity in forest ecosystems (Scherer-Lorenzen et al. 2005). Especially in grasslands (e.g. BIODEPTH) positive correlations have been found between increasing species diversity and increasing ecosystem functioning (e.g. productivity, evapotranspiration, nutrient cycling, food web interactions) (Loreau and Hector 2001, Hector et al. 1999, Tilman et al. 1996, 1997b). In Central Europe and North America, large areas of natural forests have been replaced by monocultures of coniferous and broad-leaved tree species, resulting in a reduction in tree species and structural forest diversity (Knoke et al. 2005). On the other hand, in some parts of Central Europe, forestry is recently moving from monospecific plantations to the establishment of mixed stands (Knoke et al. 2005). These large-scale anthropogenic alterations in forest diversity may have profound consequences for energy and matter fluxes and the diversity of other organism groups, but are currently only poorly understood.

1.2 Climate changes the water cycle

Atmospheric concentration of the greenhouse gas carbon dioxide has increased from 270 ppm in the 1700s to over 383 ppm at the present time (2008) at Mauna Loa Observatory, Hawaii (Raupach et al. 2007, Tans 2008). Other greenhouse gases like methane, dinitrous oxide, and chlorofluorocarbons have also increased in concentration in the earth’s atmosphere due to human activities (Gates 1990). As a result, an increase in mean annual air temperature has been observed during the industrialization stage, and further increase is predicted. Best-estimate projections from models predict for different emission scenarios an increase of 1.8°C (range from 1.1°C to 2.9°C) to 4.0°C (range from 2.4°C to 6.4°C) in mean annual temperature till 2090/99 (Bates et al. 2008, IPCC 2007a). As a further consequence of global warming, an increase in the frequency and magnitude of summer droughts is predicted for Central Europe. In particular sub-continental and continental regions may be strongly affected (Breda et al., 2006; Meehl and Tebaldi, 2004; Schär et al., 2004, Wetherald and Manabe 2002, IPCC 2007a).

Increased severity of drought conditions in several regions (Europe, parts of Latin America) during the growing season is projected to accompany increasing summer temperatures as precipitation declines, with widespread effects on net ecosystem productivity in forests (Bates et al. 2008). Global climate projections using multi-model ensembles show increases in global mean water vapor concentration, evaporation, and precipitation over the 21st century (Bates et al. 2008). A high spatial and temporal variability is predicted. General increases of precipitation in the areas of regional tropical precipitation maxima (e.g. in the monsoon regimes and the tropical Pacific regions) and at high latitude, and general decreases in the sub-tropics have been shown by various models (Bates et al. 2008).

The changes in hydrology that are projected for the 21st century will impact biodiversity on every continent. Impacts on species have already been detected in most regions of the world (IPCC 2007 a, 2007b). Approximately 80% of the changes in biodiversity all over the world were consistent with observed temperature change, but it should be recognized that temperature can also exert its influence on species performance and survival through changes in moisture availability (IPCC 2007b).

Forest ecosystems occupy roughly 4 trillion ha of land, an area comparable to the extension of the earth covered by crops and pastures. Among these, about 200 million ha are used for commercial forestry production globally (FAO, 2003). Forest ecosystems contribute to the regional water cycle, with large potential effects of land-use changes on local and regional climates (Harding 1992, Lean et al., 1996). Forest ecosystems are sensitive to climatic change (e.g. Kirschbaum and Fischlin, 1996, Sala et al., 2000), with temperature-limited biomes being sensitive to global warming (e.g. northern latitudes), and water-limited biomes being sensitive to increasing levels of drought (e.g. Central Europe) (Bates et al. 2008).

Although responses to recent climate change are difficult to identify in managed systems, due to multiple non-climate driving forces and the existence of adaptation, some effects have been detected in forests and a few agricultural systems. A significant advance in phenology has been observed for agricultural crops and forest trees over large parts of the Northern hemisphere (Bates et al. 2008). The expansion of the growing season has contributed to an observed increase in forest production in many regions, whereas extreme warm and dry conditions in certain years have already caused a significantly reduced forest productivity in Central Europe (Breda et al. 2006, Ciais et al. 2005, Granier et al. 2007, IPCC 2007b). Effects of drought on forests include mortality due to disease, drought stress and pests; a reduction in resilience; and biotic feedbacks that vary from site to site (Breda et al. 2006, IPCC 2007b).

Evaporative demand has been modeled to increase worldwide (IPCC 2007a and IPCC 2007b). The water-holding capacity of the atmosphere increases with increasing temperatures. As a result, atmospheric water vapor deficit increases, and so does the evaporation rate

(Trenberth et al. 2003). Changes in evapotranspiration over land are controlled by changes in precipitation and radiative forcing, and these changes also impact the water balance (IPCC 2007b). Changes in hydrology can affect species in a variety of ways, but the most completely understood processes are those that link moisture availability with intrinsic thresholds that govern metabolic and reproductive processes (Burkett et al. 2005). In temperate regions, the predicted rise in air temperature will induce a larger evaporative demand and a decrease in available soil water due to heat waves in summer. If these are not met by adequate water resources in the soil, concurrent drought stress will develop (Rennenberg et al. 2006). Despite substantial water losses and a marked deterioration of plant water status, it is expected that tree species confronted with water stress will respond with structural or physiological adjustment in order to maintain the integrity of the hydraulic system and to enable carbon assimilation (Breda et al., 2006). The consequences of these changes for European temperate tree species and forests are still not sufficiently understood (Bovard et al., 2005, Breda et al. 2006).

Verheyen et al. 2008 showed in a synthetic grassland study that plant species diversity influences the stand transpiration due to species differing in their functional traits such as biomass production, niche partitioning and complementarity in resource use. A corresponding study in forests differing in tree diversity is lacking.

1.3 The Graduate School 1086 / The Hainich Tree Diversity Matrix

The present investigation was conducted in the Hainich National Park, Thuringia, Central Germany, within the framework of the interdisciplinary Research Training Group ("Graduiertenkolleg") 1086 "The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests". Here, we investigated the relationship between biodiversity and productivity, biogeochemical cycles, and biotic interactions in a forest ecosystem. With the same aim, the Hainich Tree Diversity Matrix (Leuschner et al. 2008) was established in 2005. The Hainich National Park was founded in 1997, and since more than 40 years the park area was subjected to extensive management only, since it was part of a military training site. The Hainich National Park is an area of temperate deciduous forest, which contains a natural gradient in tree species diversity that has developed under similar soil and climate conditions. The Research Training Group combines the expertise of 10 different institutes in the faculties of agronomy, biology and forestry joined together in the Goettingen Centre of Biodiversity and Ecology (GCBE) and the Forschungszentrum Waldökosysteme (FZW). The Max-Planck-Institute for Biogeochemistry in Jena is integrated in the project, bringing additional expertise and knowledge in the age determination and sequestration of soil carbon. The umbrella project aims to clarify the main hypotheses:

- Increased tree diversity correlates with higher diversity of other organism groups or guilds; the slope of this relationship differs with group or guild.
- Increased tree diversity has no directed effect to stand leaf area and annual sum of plant production.
- Carbon fixation and turnover are stronger influenced by functional traits of tree species than by tree species richness.
- Increased tree diversity increases the utilization of nutrients due to niche complementarity (partitioning), so that loss of nutrients with seepage will be reduced.
- Transpiration and seepage out of the rooting zone are more influenced by functional traits of tree species than by tree species richness.
- Increased tree diversity increases the spatial heterogeneity of matter turnover.
- Increased tree diversity reduces the temporal variability of organic matter turnover during exposure to natural disturbances (increasing resilience).
- Increased tree diversity reduces herbivore pressure and increases the abundance of natural enemies in the canopy.

1.4 Water turnover in species-rich and species-poor temperate broad-leaved forests: xylem sap flow and canopy transpiration

Water turnover is an important ecosystem function. The partitioning of precipitation into transpiration, interception and seepage depends on the structure of the vegetation. The vegetation cover determines not only the quantity of seepage, but also the quality.

Investigations in Central Europe of the water balance of mixed forest stands (beech-spruce stands) showed significant species effects on the soil hydrology (Schume et al. 2003, Armbruster et al. 2004) and stand transpiration (Köstner 2001). Measurements of water fluxes in canopies of broad-leaved forests, for example beech-oak stands, support the hypothesis that tree species composition could be an important factor in forest hydrology (Leuschner 1993, Leuschner and Rode 1999, Köstner 2001). This was also indicated by studies in hardwood forests in North America (Wullschleger et al. 1998, 2001, Pataki et al. 2000, Ewers et al. 2002, Wullschleger and Hanson 2006). Neither so far, studies investigating the impact of tree diversity for canopy transpiration and seepage have not been systematically carried out neither in temperate nor in tropical forests.

Canopy transpiration of forests has been found to be influenced by several stand structural attributes, among them stem density (Breda et al. 1995, Schipka et al. 2005), leaf area index (Oren et al. 1999, Granier et al. 2000, Vincke et al. 2005), stand age and tree height (Köstner et al. 1998, 2002, Mencuccini and Grace 1996, Vertessy et al. 1994, 1995, 1997, Roberts 2000, Ryan et al. 2000, Schäfer et al. 2000, Zimmermann et al. 2000, Köstner 2001, Ewers et al. 2005). A key trait with a large influence on canopy transpiration is the cumulative sapwood area of the stand (Wullschleger et al. 1998, 2001, Oren and Pataki 2001), which is related to stem density and other stand structural attributes. Not only these structural attributes could have an influence on the transpiration of forests, but also the leaf conductance (or canopy conductance), and the boundary layer conductance. Boundary layer conductances are assumed to have similar values in species-poor and species-rich forest stands, if stand structural attributes like tree height and stem density are similar. Porometer measurements in tree crowns of mixed stands showed that the leaf conductances between co-existing tree species could vary up to two- or three-fold (Kaufmann 1985, Pallardy et al. 1995, Leuschner et al. 2001). In previous studies in a mixed stand in the Hainich, Hölscher (2004) and Hölscher et al. (2005) could reveal species-specific patterns in xylem sap fluxes, leaf conductances, $\delta\ ^{13}C$ signatures and mineral element contents of the leaves, and photosynthesis. However, it remains unclear whether these species-specific and stand structural attributes have a significant influence on canopy transpiration in stands differing in tree diversity.

This thesis-project focused on the study of water turnover in forest stands differing in tree diversity.

The main objectives are, at the tree species level,

to

(1) Determine the patterns of radial xylem flux density change in trees with different functional xylem anatomy (diffuse-porous vs. ring-porous) (chapter 3);

(2) Compare the size of the hydroactive xylem between ring-porous and diffuse-porous tree species by relating it to stem diameter (chapter 3);

(3) Compare five tree species with respect to the vapor pressure deficit (vpd) sensitivity of leaf conductance (chapter 4);

(4) Quantify the influence of vpd and soil matrix potential on xylem sap flux and leaf conductance (chapter 4), and

(5) Analyze the response of leaf water potential in five tree species to decreasing soil matrix potential (chapter 4).

At the stand level, the following working hypotheses were adopted:

(6) Canopy transpiration does not change significantly along the diversity gradient (chapter 5), but

(7) Tree species identity exerts a major influence on stand transpiration (chapter 5);

(8) The functional attributes of different tree species are more influential on stand canopy transpiration than is tree species diversity (chapter 6), and

(9) Differences in the degree of atmospheric vs. edaphic control of tree water consumption are related to the xylem anatomy of the species (diffuse- vs. ring-porous) (chapter 6).

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Chapter

2

Materials & Methods

(an overview)

2.1 Study site description

The Hainich National Park is a mixed temperate broad-leaved forest dominated by European beech (*Fagus sylvatica* L.). Linden (*Tilia cordata* Mill. and *T. platyphyllos* Scop.), common ash (*Fraxinus excelsior* L.), European hornbeam (*Carpinus betulus* L.) and different maple species (*Acer pseudoplatanus* L., *Acer platanoides* L. and *Acer campestre* L.) co-occurring in different densities; further deciduous tree species like elm (*Ulmus glabra* L.), oak (*Quercus* sp.), cherry (*Prunus avium* L.) and service tree (*Sorbus torminalis* L.) are interspersed in lower numbers within the forest.

The climate of the area is sub-continental (Klaus and Reisinger 1995) with a mean annual precipitation of 590 mm and 7.5 °C as mean annual air temperature (1973-2004, Deutscher Wetterdienst).

The soils in the study region developed from loess which is underlain by Triassic limestone (Muschelkalk). The Pleistocene loess cover varies between 60 and 120 cm in thickness. The soil texture in the upper 30 cm of the mineral soil is characterized by high silt (~ 75 %) and clay contents (17-31 %) and a low sand content (< 4 %) with a mean bulk density of 1.24 g cm^{-3}. The dominant soil type is a luvisol showing stagnant properties during winter and spring and strongly drying out during summer. The C/N ratio in the organic layers varied from 28.7 to 31.1 and in the upper 30 cm of the mineral soil from 11.8 to 13.7 whereas the C/N ratio decreases with increasing soil depth (Guckland et al., in press). The terrain is slightly inclined (between 3.0 and 4.2 %) with a mean exposition of 315° (Leuschner et al. 2008).

The Hainich Tree Diversity Matrix (see Leuschner et al. 2008) was established within this small-scale mosaic of species-poor and species-rich forest patches growing under almost homogenous climate and soil conditions (see above). Within the Research Training Group 1086, permanent forest plots of 50 m x 50 m were established in 2005. These plots are located in the north-eastern part of the National Park between 295 and 355 m a.s.l. (51°04’ N, 10°30’ E) within an area of less than 25 km^2. The plots included stands of different tree diversities:

- Level of low diversity: monospecific European beech-dominated stands
- Level of moderate diversity: mixed stands of European beech, common ash and linden
- Level of high diversity: species-rich plots composed by the tree species found in the second level and, in addition, European hornbeam and maple species.

In the following, the three diversity levels are referred to as diversity level 1 (DL1), 2 (DL2) and 3 (DL3). The mean tree diversity measured by the Shannon diversity index for the DLs were, 0.19, 1.00 and 1.47 based on the crown area of the species in the stands, and 0.27, 0.98 and 1.21, if the stem density of the species in the stands is considered. Each diversity level was represented by four plot replications (indicated by lower case letters: a, b, c, d).

Photo: V. Horna

Photo: T. Gebauer

Figure 1. Monospecific beech stand (DL1a) prior to leaf flush (left) in spring and with fully developed leaf cover (right) in summer 2005.

Photo: V. Horna

Photo: T. Gebauer

Figure 2. Moderately diverse stand (DL2c) composed of beech, linden and ash prior to leaf flush (left) in spring and fully developed leaf cover (right) in summer 2005.

Photo: V. Horna

Photo: T. Gebauer

Figure 3. Highly diverse stand (DL3a) composed of beech, linden, ash, hornbeam and maple prior to leaf flush (left) in spring and fully developed leaf cover (right) in summer 2005.

A total of 44 trees from at least 5 species along the diversity gradient were continuously monitored for xylem flux density between June 2005 and October 2006. Measurements of xylem flux density were expanded during 2006 to cover a second set of plots (DL1c, DL2a and DL3c) and 37 trees were additionally equipped with Granier sensors on these plots. During this second year, the measuring campaign in summer was focused on species differences in radial xylem flux density patterns in the sapwood (Chapter 3) and on the investigation of diurnal and seasonal variations in leaf water status using steady-state porometry and pressure chamber measurements (Chapter 4).

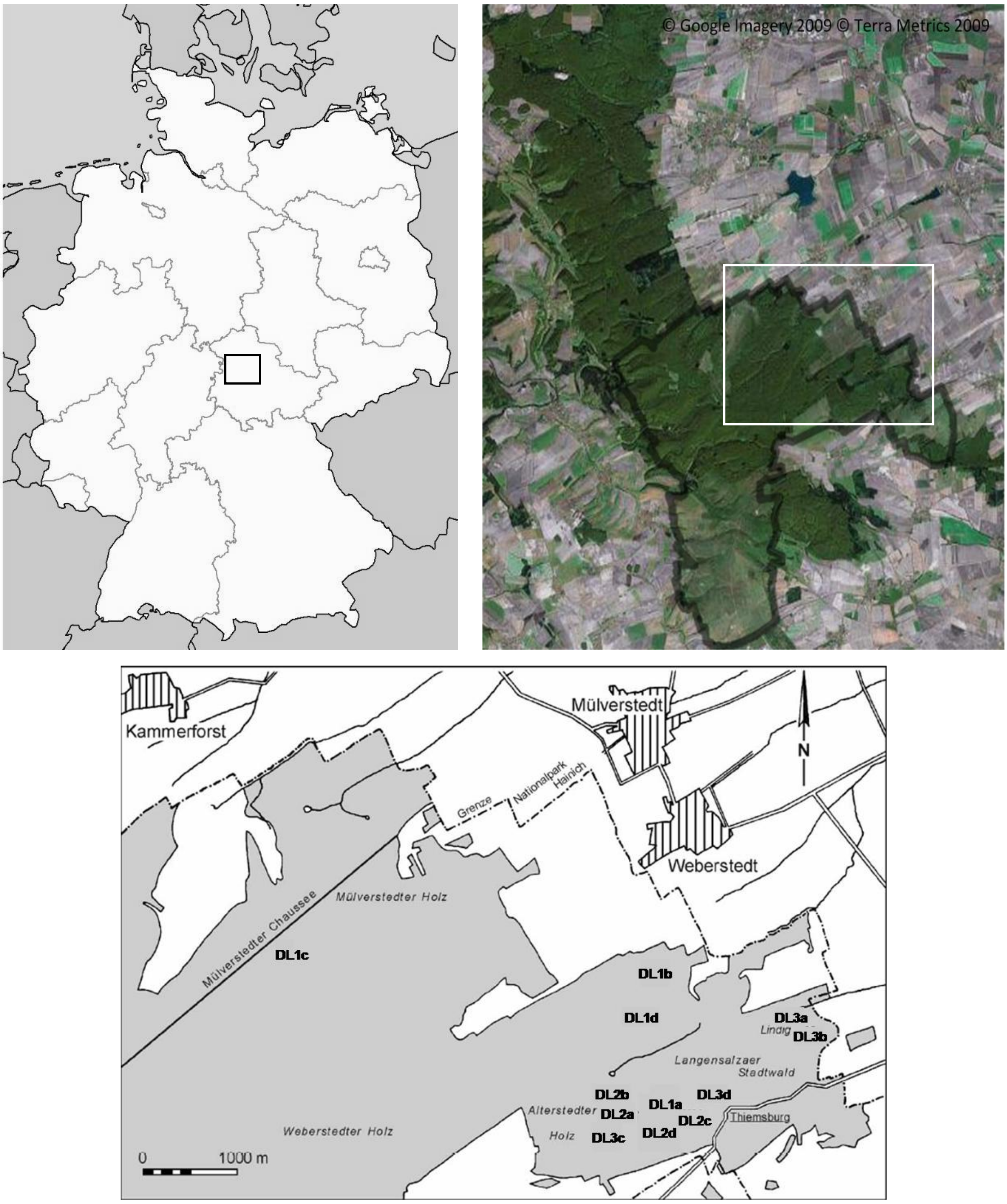


Figure 4. The upper maps show the location of the Hainich region in Germany (left, black square) and the area of the Hainich National Park (right, grey shaded). The white square indicates the detail of the lower map: the location of the twelve 50 m x 50 m study plots in the north-eastern part of the Hainich National Park (— · — · -), Thuringia, Central Germany. Satellite image is under copyright of Google (Imagery) and Terra Metrics (2009).

2.2 Sap flow

In this study, the heat-dissipation method after Granier was used. The Granier method has been particularly popular among tree physiologists and forest hydrologists owing to its simplicity, high degree of accuracy and reliability, and relatively low cost (Lu et al. 2004).

When sap flux density is analyzed across the entire sapwood depth, some studies showed uniform and others non-uniform sap flux densities (Cermak et al. 2004, Granier et al. 2000, James et al. 2002, Lu et al. 2004, Nadezhdina et al. 2002, Phillips et al. 1996). The Granier method is sensitive enough to evaluate the changes of radial sap flux density patterns of tree species with different xylem anatomy and it is thus well suited for quantitative determinations of forest transpiration.

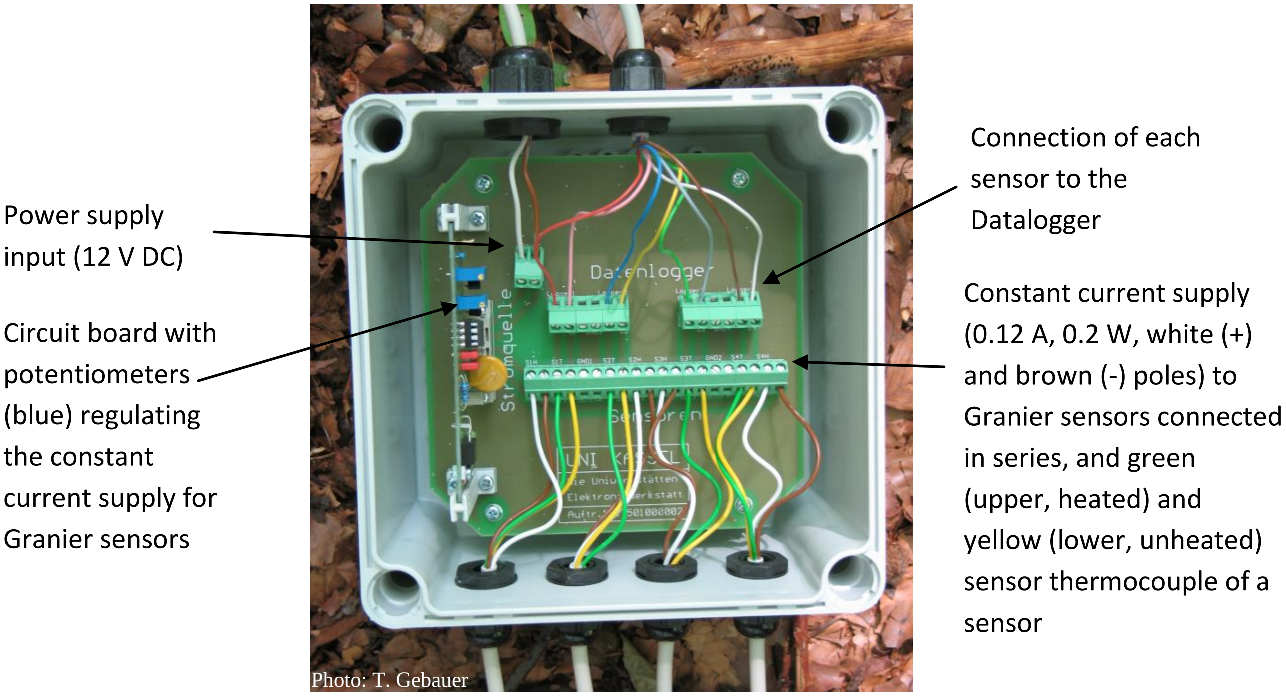
The system consists of two sensor probes each containing a heating element. The sensing part of a probe is a thermocouple placed amidst of the heating spiral. Both probes are inserted radially into the trunk, 10 to 15 cm apart from each other, into pre-installed aluminum tubes at 1.3 m trunk height (Figure 5).


Photo: V. Horna

Photo: V. Horna

Figure 5. Sensor insertion into the trunk of beech trees. Sensors were placed at 1.3 m height above the trunk base and 10-15 cm apart from each other (left) (upper (red): heated, lower (blue): unheated sensor on opposite, northern and southern directions (right).

It was found most practicable to place the two sensors 1-2 mm deeper than the depth of the cambium to avoid heat losses to the bark and surrounding air. In the centre of each heating element, a T-type copper-constantan thermocouple element is placed measuring the voltage difference between the upper (heated) and the lower (unheated) probe. The upper probe is continuously heated at a constant current (0.12 A) and power (0.2 W). Constant power supply is provided by power supply boxes with a 12 Volt DC input (manufactured by University of Kassel, see Figure 6).



Power supply input (12 V DC)

Circuit board with potentiometers (blue) regulating the constant current supply for Granier sensors

Connection of each sensor to the Datalogger

Constant current supply (0.12 A, 0.2 W, white (+) and brown (-) poles) to Granier sensors connected in series, and green (upper, heated) and yellow (lower, unheated) sensor thermocouple of a sensor

Photo: T. Gebauer

Figure 6. Power supply box manufactured for the control of constant current supply (0.12 A, 0.2 W) to four Granier sensors (manufactured by University of Kassel).

The lower probe is unheated and measures the current temperature of the wood tissue, operating as a reference probe. Heat of the upper probe dissipates into the wood till the heat uptake capacity of the tissue is nearly saturated and heat exchange is low. The main cause of a temperature difference is the heat transport via the xylem sap flow. The measured temperature difference permits to calculate the xylem sap flux density based on Granier's empirical calibration of the sensors for several ring- and diffuse-porous tree species and standardized materials with given sap flux densities (Granier 1985, 1987, and pers. comm.).

The heating spiral was typically 20-mm long when used in diffuse-porous tree species, and 10-mm long in the case of ring-porous *Fraxinus excelsior*, where the hydro-active sapwood depth is expected to be smaller. An insertion into non-hydroactive sapwood would need a correction in the calculation of sap flux density which takes into account the proportion of the hydroactive to non-hydroactive xylem along the heating spiral (Clearwater et al. 1999).

Because the northern side of the trunk guarantees the lowest influence of temperature gradients by sun flecks, one sensor pair was always placed on this side. A second pair of sensors was installed on the southern side of the trunk, to check for changes in sap flux density with trunk side. All probes were covered with an insulating polystyrene mat with a reflecting foil and a transparent plastic foil to minimize the influence of sun flecks and air temperature gradients over the sensors. Nevertheless, our tests with different covers showed no significant change in sap flux density when sensors were only insulated with the polystyrene mat and protected against rain and stem flow with duct tape and silicon/liquid pitch (Figure 7, data not shown).


Photo: T. Gebauer

Photo: T. Gebauer

Figure 7. Two methods of insulation as protection of sensor measurements against wind, rain and sun flecks in linden trees. Left: Polystyrene mat, fixed with duct tape and silicone. Right: Reflecting aluminum foil and transparent plastic foil over the polystyrene mat.

To analyze the change in sap flux density with increasing xylem depth, additional Granier sensors were placed in different sapwood depths. The set up of energy input and type of insulation was the same as for the installation of a single sensor pair. To avoid interference between the thermal fields of the different depths, the sensors should be placed between the northern and western direction of the trunk in proximity of the outermost probe (Figure 8).

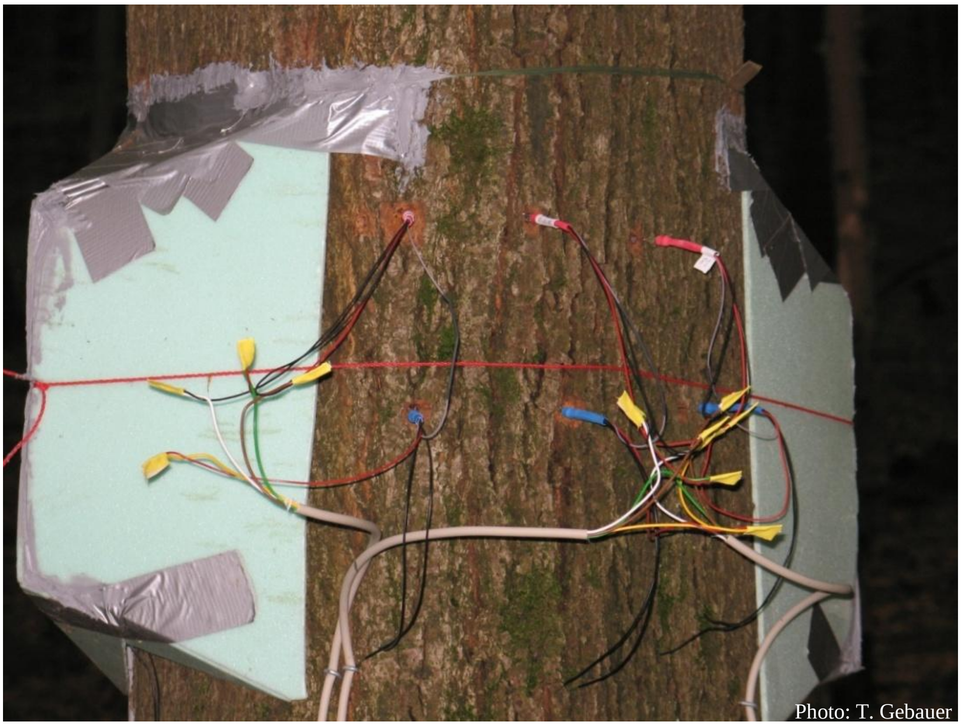


Photo: T. Gebauer

Figure 8. Installation of additional Granier sensors at different sides of the stem and in deeper xylem depths (2-4, 4-6 and 6-8 cm) between the northern and western side of the trunk.

These radial measurements of xylem flux density are needed to determine the area of hydro-active xylem and the variation in xylem flux density with sapwood depth. Both factors are important to estimate the total amount of water transported in the xylem of a tree and to more accurately scale transpiration from the tree level to the forest stand level (for further information see chapters 3 and 4).

2.3 Canopy access

Studying forest canopies requires techniques of accessing these hidden compartments of a tree, where the bulk of energy and gas exchange between plant and atmosphere occurs. Many researchers are using cranes, balloons, walkways, towers and climbing ropes to get access to tree canopies. In the Hainich National Park, the use of a mobile hydraulic canopy lifter DENKA LIFT DL30 (DENKA LIFT A/S, Holbaek, Denmark) enabled access to the upper canopy at a height of 28 to 30 meters above ground. The gondola of the lifter allowed the use of *in situ* gas exchange measurement devices in the upper sun-exposed canopy. Leaf or twig samples (*ex situ* sampling) from distant crown parts could be collected from the gondola of the lifter using a 2.5 m-long telescopic pole-pruner.

Photo: F. Beyer

Photo: T. Gebauer

Figure 9. Canopy access with a canopy lifter model DENKA Lift DL30 (left). The gondola (right) reaches up to a platform height of 30 m in the canopy.

2.4 Measurement of transpiration and conductivity for water vapor at the leaf scale using porometry

Water molecules evaporate from mesophyll cell surfaces into the intercellular space and through stomatal openings into the atmosphere driven by the evaporative demand of the ambient air. The steady-state porometer LI-1600 model M (LI-COR Inc., Lincoln, USA) - an open measuring system - permits to measure leaf transpiration and leaf conductivity for water vapor without changing the humidity of the ambient air.

The LI-1600M operates on a null balance principle. The cuvette is brought to equilibrium with ambient conditions and a transpiring leaf is clamped with its transpiring side onto an opening of the cuvette causing an increase of relative humidity in the cuvette. The flow controller immediately increases the dry air flow rate into the cuvette to balance the additional input of water transpired by the leaf in order to maintain the cuvette relative humidity at the user-determined set-point (null-point, mainly near ambient conditions, steady-state conditions).

Leaf transpiration rate (E, in mmol m^{-2} s^{-1}) is calculated by the formula:

$$E = g_{\mathrm{L}} \left(\frac{e_l - e_a}{P} \right)$$

where e_l is the vapor pressure in the leaf and e_a is the vapor pressure in the air, and P is the barometric pressure at the measurement site. Leaf conductivity (g_{L}, in mmol m^{-2} s^{-1}) is calculated directly from measured values of relative humidity, leaf and air temperature and volumetric flow rate (see von Willert et al. 1995, LI-COR, 1989).

For sampling details see chapter 4.

2.5 Leaf water potential measurements using the Scholander Pressure Chamber

Water is conducted through the xylem to the site of evaporative demand (mainly the leaves of a plant). Water ascends in the xylem of plants in a metastable state under tension (negative hydrostatic pressure), i.e., xylem pressure more negative than that of a perfect vacuum (Tyree and Zimmermann 2002). The driving force is generated by surface tension at the evaporating surfaces of the leaf and the tension is transmitted through a continuous water column from the leaves to the root apices (Tyree and Zimmermann 2002). Evidence for this negative xylem pressure was obtained using a pressure chamber (Scholander pressure probe or bomb, Scholander et al. 1965). In this method, a leaf or twig is installed into a sealed pressure chamber in the way that the cutting surface is protruding through the chamber lid. Cutting a leaf or twig off the plant relaxes the tension in the xylem and the meniscus of the water column recedes back into the conduits. The pressure inside the chamber is then increased till the meniscus is visible at the cutting surface. The rate of pressure increase should be in the range of 0.05 to 0.002 MPa s^{-1}, which prevents a temperature change in the chamber (upholding isothermal conditions). The positive pressure inside the pressure chamber at equilibrium (when the meniscus is at the cutting surface) equals the negative hydrostatic pressure in the xylem before cutting. This pressure is a first approximation for the leaf water potential (see also Cochard et al. 2001, Kirkham 2005, von Willert et al. 1995, Tyree and Zimmermann 2002 and Holbrook et al. 1995).

We used a Scholander pressure chamber manufactured by PMS Instrument Inc., Albany, Oregon, USA.

For sampling details see chapter 4.

Photo: S. Haverstock

Figure 10. Measurement of predawn and noon leaf water potentials with the Scholander pressure chamber. Here, a hornbeam twig is placed into the rubber sealing before insertion into the pressure chamber to start the predawn leaf water potential measurement.

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Chapter

3

Variability in radial sap flux density patterns and sapwood area among seven co-occurring temperate broad-leaved tree species

T. Gebauer, V. Horna and C. Leuschner

Tree Physiology 28, 1821–1830

Variability in radial sap flux density patterns and sapwood area among seven co-occurring temperate broad-leaved tree species

TOBIAS GEBAUER,[1] VIVIANA HORNA[1] and CHRISTOPH LEUSCHNER[1,2]

[1] *Plant Ecology, Albrecht-von-Haller-Institute for Plant Sciences, Georg-August-University of Göttingen, Untere Karspuele 2, 37073 Göttingen, Germany*

[2] *Corresponding author (cleusch@gwdg.de)*

Received February 15, 2008; accepted June 27, 2008; published online October 1, 2008

Summary Forest transpiration estimates are frequently based on xylem sap flux measurements in the outer sections of the hydro-active stem sapwood. We used Granier's constant-heating technique with heating probes at various xylem depths to analyze radial patterns of sap flux density in the sapwood of seven broad-leaved tree species differing in wood density and xylem structure. Study aims were to (1) compare radial sap flux density profiles between diffuse- and ring-porous trees and (2) analyze the relationship between hydro-active sapwood area and stem diameter. In all investigated species except the diffuse-porous beech (*Fagus sylvatica* L.) and ring-porous ash (*Fraxinus excelsior* L.), sap flux density peaked at a depth of 1 to 4 cm beneath the cambium, revealing a hump-shaped curve with species-specific slopes. Beech and ash reached maximum sap flux densities immediately beneath the cambium in the youngest annual growth rings. Experiments with dyes showed that the hydro-active sapwood occupied 70 to 90% of the stem cross-sectional area in mature trees of diffuse-porous species, whereas it occupied only about 21% in ring-porous ash. Dendrochronological analyses indicated that vessels in the older sapwood may remain functional for 100 years or more in diffuse-porous species and for up to 27 years in ring-porous ash. We conclude that radial sap flux density patterns are largely dependent on tree species, which may introduce serious bias in sap-flux-derived forest transpiration estimates, if non-specific sap flux profiles are assumed.

Keywords: annual growth rings, diffuse-porous, dyes, Fagus sylvatica, Fraxinus excelsior, Granier method, ring-porous, sap flow, Tilia, Weibull function.

Introduction

In forest ecosystems, transpiration estimates are frequently based on xylem sap flux measurements of individual trees assuming that the sum of the mass flow in tree stems equals total canopy transpiration with a short time lag (Kaufmann and Kelliher 1991). Total stem sap flow is estimated from the product of sap flux and the cross-sectional area of hydro-active xylem or sapwood (Granier 1985), but these estimates can result in large errors if radial xylem flux density profiles are unknown and uniform sap flux across the entire sapwood is assumed.

In some tree species, the determination of sapwood depth is difficult. Several authors have reported that sap flux density reaches a maximum in the xylem adjacent to the cambium and decreases exponentially along the radial axis toward the inner xylem (Swanson 1967, 1974, Mark and Crews 1973, Miller et al. 1980, Dye et al. 1991, Čermák et al. 1992, Becker 1996, Phillips et al. 1996, Oren et al. 1999, Fernández et al. 2001, Nadezhdina et al. 2002, Ford et al. 2004*a*, 2004*b*, Kubota et al. 2005*a*, 2005*b*). Such a pattern has been reported in the widely distributed European species *Fagus sylvatica* L. For example, Köstner et al. (1998), Granier et al. (2000) and Schäfer et al. (2000) all reported an exponential decrease in xylem sap flux density from the outer to the inner sapwood of this species. However, the same pattern may not be characteristic of other temperate tree species.

The hydraulic conductivity of the xylem in tree stems is partly dependent on the seasonal rhythm of conduit formation. Trees with ring-porous sapwood such as oak and ash conduct water only in the outermost annual growth rings (Ellmore and Evers 1986, Granier et al. 1994). In conifers and diffuse-porous broad-leaved trees, sapwood area usually occupies a greater proportion of stem cross-sectional area and is composed of relatively narrow conduits (Čermák and Nadezhdina 1998) that are typically more resistant to water transport than the larger vessels of ring-porous trees. Sapwood is the portion of wood external to the heartwood that contains living parenchyma cells, stores carbohydrates and includes that part of the xylem that is active in the transport of water and solutes from the soil to the crown (IAWA 1964, Braun 1970). However, the hydro-active sapwood area is often difficult to quantify because of the lack of a clear border between active and inactive xylem. The amount of sapwood area and its conducting role varies with species, tree age and environmental conditions (Čermák and Nadezhdina 1998). In some tree species, sapwood and heartwood (the inner, nonconductive wood) can be distinguished easily by the darker color of the heartwood or a marked drop in tissue water content (Taylor et al. 2002). However, this is not true of all tree species and it may be true of some but not all individuals of a given species. It is often difficult, therefore, to estimate sapwood area on the basis of changes in color, water content or wood density across wood core samples (e.g., Köstner et al. 1998). Furthermore, sapwood cores may change color after the release of phenols and terpenes or after alteration of precursor substances such as phenolic glycosides (Taylor et al. 2002, 2007).

A widely used method for estimating the hydro-active sapwood area is to dye the xylem. Dye is injected into living trees or applied to stem discs obtained from harvested trees or to extracted wood cores. Certain dyes such as indigo carmine (Andrade et al. 1998, Meinzer et al. 2001), safranin (Granier et al. 1994), berberine chlorine (Gessler et al. 2005) and fuchsin (Sano et al. 2005) are added to the transpiration stream and stain the cell walls of water-conducting tracheids and vessels. Other dyes are used to indicate differences in chemical properties between sapwood and heartwood. For example, bromocresol green is a pH indicator (Kutscha and Sachs 1962, Schäfer et al. 2000) and iodine-potassium iodide (Lugol's solution) is an indicator for starch (Vötter 2005). In the case of extracted wood cores, sapwood depth is usually determined at only a few points on the stem, and sapwood area is then calculated by extrapolation assuming a constant sapwood depth in all stem directions.

Dyeing of stem discs has the advantage over the use of wood cores that the whole cross-sectional sapwood area can be investigated, but the method is destructive, as is thermo-imaging (Granier et al. 1994). Computer tomography provides a nondestructive but costly technique for sapwood area determination (Habermehl et al. 1982*a*, 1982*b*, Rust 1999), and it may be limited in applicability to only a few stems in a stand. Based on a review of Granier's thermal heat dissipation probe method, Lu et al. (2004) concluded that the use of sap flux measurements may provide a suitable nondestructive method to localize the sapwood–heartwood boundary and thus to determine the sapwood area of trees. Sap flux is measured by the use of heat pulse probes (Granier et al. 1994, Hatton et al. 1995), the heat-field deformation technique (Nadezdhina et al. 2002) or the constant-heating method (Phillips et al. 1996, Lu et al. 2000, Ford et al. 2004*a*). We applied the constant-heating method with heating probes at various xylem depths to analyze radial profiles of sap flux density in the sapwood of seven broad-leaved tree species differing in wood density and xylem structure. Our study aims were to (1) compare patterns of radial sap flux density between trees with diffuse-porous and ring-porous xylem anatomy; and (2) compare the size of the hydro-active xylem between ring-porous and diffuse-porous tree species by relating it to stem diameter. Our intention was to provide a basis for more accurate estimates of stand transpiration in mixed forests obtained from sap flux measurements made exclusively in the outermost sections of the sapwood.

Materials and methods

Study site

The study was conducted in a mixed temperate broad-leaved forest in the Hainich National Park (Thuringia, Central Germany). The forest stand is located in the northeastern part of the National Park between 295 and 355 m a.s.l. (51°04′ N, 10°30′ E). European beech (*Fagus sylvatica*), linden (*Tilia sp.*), common ash (*Fraxinus excelsior* L.), hornbeam (*Carpinus betulus* L.), sycamore maple (*Acer pseudoplatanus* L.), Norway maple (*A. platanoides* L.) and field maple (*A. campestre* L.) occur at different densities within the forest. Mean tree height varies between 27.9 m in the denser part of the forest (614 stems ha^{-1}) to 32.9 m in the less dense forest area (392 stems ha^{-1}).

Mean annual temperature of the study site in the years 1973–2004 was 7.5 °C (Deutscher Wetterdienst). Mean annual temperature in 2006 (9.4 °C, Meteomedia AG, 2006) was higher than the long-term mean. Mean annual precipitation in 2006 (518 mm, Meteomedia AG, 2006) was lower than the mean for the years 1973–2004 (590 mm, Deutscher Wetterdienst).

Sap flux profiles

Xylem sap flux was measured between August and September 2006, during which period, there was no precipitation. Mean vapor pressure deficit during the light phase varied between 5 and 15 hPa, total daily radiation ranged between 6 and 19 MJ m^{-2} day^{-1}. Characteristics of the selected trees are presented in Table 1. We estimated the sapwood area of the trees by dye injection (see details below). Xylem sap flux was measured by the heat dissipation method (constant-heating method) introduced by Granier (1985, 1987). Pairs of 20-mm-long and 2.0-mm-diameter heating probes were inserted at a depth of 0–20 mm in the stem sapwood. For measurements at xylem depths of 20–40, 40–60 and 60–80 mm, longer needles with identical heating and sensing devices were driven into holes in the xylem having the same diameter as those drilled for the outermost (0–20 mm depth) sensors. The probes were manufactured according to Granier's original design (Granier, pers. comm.). The upper probe was constantly heated, whereas the lower probe was unheated and recorded the reference temperature of the wood. The electric current of the heating element was held constant at 0.12 A with a heating power of 0.2 W. All sensors were inserted at 1.3 m stem height into the sapwood on the north side of the trunk. To guarantee direct contact with the surrounding wood and uniform heat dissipation, the probes were encapsulated in aluminum tubes previously inserted into the stem. The probes were placed 10–15 cm apart to avoid thermal interference, due to heat dissipation from the upper heated probe. The sensors at insertion depths of 20–40, 40–60 and 60–80 mm were placed radially between the northern and western sides of the trunk in proximity to the 0–20 mm sensor. All probes were covered with an insulating polystyrene mat, which in turn, was covered with reflective foil and transparent plastic to minimize the influence of solar irradiance and air temperature.

For the ring-porous species, *Fraxinus excelsior*, a smaller sapwood depth was expected. Therefore, the outer probes had a length of only 10 mm, and additional probes were inserted at depths of 10–20 and 20–30 mm.

The temperature difference (ΔT) between upper and lower sensor probes was recorded every 30 s with a CR10X data log-

Table 1. Biometric characteristics of the 11 stems of seven broad-leaved tree species analyzed for sap flux density–xylem depths relationship in the Hainich forest. Abbreviations: DBH = diameter at breast height; A_B = basal area; A_S = sapwood area; and na = not available.

Species	Stem	DBH (cm)	Age[1] (years)	Tree height (m)	Crown area (m^2)	A_B (cm^2)	A_S (cm^2)	A_S/A_B	Sapwood depth (cm)	Annual rings in sapwood
Diffuse-porous										
Fagus sylvatica	Bu28	28.7	108	27.2	16.5	647	484	0.75	7.2	73
Fagus sylvatica	Bu1	39.8	104	32.7	20.1	1244	906	0.73	9.6	70
Carpinus betulus	HBu4	48.7	149	26.7	88.6	1863	1289	0.69	10.9	85
Tilia cordata	Li17	27.1	na	22.8	26.5	577	454	0.79	7.3	na
Tilia platyphyllos	Li11	28.3	30	26.2	21.9	629	486	0.77	7.4	29
Tilia platyphyllos	Li1	46.2	62	33.2	39.7	1676	1044	0.62	8.9	40
Acer pseudoplatanus	BAh4	41.1	110	26.5	36.5	1327	1127	0.85	12.6	88
Acer campestre	FAh167	26.8	92	23.9	na	564	364	0.65	5.4	46
Ring-porous										
Fraxinus excelsior	Es8	14.0	50	14.3	17.7	154	15	0.10	0.3	5
Fraxinus excelsior	Es2	27.2	108	29.6	5.1	581	88	0.15	1.1	12
Fraxinus excelsior	Es14	52.9	81	31	46.1	2198	521	0.24	3.4	11

[1] Minimum estimated tree age. Annual rings were counted from wood cores taken at 1.3-m height.

ger (Campbell Scientific, U.K.) equipped with a 16/32-channel multiplexer (AM16/32, AM416, Campbell Scientific). Thirty-minute means were calculated from the 30-s readings and stored by the data logger. Temperature differences were converted to sap flux densities (J_s; g m^{-2} s^{-1}) based on Granier's empirical calibration equation (Granier 1985, 1987):

$$J_s = 119\left(\frac{\Delta T_M - \Delta T}{\Delta T}\right)^{1.231} = 119\,K^{1.231} \qquad (1)$$

where ΔT_M is the maximum temperature difference when sap flow is assumed to be zero.

Sapwood area and diameter at breast height

Sapwood depth was determined during August 2006 for trees of *Fagus sylvatica*, *Carpinus betulus*, *Tilia cordata*, *Acer pseudoplatanus*, *A. platanoides*, *A. campestre* and *Fraxinus excelsior* with a minimum diameter at breast height (DBH) of 10 cm and a maximum diameter of 60 cm. Measurements were made on at least 12 trees per species that were not used for sap flux measurements (Table 2). Sapwood depth at breast height was estimated by a staining method (Goldstein et al. 1998, Meinzer et al. 2001). During the morning (0800–1100 h), when transpiration rates were expected to rise, a core to the center of the trunk was taken at 1.3-m height with a 5-mm diameter increment borer (Suunto Oy, Vaanta, Finland). Immediately after coring, a 0.1% indigo carmine-solution was injected into the hole, which was refilled when necessary. After 2 to 4 h, when the xylem sap should have moved upward in the active xylem, a second core was taken 3–5 cm above the injection point. The stained depth of the sapwood was determined based on the following criteria. Wood sections continuously colored by indigo-carmine and adjacent wood sections with at least two spots of dye were considered to be conducting sapwood. This border was taken as the maximum sapwood depth. Sapwood area was then calculated as the area of the stem ring with the estimated sapwood depth.

The wood core removed to allow dye injection was used for analysis of annual tree ring diameter (I. Schmidt, unpublished data) using LINTAB and TSAP-Win software (RINNTECH, Heidelberg, Germany).

The wood cores were cut into 10-mm segments for wood density determination. Fresh mass was recorded immediately after core extraction. Dry mass was measured after drying at 70 °C for 48 h to constant mass. Wood density was determined from the mass and volume of the oven-dried 10-mm segments with volume being determined by caliper measurements of length and width at several points on the fresh wood segments.

Data analysis

The relationship between sapwood area as estimated by dyeing and DBH was approximated by the following power function according to Vertessy et al. (1995) and Meinzer et al. (2001, 2005):

$$A_s = a\,\mathrm{DBH}^b \qquad (2)$$

where A_s is sapwood area (cm^2) and a and b are species-specific coefficients determined by regression techniques.

To analyze the change in J_s with sapwood depth, J_s was calculated from the data obtained at the four measuring depths (three for ash) in the xylem. By calculating daily means, we minimized time lag effects on J_s at different sapwood depths. Sap flux density tended to increase later in the morning, and decrease earlier in the evening, at increasing xylem depths. The time of peak J_s differed by up to 2 h among the xylem depths. The J_s data were normalized to the value observed at the outermost measuring point in the xylem (0–20 mm for diffuse-porous species with a midpoint at 10 mm, 0–10 mm for ash with a midpoint at 5 mm). The dependence of relative J_s on radial xylem depth (x) was described by a four-parametric

Table 2. Diameter at breast height (DBH), sapwood depth, mean number of annual rings in the hydro-active sapwood (absolute numbers) and mean annual ring width in seven broad-leaved tree species (minimum and maximum, or mean (standard deviation) of *n* stems per species).

Species	*n*	DBH (cm)		Sapwood depth (cm)		Annual rings in sapwood		Mean annual ring width in sapwood (mm)
		min.	max.	min.	max.	min.	max.	
Diffuse-porous								
Fagus sylvatica	19	13.1	57.9	3.6	13.3	25	73	2.02 (0.99)
Carpinus betulus	20	13.4	61.8	2.3	14.5	25	104	1.41 (0.71)
Tilia cordata	24	10.8	60.2	6.8	10.0	14	77	2.17 (0.88)
Acer pseudoplatanus	15	16.2	57.6	5.3	17.3	18	169	1.63 (0.74)
Acer platanoides	14	13.5	51.9	7.6	12.1	38	95	1.67 (0.61)
Acer campestre	12	13.1	42.3	1.7	11.8	29	68	1.18 (0.43)
Ring-porous								
Fraxinus excelsior	24	9.9	57.6	0.2	5.7	3	27	2.35 (1.39)

Weibull function (Kubota et al. 2005*b*):

$$J_s = \frac{c-1}{c} + a\left(\frac{c-1}{c}\right)^{\frac{1-c}{c}} \cdot e^{-\left(\frac{x-d}{b}+\left(\frac{c-1}{c}\right)^{\frac{1}{c}}\right)^{c}} \cdot \left(\frac{x-d}{b}+\left(\frac{c-1}{c}\right)^{\frac{1}{c}}\right)^{c-1} \tag{3}$$

where coefficient *a* characterizes the peak value of the function, the coefficients *b* and *c* determine the shape of the curve, and *d* is the xylem depth where maximum J_s is located.

Results

Species differences in radial sap flux density profiles

Radial patterns of J_s showed considerable variability among the 11 investigated stems of the seven tree species. In all stems, J_s peaked in the first 4 cm of the xylem directly adjacent to the cambium according to the radial sap flux density profiles modeled by four-parametric Weibull functions (Figure 1). However, radial J_s peaked in the youngest xylem elements in *Fagus sylvatica* (diffuse-porous) and *Fraxinus excelsior* (ring-porous) and decreased exponentially toward the inner sapwood, whereas radial J_s patterns in *Carpinus betulus*, *Acer pseudoplatanus*, *A. campestre* and *Tilia* sp. showed a hump-shaped curve with maximum values 2 to 4 cm beneath the cambium and lower values in the youngest xylem elements. All stems showed decreasing J_s with increasing xylem depth beyond the maximum in the modeled flux profiles, but the slope of the decrease differed markedly among species and among stems of different DBH classes. The difference in the location of maximum J_s among species is expressed by the value of *d* in the four-parametric Weibull function describing the radial J_s profiles. Coefficient *d* was < 0.5 or even negative in *Fraxinus excelsior* and *Fagus sylvatica*, but ranged between 1.9 and 3.4 in the other species (Table 3). In the *Tilia* species, radial patterns

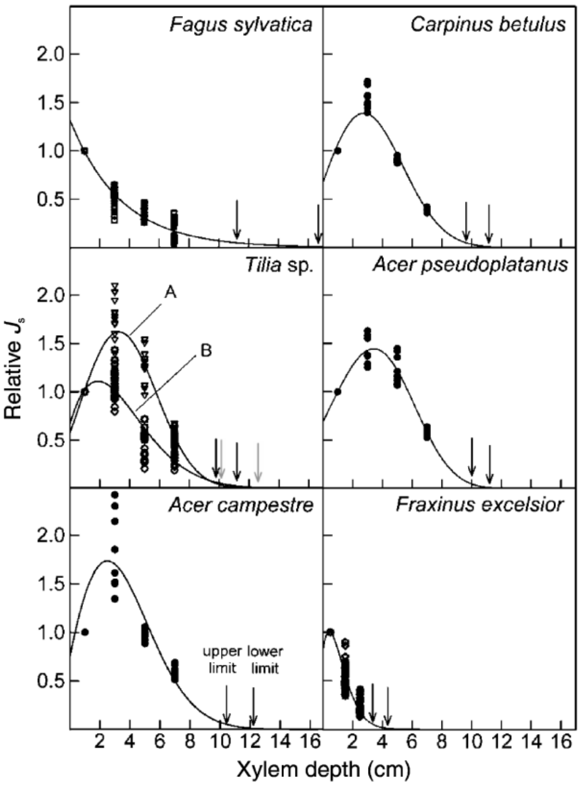

Figure 1. Xylem depth and mean daily sap flux density (J_s) normalized to the outermost measuring point. In all diffuse-porous species the outermost measuring point was at 1-cm depth, and in the ring-porous *F. excelsior* at 0.5 cm. Four-parametric Weibull functions were fitted to the data (solid lines). Values are means of 1–3 trees per species that were measured for between 8 (*A. campestre, A.pseudoplatanus*) and 22 (*F. sylvatica*) days. Sap flux density at the outermost measurement point is given a relative value of one and is the mean of up to 22 individual measurements. For *Tilia* sp. two stem size classes were analyzed separately (A = Li1: 46.2 cm, B: Li17, 27.1 cm and Li11: 28.3 cm). Arrows indicate the lower and upper limit (i.e. J_s = 0.01 or 0.05) of the transition zone from active to inactive xylem (*Tilia* sp.: A = black arrows, B = gray arrows) as estimated by modeled data from Weibull functions.

of J_s of large- and medium-diameter stems differed significantly: peak values occurred at about 3.5 cm from the cambium in the widest stem, but was within 2 cm of the cambium in the narrower stems (Figure 1, center row). Although J_s in Figure 1 is expressed relative to the outermost measuring point in the sapwood (at 1.0 or 0.5 cm depth), daily variation in patterns was observed, particularly in *Acer campestre*, where measurements on eight days yielded relative J_s values at a sapwood depth of 3 cm between 1.4 and 2.5 (Figure 1, bottom row). Temporal scatter of relative J_s was smaller in *A. pseudoplatanus* and *Carpinus betulus* which had a greater proportion of leaf area in the upper canopy of the stands than the subdominant individuals of *A. campestre*.

No distinct boundary between hydro-active and inactive xylem was detected within the 8-cm-wide flux profiles, indicating that J_s gradually approached zero flow with increasing xylem depth in all species. To estimate the hydro-active sapwood depth, we defined a relative $J_s = 0.05$ as the upper limit, and a relative $J_s = 0.01$ as the lower limit of the transition zone from active to inactive xylem based on the modeled J_s profiles. We obtained a mean sapwood depth of 11.2 cm (upper boundary) to 16.7 cm (lower boundary) for the *Fagus sylvatica* stems (Figure 1). The other diffuse-porous species had sapwood depths between 9.6 and 12.6 cm. The narrowest sapwood was found in the ring-porous species *Fraxinus excelsior* with an upper limit of 3.3 cm and a lower limit of 4.3 cm (Figure 1, bottom row). In the *Tilia* stems, there was only a minor difference in hydro-active xylem depth between the stem diameter classes (A: 46-cm DBH, B: 27–28-cm DBH) (Figure 1, center row).

In Table 4, we converted absolute xylem depth to relative depth by defining a relative J_s value of 0.01 as the boundary between hydro-active and inactive xylem (sapwood–heartwood boundary); this depth was set to 1. Accordingly, maximum J_s occurred immediately beneath the cambium in *F. sylvatica*, at a relative sapwood depth of 0.10 in *F. excelsior*, and at a relative depth of 0.15 to 0.30 in the other diffuse-porous species. Because of the differently shaped profiles of modeled radial J_s, relative J_s in the center of the hydro-active xylem (i.e., at a sapwood depth of 0.5) differed among species (*Fagus*: 0.11, *Fraxinus*: 0.28, *Tilia* sp. B: 0.39, *A. campestre*: 0.50, *Carpinus*: 0.77 and *Tilia* sp. A and *A. pseudoplatanus* > 1.00; Table 4).

Table 3. Coefficients of the four-parametric Weibull function describing the relationship between sap flux density (J_s) and xylem depth in the seven study species. For analysis, mean daily J_s normalized to the J_s at the outermost measuring point (=1) were used. For *Tilia*, the two similar species *T. platyphyllos* and *T. cordata* were pooled; however, stems of two diameter classes (A > 35 cm, B < 35 cm) were analyzed separately. Values are means of 1–3 stems per species (genus).

Species	*a*	*b*	*c*	*d*	r^2
Diffuse-porous					
Fagus sylvatica	2.69	3.42	1.00	–2.44	0.95
Carpinus betulus	1.37	5.88	2.43	2.79	0.97
Tilia sp. (A)	1.62	6.35	2.71	3.28	0.93
Tilia sp. (B)	1.11	4.52	1.67	1.88	0.77
Acer pseudoplatanus	1.44	8.98	3.47	3.42	0.91
Acer campestre	1.74	4.86	1.94	2.50	0.79
Ring-porous					
Fraxinus excelsior	1.00	1.44	1.54	0.42	0.96

Sapwood area determination

Sapwood area estimated by the dye method in 12 to 25 stems per species showed a highly significant relationship with DBH in each species (Figure 2). The coefficients of the exponential functions describing these relationships are listed in Table 5.

Table 4. Parameters characterizing the radial patterns of sap flux density (J_s) in the hydro-active xylem in seven tree species as estimated by modeled data from Weibull functions. Daily mean J_s was normalized to the flux at the respective outermost measuring point (= 1) to give relative values. Similarly, xylem depth was expressed in relative values (0 = cambium, 1 = transition from sapwood to inactive heartwood). Mean values of one to three stems per species (genus) are given. A relative J_s of 0.01 was used to define the sapwood–heartwood boundary. For the *Tilia* species, two size classes were analyzed separately (A = Li1: 46.2 cm, B: Li17, 27.1 cm and Li11: 28.3 cm).

Species	Relative J_s at different relative sapwood depths						Relative sapwood depth of maximal flux density	Relative J_s at maximal flux density
	1.0[1]	0.75	0.5	0.25	0.01	0.0[2]		
Diffuse-porous								
Fagus sylvatica	0.01	0.03	0.11	0.39	1.26	0	< 0.01[3]	1.26–1.32
Carpinus betulus	0.01	0.15	0.77	1.37	0.69	0	0.25	1.37
Tilia sp. (A)	0.01	0.2	1.05	1.59	0.62	0	0.3	1.62
Tilia sp. (B)	0.01	0.08	0.39	0.99	0.73	0	0.15	1.11
Acer pseudoplatanus	0.01	0.22	1.03	1.41	0.72	0	0.3	1.44
Acer campestre	0.01	0.09	0.50	1.14	0.57	0	0.20	1.74
Ring-porous								
Fraxinus excelsior	0.01	0.06	0.28	0.78	0.86	0	0.1	1.00

[1] Sapwood–heartwood boundary.

[2] Cambium.

[3] Close to cambium.

In all diffuse-porous species, a large proportion of the stem basal area was active in xylem sap flux. The mean sapwood area to basal area ratio in the diffuse-porous species varied from 0.66 in *A. campestre* to 0.88 in *A. pseudoplatanus*, when all stem diameter classes were pooled. The ring-porous species *F. excelsior* showed a smaller sapwood area to basal area ratio (0.21). Comparing diameter classes revealed a decrease in the ratio with increasing stem diameter. Weak DBH–sapwood area relationships were found in *F. excelsior* and *T. cordata* (r^2 = 0.63 and 0.65), whereas close relationships were found in *A. pseudoplatanus* and *A. platanoides* (0.90).

Table 2 lists the maximum and minimum number of annual rings in the hydro-active sapwood area of each species. In *A. pseudoplatanus*, up to 170 annual rings apparently participated in sap flux in the thickest stems, whereas in the largest diameter *A. platanoides*, *F. sylvatica* and *T. cordata* stems, the hydro-active sapwood included a maximum of 75 to 95 rings (Table 2). As expected, the ring-porous species *F. excelsior* had a shallower sapwood (5.7 cm at the maximum depth) with a smaller number of annual rings (less than 27). The depth of hydro-active sapwood is not only a function of the time span of vessel operation, but also of ring width. We found considerable variation in mean ring width among species with particularly wide rings in *F. sylvatica* and *T. cordata* (> 2 mm wide) and relatively narrow rings in *A. campestre* and *C. betulus* (< 1.5 mm wide, Table 2).

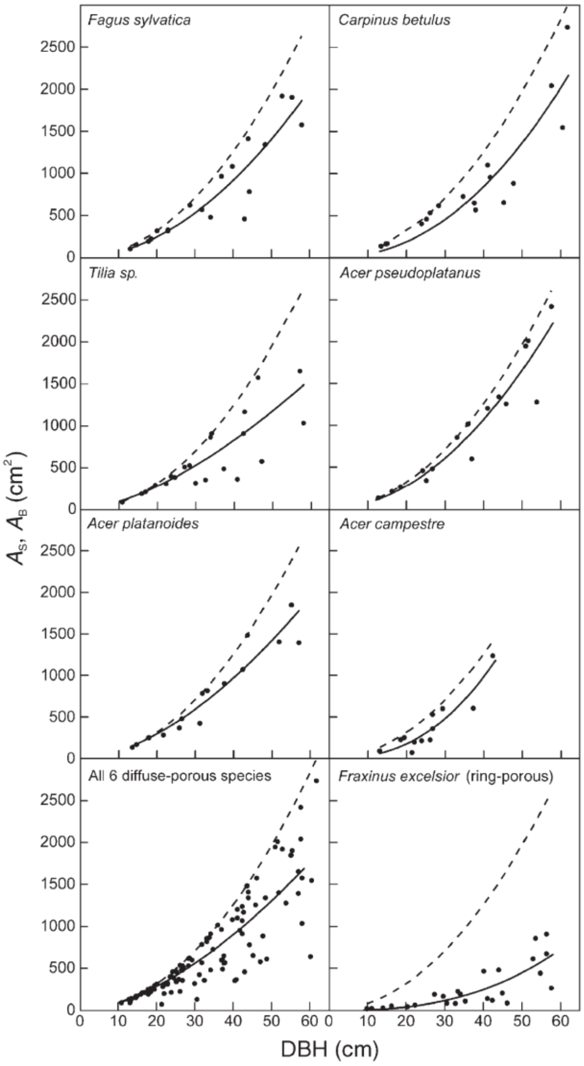

Figure 2. Relationships between stem diameter at breast height (DBH) and sapwood (A_S, solid lines) and basal area (A_B, dashed lines) in six diffuse-porous species and the ring-porous species *F. excelsior*. The relationships are described by power functions of the form $A = a\,\mathrm{DBH}^b$.

Mean wood density of each species is given in Table 5. Among the diffuse-porous species, *C. betulus* and *F. sylvatica* had the highest mean wood densities (0.67 and 0.65 g cm^{-3}, respectively) and *T. cordata* had the lowest (0.43 g cm^{-3}). The ring-porous *F. excelsior* had a mean wood density of 0.59 g cm^{-3}. All three *Acer* species had similar wood densities (0.59–0.60 g cm^{-3}). No study species showed a significant change in wood density from the cambium toward the sapwood–heartwood boundary or beyond this point (data not shown).

Discussion

Sap flux density and sapwood depth

Various factors influence the radial patterns of xylem J_s in a tree stem, among them stem diameter, tree age, social status and species, and evaporative demand. In general, J_s decreases rapidly with increasing sapwood depth in temperate tree species (Cohen et al. 1981, Phillips et al. 1996). This is particularly evident in tall trees with large stem diameters, which position their leaf area in more exposed areas of the upper forest canopy and, thus, are forced to maximize hydraulic conductivity in the stem sapwood to meet the high demand of water consumed by transpiration. Failing to do so would mean a high risk of vessel embolism because of a drop in xylem water potential (Sperry et al. 1998, Koch et al. 2004). Jimenez et al. (2000) emphasized that leaf distribution within the crown has an important influence on radial sap flux density patterns, at least in dominant trees.

In our sample of six broad-leaved species, we found considerable variation in radial pattern of J_s among species, as is evident when comparing the modeled J_s profiles in Table 3. *Fagus sylvatica* was the only species to show an exponential decrease in J_s with sapwood depth; thus, maximum J_s occurred in the youngest xylem elements. This observation is in agreement with results for this species obtained by Granier et al. (2000), Hölscher et al. (2005), Köstner et al. (1998) and Schäfer et al. (2000). According to Hölscher et al. (2005), the decrease in J_s was particularly steep in large diameter stems, as in 140-year-old beech trees. This contrasts with results obtained by Gessler et al. (2005) who detected a less steep radial decrease in sap flux density in older (95-year-old) *F. sylvatica* trees than reported by Granier et al. (2000) for younger

Table 5. Coefficients of the power function (with coefficients of determination) describing the relationships between stem diameter at breast height and sapwood area ($A_S = a\mathrm{DBH}^b$) in the seven tree species. Different letters indicate significant differences between species in wood density (Wilcoxon rank sum test). n_1 and n_2 are the numbers of trees sampled for A_S and wood density determination, respectively.

Species	n_1	a	b	r^2	Wood density (g cm^{-3})	n_2
Diffuse-porous						
Fagus sylvatica	19	0.778	1.917	0.86	0.65 (0.025) a	18
Tilia cordata	21	2.635	1.561	0.65	0.43 (0.063) c	21
Carpinus betulus	18	0.305	2.149	0.85	0.67 (0.024) a	11
Acer pseudoplatanus	16	0.754	1.967	0.90	0.59 (0.030) b	11
Acer platanoides	15	1.794	1.706	0.90	0.59 (0.032) b	7
Acer campestre	12	0.103	2.484	0.86	0.60 (0.015) b	2
All diffuse-porous species	101	1.151	1.801	0.75		
Ring-porous						
Fraxinus excelsior	25	0.013	2.671	0.63	0.59 (0.045) b	18

(32-year-old) beech trees. Our data and those of Schäfer et al. (2000) provide no evidence of a difference in the radial decrease in sap flux density between large and small *Fagus* stems.

Compared with *Fagus sylvatica*, the other species studied showed an initial increase in J_s from the youngest xylem elements toward older annual rings and then a decrease. In general, our results on radial J_s patterns were similar to those obtained in other temperate and subtropical tree species (e.g., Mark and Crews 1973, Hatton et al. 1995, Phillips et al. 1996, Jimenez et al. 2000, Lu et al. 2000, James et al. 2002, Nadezhdina et al. 2002, Ford et al. 2004*a*, Kubota et al. 2005*a*, 2005*b*). In the case of ring-porous *F. excelsior*, our regression model revealed a peak in J_s close to the cambium, i.e., in the second or third annual ring, which is similar to beech. However, our sensors could not give an accurate picture of J_s in the first mm beneath the cambium because the signal was integrated over the entire sensor length. Other methods of measuring J_s, for example, with heat pulse probes, are more appropriate for point measurements in one or two annual rings. In the diffuse-porous genus *Populus*, Edwards and Booker (1984), using heat pulse probes, observed maximum J_s in the second growth ring and lower J_s in the youngest (first) and third rings. Similarly, the highest J_s was reported in the second and third annual rings of 24-year-old *Pseudotsuga menziesii* (Mirb.) Franco trees (Domec et al. 2006).

In contrast, stems of *Carpinus*, *Tilia* and *Acer* showed maximum J_s at a xylem depth of about 3 cm, which corresponds to a growth ring age of about 15 to 30 years. Thus, J_s is comparatively low in the young, recently formed xylem elements and increases over years or decades to reach maximum values in these diffuse-porous species. However, differences in radial J_s patterns are not only related to species, stem size and tree age, but may also result from differences in measurement technique. For example, Gessler et al. (2005) used multi-point sensors where an overlap of neighboring heat fields can increase the uncertainty of measurement (Clearwater et al. 1999, Lu et al. 2000, James et al. 2002); however, Jimenez et al. (2000) found no significant interference among neighboring measurement points along their radial sap flow probe.

A further source of bias in radial sap flux data when only a single sap flow sensor in the outermost sapwood is used, is the diurnal variation in the radial profile of J_s. According to Ford et al. (2004*a*, 2004*b*; see also Nadezhdina et al. 2002), the radial profile of J_s in *Pinus* stems does change diurnally in response to daily variation in the evaporative demand. In the course of a day, the inner part of the xylem contributed more to J_s later in the day. Similarly, J_s was greater in the innermost sapwood on days when vapor pressure deficit was high. Finally, Nadezhdina et al. (2002) showed that changes in soil water content may influence radial J_s profiles and the size of hydro-active sapwood area. Such observations point to the capacity of trees to extend their hydro-active area on a daily or seasonal basis to accommodate changes in the demand for water transport. This may also indicate plasticity in the xylem and a capacity to overcome vessel embolism. *Fagus* species are unable to refill embolized xylem vessels as efficiently as other diffuse-porous species (Hacke and Sauter 1995, 1996, Sperry 1995, Améglio et al. 2004). This may explain the typical sharp decrease in J_s from the outer to the inner sapwood in *F. sylvatica*, and also in ring-porous *F. excelsior*.

To extrapolate the radial J_s profiles to different tree size classes, we suggest that the profiles be expressed in relative terms with maximum sapwood depth being set at 100%. By assuming that the radial J_s patterns are similar among the size classes of a species, this approach may yield the most realistic whole-tree transpiration estimates. Clearly, a set of species-specific sapwood area–DBH relationships and species-specific radial J_s profiles for different size classes of trees is required to accurately extrapolate mass flow in mixed stands, which makes this approach labor intensive.

Tree ring formation and hydro-active sapwood area

The dichotomy between diffuse-porous and ring-porous temperate tree species in the depth of the hydro-active sapwood is well documented (Wang et al. 1992). For example, Meinzer et al. (2005) found a sapwood-to-basal-area ratio of 0.15 in the ring-porous species *Quercus garryana* Dougl. ex Hook, and similarly low values in the North American conifers *Pseudotsuga menziesii* and *Thuja plicata* Donn ex D.Don. In contrast, much higher ratios were observed in Central European diffuse-porous broad-leaved trees (0.78, Hölscher et al. 2005) and in 17 tropical trees (0.72, Meinzer et al. 2005). For 94-year-old *F. sylvatica* trees, Gessler et al. (2005) found a sapwood-to-basal-area ratio of 0.8, which matches well with our results for this species (0.76). Similarly, the other diffuse-porous species in our study had sapwood-to-basal-area ratios of 0.7 to 0.9, whereas a value of 0.21 was found for ring-porous *F. excelsior.* To ensure water flow to recently expanded foliage in spring, ring-porous trees produce earlywood composed mainly of large-diameter vessels. Such wide vessels are at greater risk of embolism than narrow latewood vessels, and they are thought to lose their capacity to transport water by the end of the first winter. No refilling occurs in these vessels during the following spring (Tyree and Zimmermann 2002). For example, the large vessels from the earlywood of ring-porous *Quercus alba* L. are dysfunctional after the year of formation (Miller et al. 1980), whereas small latewood vessels continue to function, or can be reactivated after each winter, and thus will continue to function for several years after ring formation (Granier et al. 1994). Because of the dependence of bud break on hydraulic capacity (Lechowicz 1984), ring-porous trees tend to produce new leaves later in spring than diffuse-porous trees.

Although our data generally support the above-mentioned concept of xylem function in diffuse- and ring-porous species, they provide a different insight into the maximum time span that xylem elements remain functional in the hydro-active sapwood. According to the radial J_s profile data, certain vessels seem to maintain their transport functions in ring-porous *F. excelsior* much longer than one or two years as is expected from general theory. For example, we measured significant sap flux in the outermost 3 cm of the sapwood of medium-sized ash stems (Figure 1) and counted five to 12 annual rings in the hydro-active sapwood (Table 1). Even if most vessels lose their functionality because of embolism after one year, a minority of xylem elements must remain active for several years in this ring-porous species.

Some diffuse-porous species recover conductivity through embolism reversal promoted by root pressure after winter freezing (Hacke and Sauter 1996), which plays no role in conduit refilling at tree heights above about 20 m. This recovery in conductivity may recur for several years in narrow vessels until irreversible embolism occurs (Utsumi et al. 1998). Our data from six diffuse-porous broad-leaved species indicate that certain xylem elements may fulfill transport functions in the older sapwood for as long as 100 years or more (see Table 2), even though they may be of marginal importance for mass flow during periods of peak flow. Sapwood parenchyma cells may be important in prolonging the active life of vessels. For example, Braun (1970) states that trees are able to maintain functional vessels if they have a high proportion of parenchyma cells in their sapwood, which act either as a protective shield against the diffusion of air into the xylem or by extracting air from the sap stream. This may hold true for *Tilia*, *Carpinus* and *Acer* species which have paratracheal contact parenchyma cells surrounding the vessels and wood rays within their woody tissue. *Fagus* wood also contains paratracheal contact parenchyma cells, but only in short single-layer structures without shield formation. *Fraxinus* has contact parenchyma shields around the vessels with a high proportion of interfibrous parenchyma cells (Braun 1970).

How much water moves in a given sapwood ring depends partly on the transpiration rate of the foliage connected to that ring (Domec et al. 2006). In conifers with long-lived needles, these connections remain active for 3–5 years (Balster and Marshall 2000, Maton and Gartner 2005). Dye et al. (1991) hypothesized that the reduction in J_s along the radial sapwood profile of *Pinus* trees was the result of a decreasing participation of older xylem elements in the supply of water to transpiring surfaces. The initial hydraulic connection of early formed xylem as the primary conduit for the supply of water to young branches breaks when these branches die or become shaded. For deciduous broad-leaved species it is unknown how these connections are maintained or renewed each year with new foliage production or how relevant the connection to inner or to outer sapwood is.

No relationship between the reduction in J_s with sapwood depth and wood density was found in our sample. We observed no change in wood density with sapwood depth in the seven investigated species, nor did we find a relationship between wood density and number of annual rings in the sapwood. Similarly, other authors detected no general relationship between decreasing J_s and wood density (Phillips et al. 1996, Čermák and Nadezhdina 1998, Schäfer et al. 2000, but see Delzon et al. 2004).

In conclusion, the dye injection technique can give a first approximation of the size of the hydro-active sapwood area of tree stems. Our study revealed considerable variation in radial J_s patterns among seven co-occurring tree species. This variation is relevant for up-scaling from point measurements in the stem to the whole-tree and to the stand. Further investigations in a larger set of tree species and diameter classes are required to draw more general conclusions on possible relationships between tree functional types, xylem structural types and radial sap flux patterns.

Acknowledgments

We are grateful to the management of the Hainich National Park, Thuringia, for their cooperation. We thank Sarah Haverstock for help in the field, Inga Schmidt for supporting this study with tree ring data and Heinz Coners for technical support. This study was conducted within the framework of the Graduiertenkolleg 1086 with funding from the German Research Foundation (DFG).

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Chapter
4

Leaf water status and stem xylem flux in relation to soil drought in five temperate broad-leaved tree species with contrasting water use strategies

Köcher P., T. Gebauer, V. Horna and C. Leuschner

Ann. For. Sci. 66 (2009) 101
© INRA, EDP Sciences, 2009
DOI: 10.1051/forest/2008076

Available online at:
www.afs-journals.org

Original article

Leaf water status and stem xylem flux in relation to soil drought in five temperate broad-leaved tree species with contrasting water use strategies

Paul KÖCHER, Tobias GEBAUER, Viviana HORNA*, Christoph LEUSCHNER

Department of Plant Ecology, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2,
37073 Göttingen, Germany

(Received 9 May 2008; accepted 29 Octobre 2008)

Keywords:
leaf conductance /
leaf water potential /
drought sensitivity /
mixed forest /
xylem sap flux

Abstract

- Five temperate broad-leaved tree species were compared with respect to their water consumption strategies under ample and restricted water supply. We measured synchronously leaf conductance (g_L) in the sun canopy, xylem sap flux (J_s) and leaf water potential (predawn, Ψ_{pd} and noon, Ψ_{noon}) in adult trees in a mixed stand and related them to the fluctuations in vapor pressure deficit (D) and soil moisture.
- Maximum g_L was particularly high in *F. excelsior*, *C. betulus* and *T. cordata* and revealed a higher D sensitivity. Ψ_{pd} remained constantly high in *A. pseudoplatanus*, *C. betulus* and *F. excelsior*, but decreased in *T. cordata* and *F. sylvatica* with decreasing soil moisture.
- J_{sd} decreased linearly with decreasing soil matrix potential in all species except for *F. excelsior*. Apparent hydraulic conductance in the soil-to-leaf flow path (L_c) was higher in *A. pseudoplatanus* than in the other species.
- *F. sylvatica* maintained a low maximum g_L and reduced J_{sd} markedly upon drought, but faced severe decreases in Ψ_{pd} and Ψ_{noon}. *F. excelsior* represents an opposite strategy with high maximum g_L and stable Ψ_{pd}.
- The species drought sensitivity increases in the sequence *F. excelsior* < *C. betulus* < *T. cordata* < *A. pseudoplatanus* < *F. sylvatica*.

Mots-clés :
conductance foliaire /
potentiel hydrique foliaire /
sensibilité à la sécheresse /
forêt mixte /
flux de sève xylèmique

Résumé – Statut hydrique des feuilles et flux xylèmique dans le tronc en relation avec la sécheresse du sol pour cinq espèces d'arbres feuillus tempérés à stratégies de consommation d'eau différentes.

- Les stratégies de consommation d'eau de cinq espèces d'arbres feuillus tempérés ont été comparées sous approvisionnement en eau suffisant ou limité. De façon synchrone nous avons mesuré la conductance hydraulique des feuilles (g_L) dans la partie du couvert exposée au soleil, le flux de sève xylémique (J_s) et le potentiel hydrique foliaire (potentiel de base (Ψ_{pd}) et potentiel minimum (Ψ_{noon})) d'arbres adultes en peuplement mixte et nous les avons reliés aux fluctuations du déficit de pression de vapeur (D) et à l'humidité du sol.
- g_L maximum était particulièrement élevée chez *F. excelsior*, *C. betulus* et *T. cordata* et a révélé une plus grande sensibilité à D. Ψ_{pd} est resté constamment élevé *chez A. pseudoplatanus*, *C. betulus* et *F. excelsior*, mais a diminué chez *T. cordata* et *F. sylvatica* lorsque l'humidité du sol diminuait.
- J_{sd} a diminué linéairement avec le potentiel matriciel du sol pour toutes les espèces excepté *F. excelsior*. La conductivité hydraulique apparente du trajet sol-feuille (L_c) était plus élevée chez *A. pseudoplatanus* que dans les autres espèces.
- *F. sylvatica* a maintenu une faible g_L maximum et a réduit sensiblement J_{sd} face à la sécheresse, mais a connu de graves diminutions de Ψ_{pd} et Ψ_{noon}. *F. excelsior* présentait une stratégie opposée avec une g_L maximum élevée et un Ψ_{pd} stable.
- La sensibilité des espèces à la sécheresse augmente selon la séquence *F. excelsior* < *C. betulus* < *T. cordata* < *A. pseudoplatanus* < *F. sylvatica*.

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* Corresponding author: vhorna@gwdg.de

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1. INTRODUCTION

As a consequence of global warming, an increase in the frequency and magnitude of summer droughts is predicted for Central Europe (Bréda et al., 2006; Meehl and Tebaldi, 2004; Schär et al., 2004). An expected rise in air temperature in temperate regions would increase the evaporative demand and should decrease available soil water relative to current conditions. The consequences of these changes for European temperate tree species and forests are still not sufficiently understood (Bovard et al., 2005).

Transpiration of co-existing tree species often varies greatly due to species-specific responses to variation in microclimatic and edaphic parameters (Granier et al., 1996; Oren et al., 2001; Pataki and Oren, 2003; Pataki et al., 2000). How tree species cope with a drier climate will depend on the species' capability to ensure water uptake under decreasing soil humidity. Tree species confronted with water stress will incur in structural or physiological adjustment in order to maintain the integrity of the hydraulic system and to enable carbon assimilation despite substantial water losses and a marked deterioration of plant water status (Bréda et al., 2006). Short term dynamic adaptation of trees to drought is achieved reducing transpiration via stomatal closure or reducing leaf water potential through active osmotic adjustment (Sperry, 2000). Long-term plastic responses to drought include regulation strategies like growing a deep rooting system, reducing leaf area or developing stems with high hydraulic conductivity and low cavitation risk (Sperry et al., 2002). Typically, trees combine elements of both strategies, but differ considerably in terms of stomatal regulation, hydraulic properties and growth sensitivity to drought. These traits may be crucial when temperate forests are exposed to increased summer drought, favouring species that are better adapted to avoid and/or tolerate water shortage and possibly inducing alterations in tree species composition.

In this study, we investigated leaf and whole tree water use and short-term regulation mechanisms in five co-occurring tree species growing in a species-rich temperate broad-leaved forest in Central Germany. Sycamore (*Acer pseudoplatanus* L.), European beech (*Fagus sylvatica* L.), European ash (*Fraxinus excelsior* L.), hornbeam (*Carpinus betulus* L.) and little-leaf linden (*Tilia cordata* Mill.) represent species with a contrasting distribution range in Europe and, thus, putatively differing in drought avoidance and tolerance strategies (Marigo et al., 2000; Bolte et al., 2007; Ellenberg and Leuschner, 2009). Except for beech, data on the drought response of the important Central European tree species is scarce (Aranda et al., 2005; Bréda et al., 2006; Cochard et al., 1996; Leuzinger et al., 2005; Magnani and Borguetti, 1995; Marek et al., 1989; Nardini and Salleo, 2000).

This study was conducted on adult trees growing under similar soil moisture and microclimate conditions. We used a canopy lifter which allowed access to the upper sun crown of two different trees of each of the five species listed above. By synchronously measuring leaf conductance for water vapour, apparent hydraulic conductance in the root and stem flow path, and leaf water potential in relation to atmospheric and soil water status, we aimed at a characterization of the five tree species' water consumption strategies under conditions of ample and limited soil water supply. Study objectives were (i) to compare the five tree species with respect to the D sensitivity of leaf conductance, (ii) to quantify the influence of D and soil matrix potential on xylem sap flux and leaf conductance, and (iii) to analyze the response of leaf water potential in these five species to decreasing soil matrix potential. These investigations in adult trees should help to improve our understanding of how temperate trees differ in their short-term strategies of controlling water flux in the soil-plant atmosphere continuum under field conditions and to predict more precisely how different tree species will respond to a future drier climate.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted in a temperate mixed broad-leaved forest in the Hainich National Park in western Thuringia, Central Germany (51° 04' N, 10° 30' E). The Hainich is a forested plateau range (350 m a.s.l.) that encompasses an area of 22 000 ha, constituting the largest non-fragmented beech-woodland block on calcareous soil in Germany (Hiekel et al., 2004). Mean annual temperature recorded at the nearby Weberstedt meteorological station is 7.5 °C and mean annual rainfall is 590 mm (Deutscher Wetterdienst, 2005).

In the study, we selected two individuals each of *F. sylvatica*, *T. cordata*, *C. betulus*, *F. excelsior* and *A. pseudoplatanus* with a maximum distance of 50 m to each other. The criteria used for tree selection were that trees were within a similar DBH size class (about 35 to 70 cm) and that the tree crown was located within the upper canopy (Tab. I). To access the uppermost sun canopy we used a mobile canopy lifter (model DL30, Denka-Lift A/S, Denmark) that allowed reaching at 30 m height.

The investigation was conducted between July and October 2006. Diurnal measurements were related to solar time which is 80 min behind of Central European Summer Time (CEST).

2.2. Microclimatic measurements

Hourly values of precipitation, global radiation, air temperature and relative air humidity for the whole year 2006 were obtained from the weather station Weberstedt/Hainich (Meteomedia GmbH) located about 2 km from the study plot. Additionally, for calculating vapor pressure deficit D directly above the crown of the study trees, we measured air temperature and relative air humidity in the upper canopy at the study plot with a Rotronic temperature and humidity probe (MP 100A Hygromer, Rotronic, Ettlingen, Germany). Measurements were taken every 15 s and stored as half-hourly means in a Campell CR10X data logger (Campbell Scientific, UK). To compare tree water status to the variation in climatic parameters on a daily scale, we removed the effect of different day lengths and used the daytime mean of D.

2.3. Soil water content and soil water potential

Volumetric soil water content (Θ_V, vol. %) was measured with TDR sensors installed at three different depths (10, 30 and 50 cm) in

Table I. Biometric data of all studied trees: diameter at breast height (DBH), tree height (H), basal area (A_B), average leaf size (LS) and specific leaf area (SLA). LS and SLA are means of $n = 35$ and $n = 44$ leaves collected from the upper crown, respectively. Values in parentheses are the standard error.

Species	DBH (cm)	H (m)	A_B (cm^2)	LS (cm^2)	SLA (cm^2 g^{-1})
A. pseudoplatanus #1	77.7	34.5	4737.7	75.16 (3.38)	80.81 (1.3)
A. pseudoplatanus #2	53.8	29.0	2272.8	76.40 (5.02)	127.50 (3.35)
F. sylvatica #1	40.1	29.2	1263.4	16.41 (0.57)	107.01 (2.86)
F. sylvatica #2	48.4	32.5	1838.6	22.54 (0.8)	112.95 (4.12)
F. excelsior #1	39.5	27.4	1223.6	165.74 (6.33)	105.11 (3.74)
F. excelsior #2	35.0	26.3	962.9	171.04 (7.04)	109.66 (5.97)
C. betulus #1	34.4	24.3	928.2	24.26 (0.56)	114.21 (2.45)
C. betulus #2	37.2	24.7	1089.3	30.57 (0.91)	137.16 (7.29)
T. cordata #1	40.1	28.9	1263.4	30.15 (1.39)	138.83 (8.58)
T. cordata #2	64.6	33.6	3279.3	23.57 (0.74)	128.90 (4.8)

close proximity to the studied trees. Between July and October 2006, two measurements were taken per day (0:00h and 12:00h).

Soil matrix potential (Ψ_s, MPa), which is a more important parameter to asses plant response to soil drought than volumetric soil water content, could not be measured with tensiometers because of low Ψ_S values (beyond the measuring range of the tensiometers) during part of the study period. Instead, we used the program Rosetta Lite Version 1.0 (Schaap et al., 1998) to calculate soil water potential from soil water content (Θ_v) data. Necessary soil parameters (e.g. clay content, bulk density) were provided by Guckland et al. (2008).

2.4. Leaf water potential, transpiration rate and leaf conductance

Leaf water potential (Ψ_L, MPa) was measured with a Scholander pressure chamber (Scholander et al., 1965). Leaf (or shoot) samples were collected from the exposed sun crown of the 10 selected trees. Predawn leaf water potential (Ψ_{pd}, MPa) was measured before sunrise between 2:00h and 4:30h. Noon leaf water potential (Ψ_{noon}, MPa) was recorded between 12:00h and 13:30h. Three to four leaf (shoot) samples were measured per tree.

Leaf transpiration (E, mmol m^{-2} s^{-1}) and leaf conductance (g_L, mmol m^{-2} s^{-1}) were measured with a Li-Cor-1600M steady state porometer (Li-Cor, Lincoln Nebraska, USA). We conducted measurements between 6:00 and 7:00, 9:00 and 10:00, 12:00 and 13:00, 15:00 and 16:00h. Each time we sampled ten leaves per tree from the upper sun crown. Per field working day, we were able to measure 3 or 4 different trees synchronously because of the limited mobility range of the canopy lifter. To complete measurements in all 10 trees we needed three consecutive days with similar light conditions. Four complete field campaigns and additional single-day measurements could be conducted between July and September 2006, a period which included contrasting soil moisture conditions.

2.5. Xylem sap flux

Sap flux density in the stem (J_s, g m^{-2} s^{-1}) was monitored with the constant-heat method after Granier (1987). Two 20 mm-long Granier-type probes were inserted at a distance of 15 cm from each other at lower and higher insertion points into the stem at 1.3 m height. The upper probe was constantly heated (200 mW), while the lower one served for monitoring the reference temperature of the stem. The temperature difference between the heated and the reference probe was recorded continuously and related to the maximum temperature difference occurring at predawn when minimum or no flow occurred. Sap flux density was calculated according to the empirical equation given by Granier (1987). To avoid disturbance by thermal gradients or stem flow runoff at the measuring points, the sensors were insulated by polystyrene mats and covered with a reflecting foil and a transparent plastic cover. Sap flux data were logged every 30 s and a mean value was recorded every 30 min. Half-hourly sap flux density values were summed to obtain daily flux density in g cm^{-2} d^{-1}. We used data from a prior study (Gebauer et. al., 2008) which investigated radial patterns and changes in sapwood area with tree size of the same tree species at the same forest site. No corrections of sap fluxes as suggested by Clearwater et al. (1999) were necessary for our study trees.

2.6. Whole-tree hydraulic conductance

The amount of water which flows under a given pressure gradient through a tree is determined by the hydraulic conductance (L_c, g MPa^{-1} s^{-1} m^{-2}) of the flow path between soil and leaf, and the water potential gradient along this flow path. L_c was calculated from J_s and the difference in Ψ_{pd} and Ψ_{noon} after Loustau and Granier (1993) and Pataki et al. (2000). We used J_s data that were recorded synchronously to the Ψ_{noon} values. L_c was calculated as follows:

$$L_c = \frac{J_s}{(\Psi_{pd} - \Psi_{noon})}. \tag{1}$$

2.7. Statistical analyses

The data sets showed a non-Gaussian distribution according to a Shapiro & Wilk test. Parameters of leaf morphology were compared pairwise among species with the Wilcoxon U-Test after Mann & Whitney. The relationship between D or Ψ_S and Ψ_L, g_L and J_{sd} was analyzed with linear and non-linear regressions using the program Xact 7.20g (SciLab GmbH, Hamburg, Germany). All other calculations were conducted with SAS statistical software, version 8.02 (SAS Institute, Cary, NC, USA). Significance was determined at $p \leqslant 0.05$ in all tests.

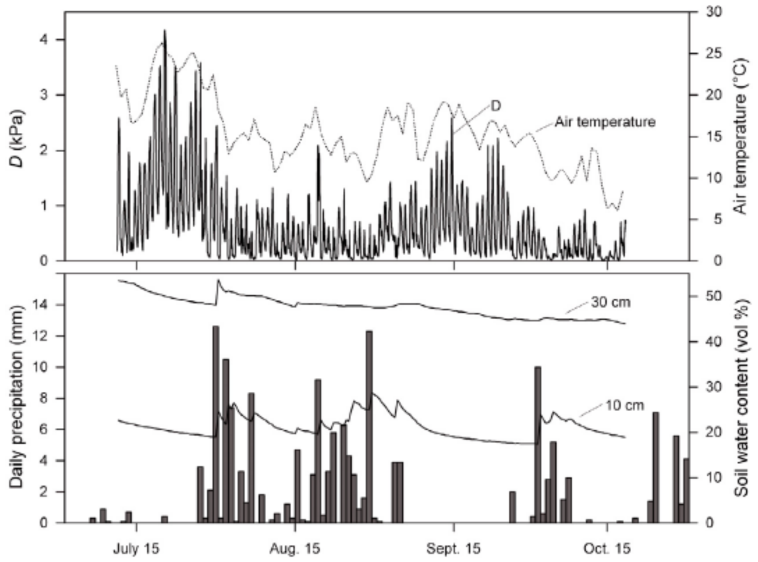

Figure 1. Top: Seasonal courses of vapor pressure deficit (*D*) and air temperature (daily means) from July to October 2006. Bottom: Daily precipitation (*P*, bars) and soil moisture content (Θ_V) at 10 and 30 cm depth during the study period.

3. RESULTS

3.1. Climate conditions and soil water content

The daily means of air temperature during the study period (July 11th to October 18th, 2006) varied between 6 and 26 °C (Fig. 1) which was higher than the average except in August. During the second half of July, *D* achieved highest values with about 4 kPa (Fig. 1). In September, *D* declined due to lower temperatures. Annual precipitation in 2006 was 72 mm less than the long-term precipitation average (590 mm). July and September were almost rainless months, while rainfall was relatively high in August. At 30 cm soil depths, Θ_V decreased continuously from 54 vol. % to 44 vol. % between mid July and mid October, only interrupted by an infiltration event at the beginning of August. In contrast, Θ_V closely followed the rainfall events at 10 cm depth (Fig. 1). During the dry periods in July and September, Θ_V at 10 cm decreased continuously from 29 to 17 vol. %.

3.2. Biometric data

Biometric characteristics of the studied trees are shown in Table I. Diameter at breast height (DBH) of the trees varied between 34.4 cm and 77.7 cm and tree height ranged from 24.3 to 34.5 m. Leaf size and specific leaf area (SLA) showed considerable species-specific differences: *T. cordata* and *C. betulus* had a significantly higher SLA than the other species, *A. pseudoplatanus* had the smallest value. SLA between individuals of the two *A. pseudoplatanus* differed considerably (80.81 and 127.5). This is probably due to the spatial position of the two trees in the canopy.

3.3. Leaf conductance and leaf water potential in their dependence on soil and atmospheric water status

The five species differed considerably with respect to the daily maxima of leaf conductance (g_L) that were observed in sun canopy leaves during the study period. Peak values of g_L reached 270–280 mmol m^{-2} s^{-1} in *F. excelsior* and *C. betulus*, and 250 mmol m^{-2} s^{-1} in *T. cordata*, but did not exceed 150–170 mmol m^{-2} s^{-1} in *A. pseudoplatanus* and *F. sylvatica* (Fig. 2). Daily maxima of g_L decreased linearly with a decrease in soil matrix potential at 10 cm depth (Ψ_s) in all species except for *F. excelsior*; however, the slope of the conductance decrease was steeper in the species with higher maximum g_L (*T. cordata* and *C. betulus*) than in *F. sylvatica* and *A. pseudoplatanus* with low maximum g_L (Fig. 2). Higher maximum conductances were associated with much higher day-to-day variation in g_L levels as is visible when comparing the plots of *T. cordata* and *A. pseudoplatanus* in Figure 2.

Leaf conductance decreased exponentially with increasing atmospheric saturation deficit (*D*) in the species with high maximum g_L (*F. excelsior*, *T. cordata* and *C. betulus*), but showed a more gentle decrease in *F. sylvatica* and *A. pseudoplatanus*, the two species with low maximum g_L (Fig. 3).

The water potential of sun canopy leaves measured at noon (Ψ_{noon}) responded differently to increasing soil drought in the five tree species. We assumed the same matrix potential in the soil for all species because of the absence of a clear spatial segregation of the rooting systems of these species in the study area (Meinen, 2008). In *C. betulus* and *T. cordata*, Ψ_{noon} remained unchanged upon a decrease in soil matrix potential from –0.05 to –0.17 MPa, while Ψ_{noon} significantly decreased from –2.0 to –2.5 MPa in *F. sylvatica* with increasing soil drought (Fig. 4). No trend was visible in the Ψ_{noon}

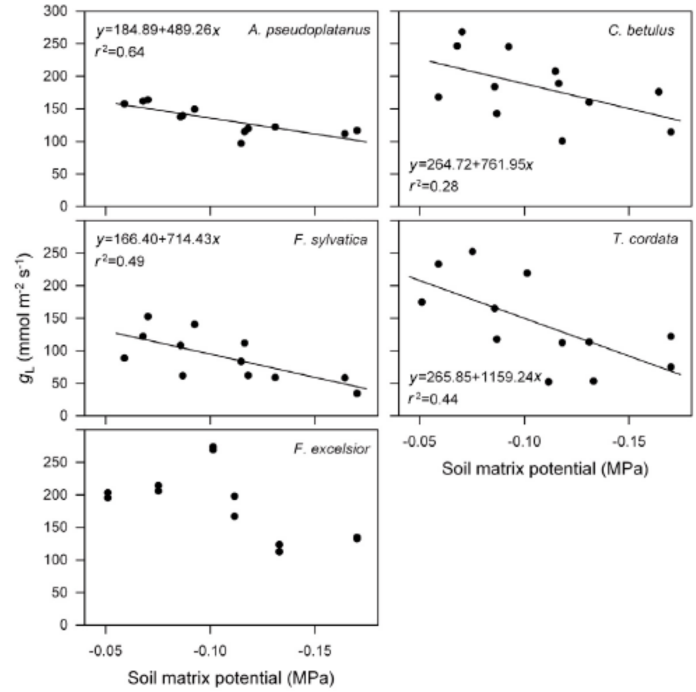

Figure 2. Relationship between daily maxima of leaf conductance (g_L) and the corresponding soil matrix potential (Ψ_s) at 10 cm depth for the five studied tree species. Values are means of $n = 10$ sampled leaves (per individual).

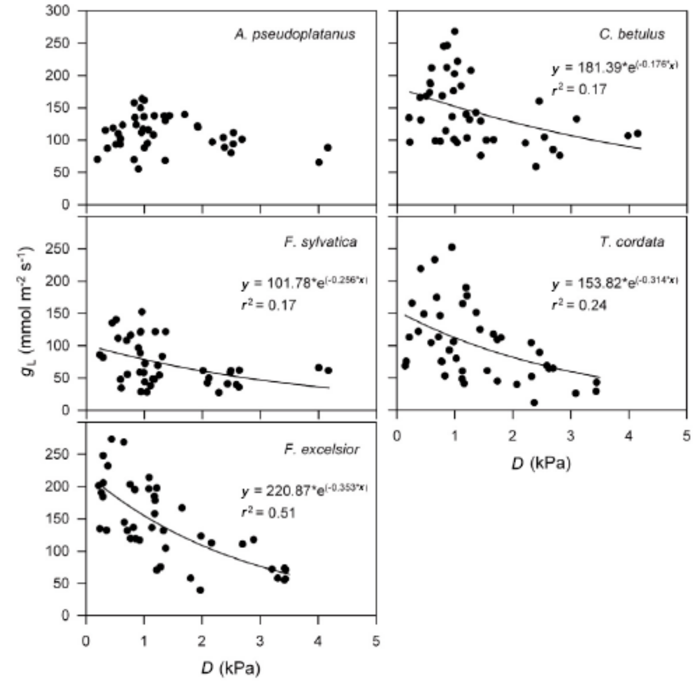

Figure 3. Leaf conductance (g_L) as a function of vapor pressure deficit (D) for the five tree species in data sets of up to 43 measurements taken between July and September 2006. All regressions are significant ($p < 0.05$) except for that of *A. pseudoplatanus*.

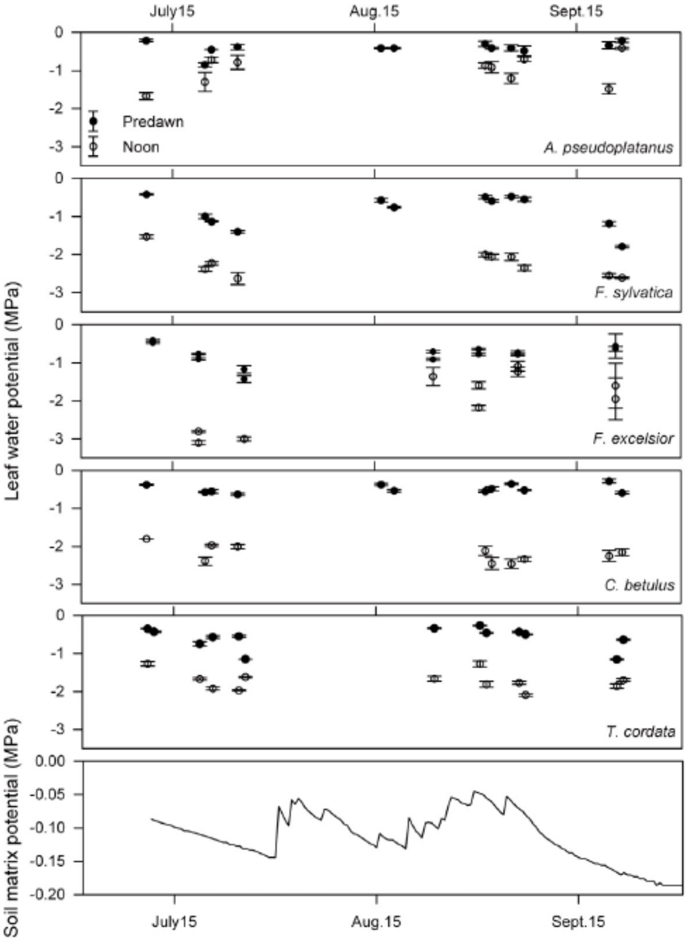

Figure 4. Seasonal course of predawn and noon leaf water potential (Ψ_{pd} and Ψ_{noon}) for the five studied tree species. Error bars indicate the standard error (n = 3–4). Bottom: Seasonal course of soil matrix potential (Ψ_S) at 10 cm soil depth.

values of *A. pseudoplatanus* and *F. excelsior*, but the day-to-day fluctuation in leaf water potential minima was much higher in these two species than in *C. betulus*, *T. cordata* and *F. sylvatica*. Lowest Ψ_{noon} values were measured in *F. excelsior* (< –3.0 MPa), followed by *F. sylvatica* (–2.6 MPa) and *C. betulus* (–2.5 MPa) while *A. pseudoplatanus* differed from the other species because of its high daily Ψ_{noon} which typically did not fall below –1.5 MPa (Fig. 4). The species also contrasted with respect to the daily leaf water potential maxima (predawn value, Ψ_{pd}): *A. pseudoplatanus* and *C. betulus* maintained high predawn potentials (typically > –0.5 MPa) in the sun canopy throughout the measuring season with no significant effect of drought. Similarly, Ψ_{pd} of *F. excelsior* did not decrease upon a decrease in soil matrix potential, but the day-to-day variation was considerable. In contrast, *F. sylvatica* and *T. cordata* exhibited a significant and (in beech) steep decrease of Ψ_{pd} with a drop in Ψ_S from –0.05 to –0.17 MPa (Fig. 4). The lowest absolute minima of Ψ_{pd} were recorded in *F. sylvatica* (–1.79 MPa).

3.4. Xylem sap flux response to soil and atmospheric water status

The five tree species showed rather similar average and maximum xylem sap flux densities in the stem (J_{sd}, flux density per day) during the study period (Tab. II). Remarkably, ring-porous *F. excelsior* differed not significantly from the four diffuse-porous species. Highest flux densities were observed in *C. betulus* #1 with 171.4 g cm^{-2} d^{-1}. We observed large differences in the average flux density between different trees of a species (*F. sylvatica* and *C. betulus*, Tab. II) in spite of the similar tree sizes. We suspect that these differences may be due the location of the flux sensors in sapwood areas with different conductivities.

A decrease of soil matrix potential from –0.08 to –0.18 MPa reduced xylem sap flux to about a third in *A. pseudoplatanus*, *F. sylvatica* and *C. betulus*, and to about the half in *T. cordata* (Fig. 5). In contrast, no decrease in xylem sap flux with increasing soil drought occurred in *F. excelsior*, but J_{sd} rather

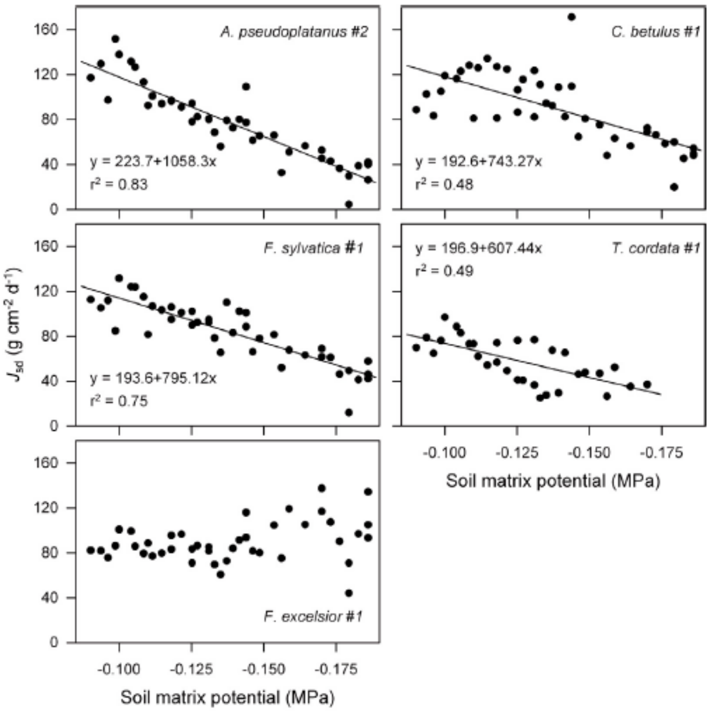

Figure 5. Daily sap flux density (J_{sd}) as a function of the soil matrix potential (Ψ_S) at 10 cm soil depth. One individual each of the five species is shown. Values correspond to the dry periods in July (July 12–July 30, 2006) and September (Sept. 08–Sept. 30, 2006). For trees with a significant correlation ($p < 0.05$), the linear regression lines are drawn.

tended to increase at soil matrix potentials < –0.15 MPa, while the data showed increasing variability. The spread in J_{sd} values towards decreasing soil matrix potential coincided with a lack of a relationship between J_{sd} and D under soil drought (Fig. 6). This may indicate a lack of stomatal control; however, we had very few data of g_L at low Ψ_S to confirm this theory.

The response of J_{sd} to variable atmospheric saturation deficits was studied with data sets from a "wet period" with soil water contents > 21 vol. % and soil matrix potentials > –0.107 MPa, and from a "dry period" with $\Theta_s < 21$ vol. % and $\Psi_S < -0.107$ MPa. At this threshold soil moisture, leaf water potential and sap flux density were found to decrease significantly in the majority of species (Fig. 4). The dependence of J_{sd} on D was described with logarithmic functions for the wet and the dry period in the five species in Figure 6. In all species, the relationship was stronger in the wet than in the dry period as reflected in higher coefficients of determination (r^2) and also in steeper slopes. In the case of *T. cordata* #1 and *F. excelsior* #1, no significant J_{sd}/D-relationship appeared in the dry period.

Based on sap flux data (measured around noon) and corresponding Ψ_{noon} and Ψ_{pd}, we calculated maximum L_c of the flow path soil-to-leaf in the five species (Tab. II). In *T. cordata*, *C. betulus, F. excelsior* and *F. sylvatica*, we obtained conductivities in the range of 0.82 to 2.88 mol m^{-2} s^{-1} MPa^{-1} in the wet period and of 0.53 to 0.99 mol m^{-2} s^{-1} MPa^{-1} in the dry period, respectively. Thus, L_c was markedly smaller in the dry period in all species. An exception was the tree *F. sylvatica* #2, which had unusually small conductivities in both the dry and the wet period (0.45 and 0.36 mol m^{-2} s^{-1} MPa^{-1}). *A. pseudoplatanus* differed from all other tree species by having significantly higher L_c values both in the wet and the dry period (Tab. II).

4. DISCUSSION

4.1. Species differences in leaf conductance and leaf water potential

Our measurements in sun canopy leaves of adult trees revealed considerable differences in maximum g_L among the five co-occurring tree species. High peak g_L values (up to 280 mmol m^{-2} s^{-1}) were recorded in *C. betulus*, *F. excelsior* and *T. cordata*. These species are known to be drought-tolerant and to have large distribution ranges that include continental Eastern Europe (Ellenberg and Leuschner, 2009). In contrast, the drought-sensitive species *F. sylvatica* and *A. pseudoplatanus* with known distribution range restricted to sub-oceanic Central and Western Europe (Ellenberg and Leuschner, 2009) reached g_L maxima not higher than 160 to 180 mmol m^{-2} s^{-1}. These values are closed to the g_L means given by Körner (1994) for temperate forest. Higher g_L in adult *F. sylvatica*

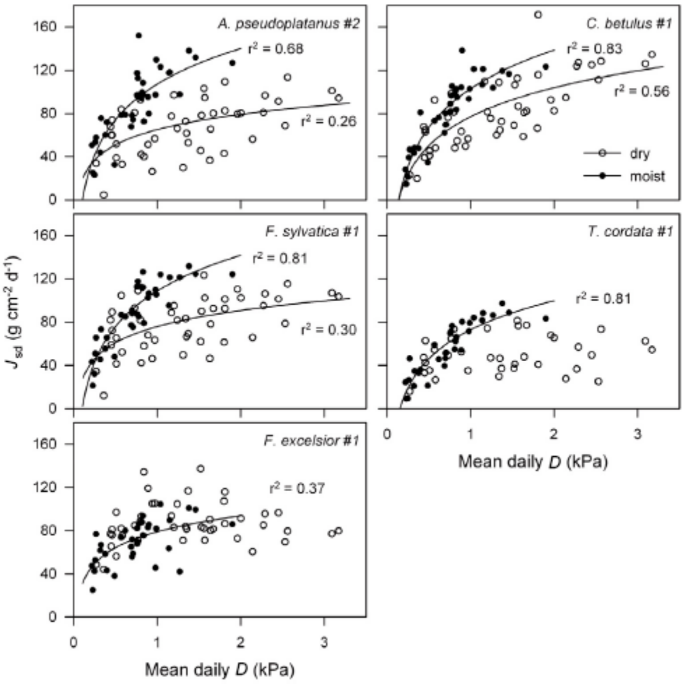

Figure 6. Daily sap flux density (J_{sd}) as a function of vapor pressure deficit (D) for periods with high (filled circles) and low (open circles) soil moisture content (Θ_V). Periods of different soil humidity were defined according to the criteria: ($\Theta_{high} > 21$ vol. % $> \Theta_{low}$) or ($\Psi_{S\ high} > -0.107$ MPa $> \Psi_{S\ low}$). For each species, one individual is shown. For trees with a significant relationship ($p < 0.05$) logarithmic functions of the type $y = a + b \times \ln(D)$ are drawn.

Table II. Mean values of daily sap flux density (J_{sd}), hydraulic conductivity (L_c) and leaf conductance (g_L) of all studied trees during wet and dry periods. For comparison, the maximum value of each tree recorded over the whole study period is given as well. Wet and dry periods are defined by soil moistures > 21 or < 21 vol. %. In the dry period, air temperature and saturation deficit were generally higher than in the wet period, resulting partly in higher fluxes (* means $n = 1$).

Species	J_{sd} (g cm^{-2} d^{-1})			L_c (mol m^{-2} s^{-1} MPa^{-1})			g_L (mmol m^{-2} s^{-1})		
	Max.	Wet	Dry	Max.	Wet	Dry	Max.	Wet	Dry
A. pseudoplatanus #1	103.0	66.5	65.2	3.95	2.95	2.60*	164.1	158.6	104.5
A. pseudoplatanus #2	152.0	87.7	67.9	10.87	5.10	3.27	157.9	145.1	119.7
F. sylvatica #1	131.7	89.2	78.7	1.37	1.30	0.99	152.6	138.5	71.2
F. sylvatica #2	123.2	21.0	31.1	0.45*	0.36	0.45*	108.5	86.4	52.0
F. excelsior #1	137.4	70.2	86.4	4.09	1.91	0.57	273.8	230.6	150.2
F. excelsior #2	96.8	56.6	64.5	4.88	2.88	0.69	269.1	223.6	137.5
C. betulus #1	171.4	81.7	82.3	1.02	0.95	0.78	268.3	253.4	192.0
C. betulus #2	108.4	45.5	39.4	0.88	0.82	0.53	184.1	165.1	125.2
T. cordata #1	97.2	55.1	50.0	1.25	1.06	0.57	252.3	215.4	60.3
T. cordata #2	98.8	44.9	59.7	1.66	1.20	0.83	233.2	172.1	116.1

trees (up to 250–290 mmol m^{-2} s^{-1}) have been reported by Backes (1996); Backes and Leuschner (2000); Roberts and Rosier (1994); Tognetti et al. (1995).

Our g_L for *C. betulus* are in the middle range of the values reported by Keel et al. (2007). They found mean maximum g_L between 100 and 300 mmol m^{-2} s^{-1} in a four-year period with the lowest values reported during the dry year 2003. For *T. cordata*, our diurnal mean maximum g_L values agree with the measurements reported by Niinemets et al. (1999), and Sellin and Kupper (2007).

Differences between our measurements and literature data (both using leaf porometry) may reflect intraspecific variation in g_L, or may be a consequence of reduced conductivities in dry summers, or might result from the investigation of different measuring objects (upper vs. lower canopy, large vs. small trees).

Changes in Ψ_{pd} are a meaningful indicator of the development of plant water deficit during drought periods because it expresses the failure of a tree to compensate daytime water deficits during the night. For example, in beech, Ψ_{pd} values of –1.66 MPa have been considered as indicative of severe drought stress (Leuzinger et al., 2005). We recorded Ψ_{pd} values as low as –1.76 MPa in beech which points to severe water shortage. Annual precipitation during 2006 was only 518 mm.

Daily minima of Ψ_{noon} in beech fell below the threshold value of –1.9 MPa determined by Hacke and Sauter (1995). Below this value beech shoots rapidly lost hydraulic conductivity due to embolism. However, Lemoine et al. (2002) reported significant variation in Ψ_L within the crown of beech trees and found that stomatal closure and the percentage of loss conductivity in the xylem was more than 50% in sun exposed branches only when Ψ_L dropped to almost –2.5 MPa.

In *F. excelsior*, Lemoine et al. (2001) found the minimum threshold of leaf water potential to vary between –1.5 and –2.8 MPa depending on habitat, water supply and drought acclimation. Other authors reported loss of hydraulic conductivity starting with water potentials of –2 MPa (Cochard et al., 1997; Crombie et al., 1985). Thus, given the low water potentials measured in ash (–3 MPa), cavitation in shoots most likely occurred during the study period. Much lower and highly variable Ψ_L have been reported by Carlier et al. (1992), with minima ranging between –5.54 MPa on shallow soils and –1.94 MPa on alluvial deposits. *F. excelsior* has an ample plasticity range of adaptation to wet and dry environments (Marigo et al., 2000).

During the whole study period, *A. pseudoplatanus* showed the highest Ψ_{pd} and Ψ_{noon} values of the five species and the smallest daily water potential amplitudes ($\Psi_{pd} - \Psi_{noon}$). Korn (2004) reported similar values on sycamore. Lemoine et al. (2001) found remarkably high (less negative) daily minima of Ψ_L in *A. pseudoplatanus* which they explained by a high shoot hydraulic conductivity. This matches well to our findings of a particularly high root-to-leaf hydraulic conductivity in sycamore.

T. cordata and *C. betulus* did not reach their physiological drought limit in the Hainich forest. With Ψ_{pd} minima not below –1.0 MPa and Ψ_{noon} values at the lowest at –2.09 MPa, *T. cordata* was above the threshold of –2.1 MPa for the beginning of wilting, leaf shedding and shoot growth reduction (Pigott and Pigott, 1993). *C. betulus* reached Ψ_{pd} minima of only –0.7 MPa, which is much less than the predawn potentials of –1.74 MPa recorded by Leuzinger et al. (2005) in the dry summer 2003 in Switzerland.

4.2. Interspecific variation in the relationship between xylem flux density and microclimate

Our results of mean daily xylem flux density (J_{sd}) in the five tree species are relatively low in comparison to the results obtained by Hölscher et al. (2005) in 2001 in a similar forest stand. They measured a mean daily J_{sd} of 102 g cm^{-2} d^{-1} for sycamore, 86 g cm^{-2} d^{-1} for little-leaf linden, 77 g cm^{-2} d^{-1} for hornbeam and 67 g cm^{-2} d^{-1} for ash stems of comparable diameter. The summer of 2006 was, on average, drier than the summer of 2001 and thus resulted in lower mean J_{sd} values in all species. In a very similar manner we found a linear decrease of J_{sd} with decreasing soil water content in sycamore, beech, hornbeam and little-leaf linden; however, the daily J_{sd} values continued to decline below the minimum values found by Hölscher et al. (2005) in the wetter summer 2001. In the case of *F. excelsior*, it is remarkable that even under the much lower soil moisture of the summer 2006 the trees maintained constant J_{sd} rates throughout the drought period with flux rates comparable to the values measured by Hölscher et al. (2005) under a more favorable moist soil water regime. It appears that continuous water supply is secured by the capacity of the species to develop low leaf water potentials and its ability to maintain a large and vital fine root system even during drought (Carlier et al., 1992; Korn, 2004; Stöhr and Lösch, 2004). Apparent hydraulic conductivity in the root-to-leaf flow path was not higher than in the other species, as we would have expected from a ring-porous tree.

The relationship between J_{sd} and D changed with increasing soil drought in all species except for *F. excelsior*. The characteristic plateau in J_{sd} at high D values which indicates stomatal regulation (Phillips et al., 1999) was reached at lower D values under water shortage. This result and the negative relationship between g_L and soil matrix potential indicate that the stomatal regulation was directly or indirectly influenced by soil drought in sycamore, hornbeam and beech. In the case of little-leaf linden, it appears that the stomata lost their sensitivity to air humidity under soil drought resulting in low daily sap fluxes which did not respond to variation in D during the whole drought period. Even though g_L was sensitive to D in ash, no additional effect of soil drought could be observed in this species and no reduction in J_{sd} occurred during dry periods. Several factors may allow this species to sustain constant transpiration rates throughout the growing season. First, the low Ψ_{noon} values observed during the dry period indicate a high capacity of ash trees to absorb water even from relatively dry soils. Active osmotic adjustment during water shortage has been documented in this species by Guicherd et al. (1997), based on the accumulation of malate and mannitol in the leaf symplasm.

4.3. Species adaptation to drought

Despite the limited number of tree individuals investigated in our study, we shall attempt to classify the five species with respect to water consumption and drought tolerance strategies, based on own data and information in the literature.

Beech and sycamore respond sensitively to extended soil drought events and show a strong reduction in J_s and E with decreasing soil water content. High Ψ_L with low daily and seasonal amplitudes and a high apparent L_c in the root-to-leaf path characterize sycamore as a drought avoiding species (Tognetti et al., 1995). Beech can not avoid daily fluctuations in Ψ_L and often large and severe drops in Ψ_{pd} and Ψ_{noon} during extended drought (Backes and Leuschner, 2000). We propose that high J_{sd} and therefore a strongly decreasing Ψ_{noon}

despite of stomatal control (g_L measured in the sun canopy) are partly responsible for the inability of beech to secure stable Ψ_{pd} during soil drought. A low capacity of beech for active osmotic adjustment upon drought (Schipka, 2003) may aggravate symptoms of water shortage during dry periods.

A classification of hornbeam and little leaf linden with respect to their water consumption strategy is less clear. Both species revealed a high maximum g_L and lower effect of drought on stem increment (Frech, 2006) in the Hainich forest. Both traits would suggest the species to be drought tolerators. However, hornbeam and little leaf linden reduced g_L substantially with increasing D and decreasing Ψ_s which would be elements of a drought avoiding strategy. Even though *T. cordata* is normally categorized as a drought tolerating species, our results provide evidence of a moderate sensitivity of this species to extended summer drought as is shown by the significant decrease in Ψ_{pd} upon soil drought. Therefore, in contrast to *C. betulus*, *T. cordata* must be classified as a partly drought-sensitive species, matching the assessment of Aasamaa et al. (2004).

The species which can deal best with prolonged drought period is European ash.

This species occurs in a broad variety of habitats, from occasionally flooded areas to xeric environments, and its ability to withstand drought is remarkable. The species can develop very low Ψ_L (up to –6 MPa, Marigo et al. (2000)), and is able to maintain sufficient leaf conductance and CO_2 assimilation during drought (Carlier et al., 1992; Guicherd et al., 1997; Korn, 2004; Marigo et al., 2000). A high maximum g_L and a low sensitivity of sap flow to water shortage are elements of a drought-tolerating strategy.

The Hainich forest represents a dry site with relative low annual precipitation (590 mm) and clay-rich soils which develop water shortage in summer. We believe that the drought-sensitive species *F. sylvatica* and *A. pseudoplatanus* are coming close to their drought tolerance limit at this site, hence trees exhibit reduced leaf conductance. Furthermore, the lower responsiveness of g_L to D in beech and sycamore supports a common observation that species with inherently low or reduced leaf conductance are less sensitive to D than species with a high maximum g_L (Meinzer, 2003; Oren et al., 1999). As a result of this work, the five species can be arranged with regard to their drought sensitivity at the leaf or canopy level in the sequence ash < hornbeam < little-leaf linden < sycamore < beech if the following tree responses are used as criteria of a low sensitivity: (i) to maintain Ψ_{pd} at a high level during drought periods, (ii) to reach high leaf conductances in periods with not too dry soils, and (iii) to reduce sap flux only moderately upon soil drought. With an increase in the frequency and intensity of summer heat waves as is predicted for parts of Central Europe, species like ash and hornbeam will be in advantage over beech which dominates many forests today. However, the vitality and productivity of the five tree species does not only depend on the regulation of leaf water status, but is also a function of the drought sensitivity of stem growth and leaf and root production, and the success of rejuvenation under a drier climate.

Acknowledgements: We would like to acknowledge the good cooperation with the headquarters of the Hainich National Park, Thuringia. We also thank Hermann Jungkunst for his help with the calculation of soil matrix potentials. We further thank Sarah Haverstock for her help in the field, Heinz Coners for technical support and Dirk Deilke for his help in transporting the crown lift. This study was enabled by a scholarship granted through the Graduiertenkolleg 1086 "Biodiversity Functions in Temperate Forests" funded by Deutsche Forschungsgemeinschaft (DFG).

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Chapter

5

Canopy transpiration in temperate broad-leaved forests of low, moderate and high tree species diversity

Leuschner C., T. Gebauer and V. Horna

Abstract

The importance of tree species diversity for biogeochemical cycles in forests is not well understood. By establishing plantations, forestry has widely reduced tree species diversity, while the consequences for the forest water cycle remain unclear. We aimed at isolating species diversity and species identity effects on canopy transpiration (E_c) in temperate broad-leaved forests and tested the hypotheses that (i) E_c is a function of tree species diversity and (ii) tree species identity (or specific tree functional traits) exerts a major influence on the temporal variation of E_c. We measured xylem sap flux during two years (2005: average precipitation, 2006: relatively dry) synchronously in three nearby old-growth forest stands on similar soil that differed in Shannon-Wiener diversity index *H*' (diversity level [DL] 1 – mostly *Fagus*, *H*'= 0.31; DL2 – dominated by *Fagus*, *Tilia* and *Fraxinus*, *H*'= 0.82; DL3 – dominated by *Fagus, Tilia, Fraxinus, Carpinus* and *Acer*, *H*'= 1.16). In the average summer 2005, E_c was by 50 % higher in the DL3 stand than in the DL1 and DL2 stands (158 vs. 97 and 101 mm yr^{-1}). In contrast, in the dry summer 2006, all stands had similar E_c totals (128 to 139 mm yr^{-1}). Transpiration per crown projection area differed up to 5-fold among the five most common coexisting tree species, probably as a consequence of contrasting sapwood/crown area ratios. However, species differences in E_c were also large on a sapwood area basis, reflecting a considerable variation in hydraulic architecture and leaf conductance regulation among the co-existing species. We could not prove a species diversity effect on E_c, but obtained some evidence of tree-specific traits affecting the seasonal variation of E_c. Contrasting seasonal patterns of stand water use in 2005 and 2006 indicate that species with a relatively high transpiration per projected canopy area (notably *Tilia*) may exhaust soil water reserves early in summer, thereby increasing drought stress in dry years and possibly reducing ecosystem stability in mixed forests.

Keywords

Fagus, *Fraxinus*, Hydraulic architecture, Sap flux, Seasonality, Species composition, *Tilia*, Water use

Introduction

The significance of plant diversity for ecosystem functioning has been one of the central research topics in ecology during the past 15 years. While most research has focused on the role of species diversity, or the diversity of plant functional types, for plant biomass and plant productivity in grasslands and old-field communities (Cardinale et al., 2007, Flombaum and Sala, 2008, Hector et al., 1999, Loreau et al., 2001, 2002, Tilman et al., 2001, van Ruijven and Berendse, 2005), less is known about the functional role of tree species diversity in forest ecosystems (Scherer-Lorenzen et al., 2005, Stoy et al., 2006, 2007). In Central Europe, North America and elsewhere, large areas of natural forest have been replaced by monocultures of coniferous and broad-leaved tree species, resulting not only in a reduction of tree species diversity, but also in a completely modified forest structure. These large-scale man-made alterations in forest diversity may have profound consequences for energy and matter fluxes and the diversity of other organism groups (Ellenberg and Leuschner, in press).

A multitude of forest hydrological studies at different spatial and temporal scales does exist that provide evidence of a considerable tree species effect on the hydrological processes in forests. Stand-level studies on canopy transpiration (E_c) using xylem sap flux measurement, or investigations on stand evapoptranspiration applying the eddy covariance technique, micro-climatological gradient studies or soil moisture budgeting approaches, have revealed a considerable variation in the water use of forest stands composed by different species but growing under similar edaphic and climatic conditions. For example, Stoy et al. (2006) reported that pine plantations in the south-eastern U.S. used more water than neighboring mixed hardwood forests. They concluded that this type of man-made vegetation was better coupled to the atmosphere but was more sensitive to drought. More important, pine plantations even may significantly influence the local precipitation regime due to their higher transpirative water losses. In Central Europe, in contrast, the transpiration rate of mature European beech (*Fagus sylvatica* L.) stands is in most cases higher than that of nearby planted Norway spruce (*Picea abies* Karst) stands growing on similar soil (Benecke, 1984, Bücking and Krebs, 1986).

Co-existing tree species were found to differ up to four-fold in canopy transpiration per ground area when largely different tree functional groups (e.g. broad-leaved vs. needle-leaved or diffuse- vs. ring-porous trees) were contrasted (Baldocchi, 2005, Ewers et al., 2002, Granier et al., 1996, Wullschleger et al., 2001). Tree species differences in E_c are mostly the consequence of species-specific differences in (i) the area of hydroactive sapwood in the stem, (ii) xylem anatomy (ring- vs. diffuse-porous, micro- vs. macroporous), (iii) maximum rooting depth, (iv) leaf area index, (v) the sensitivity of stomatal conductance regulation, and (vi) stem density in the stand (e.g. Baldocchi, 2005, Bush et al., 2008, Ewers et al., 2002, Granier et al., 2000, Vincke et al., 2005, Wullschleger et al., 2001). If tree species differ in the leaf emergence and senescence patterns during the vegetation period or in the sensitivity of their earlywood vessels to embolism, contrasting seasonal courses of E_c may be the consequence.

While canopy transpiration is the only component of forest evapotranspiration directly related to water uptake and release and thus linked to the activity of leaves and roots (Wilson et al., 2001), other components of the hydrological cycle in forests such as canopy interception, soil evaporation, deep seepage or runoff have also been found to be influenced by tree species. Numerous catchment studies have documented the influence of tree species conversions (e.g. mixed hardwood to conifers) on the water cycle of forests over longer time spans (e.g. Brown et al., 2005, Farley et al., 2005). Changes in stand evapotranspiration with successional dynamics, that cover different woody vegetation stages growing under similar soil and climate conditions, were investigated, for example, by Leuschner (2002) and Stoy et al. (2006).

The multitude of evidence in support of profound tree species effects on $\mathrm{E_c}$ contrasts with the scarcity of information existing on putative effects of tree species diversity on canopy transpiration. Baldocchi (2005) was the first to tackle this question by relating the normalized transpiration rates of six forest stands to tree diversity. Surprisingly, he found a negative diversity-evapotranspiration relationship. However, this analysis included stands growing under contrasting edaphic conditions which make conclusions about the effect of tree species diversity (or identity) on evapotranspiration difficult. To our knowledge, only one study in synthetic grasslands does exist so far that systematically addressed the question as to how plant species diversity influences stand evaportranspiration while other variables were held constant (Verheyen et al., 2008). A corresponding study in hardwood stands differeing in tree species diversity and growing under similar climatic and edaphic conditions is lacking. From a theoretical point of view, rare tree species in more diverse forests are unlikely to exert a significant influence on the boundary layer conductance and radiation interception of a stand, two factors which have a large effect on E_c. However, rare tree species could influence stand-level E_c if their traits controlling stomatal conductance were greatly deviating from those of the dominant species. Nevertheless, species with very low stem numbers in the stand will always have a small or negligible effect on stand transpiration.

In this study, we measured canopy transpiration with the xylem sap flux method after Granier (1985, 1987) in three nearby temperate broad-leaved forest stands that differed in the levels of tree diversity. Our aim was to analyze the relationship between tree species diversity and/or tree species identity and forest water use. We focused on canopy transpiration because this is the component of evapotranspiration that is most closely related to species composition. In order to isolate the effect of tree species composition from other environmental factors influencing E_c, the stands were selected in a forest area where a variety of stands with different tree diversities is present under more or less homogenous edaphic and climatic conditions. The selected stands are part of the Hainich Tree Diversity Matrix (Leuschner et al., 2009), a set of old-growth forest stands encompassing plots with low to high tree species numbers (1 to ≥ 5 species) in close neighborhood to each other. The remarkable heterogeneity in forest structure is the consequence of a mosaic of different former land ownerships and management practices that coexisted in the area for centuries (Leuschner et al., 2009). Three levels of tree diversity (DL) are most common in the forest and were selected for comparative study. Canopy layer diversity was characterized by the Shannon-Wiener diversity index *H*' ranging between 0.31 and 1.16 in the three diversity levels.

The study had two objectives: by comparing annual totals of canopy transpiration of the DL1, DL2 and D3 stands during two consecutive years with contrasting precipitation amounts, we aimed at testing the hypothesis that canopy transpiration is significantly influenced by tree diversity. Second, we hypothesized that the seasonal patterns of E_c are dependent on tree species identity because they depend on those tree functionals traits that regulate the water flux in trees. Throughout the growing seasons of 2005 and 2006 we attempted to quantify the relative contribution of the different species to stand canopy transpiration in the mixed stands.

Materials and Methods

Study sites and tree layer diversity

The study sites are located in the north-eastern part of the Hainich National Park, Thuringia, Central Germany, between 295 and 355 m a.s.l. (51°04' N, 10°30' E). The Hainich National Park is a mixed temperate broad-leaved forest dominated by European beech (*Fagus sylvatica* L.). Linden (*Tilia cordata* Mill. and *T. platyphyllos* Scop.), common ash (*Fraxinus excelsior* L.), European hornbeam (*Carpinus betulus* L.) and different maple species (*Acer* *pseudoplatanus* L., *Acer platanoides* L. and *Acer campestre* L.) are co-occurring in different densities; further deciduous tree species like elm (*Ulmus glabra* L.), oak (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.), cherry (*Prunus avium* L.) and service tree (*Sorbus torminalis* L.) are interspersed in lower numbers within the forest. In the study region, hybrids of *Tilia cordata* and *T. platyphyllos* are also occurring. Because of variable degrees of hybridization between these two species, we did not differentiate between them at the species level but refer solely to the genus *Tilia*.

The climate is sub-continental (Klaus and Reisinger, 1995) with a mean annual precipitation of 590 mm and 7.5 °C as mean annual air temperature (1973-2004, Deutscher Wetterdienst, Offenbach, Germany). The study year 2005 received average rainfall amounts with 601 mm, while 2006 was drier than the average (518 mm, Meteomedia AG, Germany).

The soils in the study region developed from loess which is underlain by Triassic limestone (Muschelkalk). The loess cover varies between 75 and 120 cm in thickness. The soil texture in the upper 30 cm of the mineral soil is characterized by high silt (~ 75%) and clay contents (16-25%) but a low sand content (< 5%). The dominant soil type is a Luvisol showing stagnant properties during winter and spring, while the soils are drying out strongly during summer (Guckland et al., 2009).

The study was conducted in three stands of the Hainich Tree Diversity Matrix in plots of 50 m x 50 m size which were classed with three levels differing markedly in tree species diversity (DL). The diversity levels have been determined using the Shannon-Wiener index H' as a measure of tree diversity based on stem density data of all individuals reaching the upper canopy and with a diameter at breast height (DBH, measured at 1.3 m from the base) of at least 7 cm. One plot per diversity level at a maximum distance to the other plots of 2 km was selected for study. In the following, the three stands are referred to as DL1a (i.e. plot # a of diversity level 1), DL2c (plot # c of diversity level 2) and DL3a (plot # a of diversity level 3). H' increased from 0.31 in stand DL1a to 0.82 in DL2c and 1.16 in DL3a (Table 1).

Table 1. Species composition and stand structural characteristics of the three study plots. Mean tree age was determined in wood cores (Schmidt and others, in press). Stem density includes all trees > 7 cm in DBH. Shannon-Wiener index (*H′*) bases on stem density data. Leaf area index (LAI) for 2005 and 2006 was estimated from leaf litter samples (M. Brauns, unpublished data). *H′* - Shannon-Wiener index; BAI - basal area index; SAI - sapwood area index; CAI - crown area index; LAI - leaf area index.

Plot	**Tree species**	**Mean age** (yrs)	**Stem density (all trees)** (ha^{-1})	**Stem density (upper canopy trees)** (ha^{-1})	***H′***	**Mean tree height** (m)	**BAI** ($m^2\ ha^{-1}$)	**SAI** ($m^2\ ha^{-1}$)	**CAI** ($m^2\ ha^{-1}$)	**LAI** ($ha\ ha^{-1}$)		**Soil profile depth** (cm)
										2005	**2006**	
DL1a	**Stand**	**109 (±12.0)**	**428**	**232**	**0.31**	**33.3 (±2.2)**	**46.13**	**33.35**	**12446.8**	**6.5**	**7.3**	**120**
	Fagus sylvatica		400	224			44.01	31.78	11753.2			
DL2c	**Stand**	**83 (±17.8)**	**776**	**376**	**0.82**	**29.2 (±2.1)**	**45.00**	**29.02**	**14874.0**	**6.6**	**6.5**	**120**
	Fagus sylvatica		572	264			30.12	22.45	10832.4			
	Tilia sp.		84	40			5.68	4.48	2050.4			
	Fraxinus excelsior		100	64			7.98	1.62	1473.2			
DL3a	**Stand**	**116 (±16.8)**	**392**	**188**	**1.16**	**27.4 (±1.9)**	**35.73**	**23.64**	**12557.6**	**7.3**	**7.6**	**75**
	Fagus sylvatica		12	12			3.76	2.67	875.6			
	Tilia sp.		264	108			19.59	13.58	6851.6			
	Fraxinus excelsior		28	20			3.35	1.31	1163.6			
	Carpinus betulus		36	20			3.58	2.42	1770.4			
	Acer sp.		32	12			2.26	1.65	724.8			

All stands had a closed canopy (gap fraction < 0.1) and roughly comparable stand basal areas (36 to 45 $m^2\ ha^{-1}$) and mean tree ages (83 to 116 years, Schmidt et al., 2009). Leaf area index (LAI, unit: $m^2\ m^{-2}$) varied between 6.5 and 7.3 in 2005, and between 6.5 and 7.6 in 2006 (Jacob et al, in press). While the DL2c plot had a considerably higher total number of stems per hectare than the DL1a and DL3a plots due to abundant beech trees in the subcanopy layer, the number of tree individuals participating in the upper canopy layer was more similar among the stands (188 to 376 trees ha^{-1}). The DL1a plot was mainly composed of beech (93.5% of the stems); the DL2c plot was dominated by beech, linden and ash. The species-richest DL3a plot included all tree species of DL2c and, in addition, contained hornbeam and several maple species (mainly *A. pseudoplatanus* and *A. platanoides*) (Table 1 and Figure 1).

Tree selection for sap flux measurement followed the objective to reach at reliable estimates of stand-level transpiration at the three plots. Thus, stems were selected that represented the different tree species and the most important diameter at breast height (DBH) classes in the respective stands. In the DL1a plot, 8 beech trees were instrumentated, in DL2c, 8 beech, 3 linden and 5 ash trees (16 in total), and in DL3a, 3 beech, 8 linden, 3 ash, 3 maple and 3 hornbeam trees (20 in total). Thus, the total number of measured trees in the stands increased with the diversity level from 8 in DL1a to 20 in DL3a, adding up to 44 in the whole study. All trees were individuals that reached the middle or upper canopy.

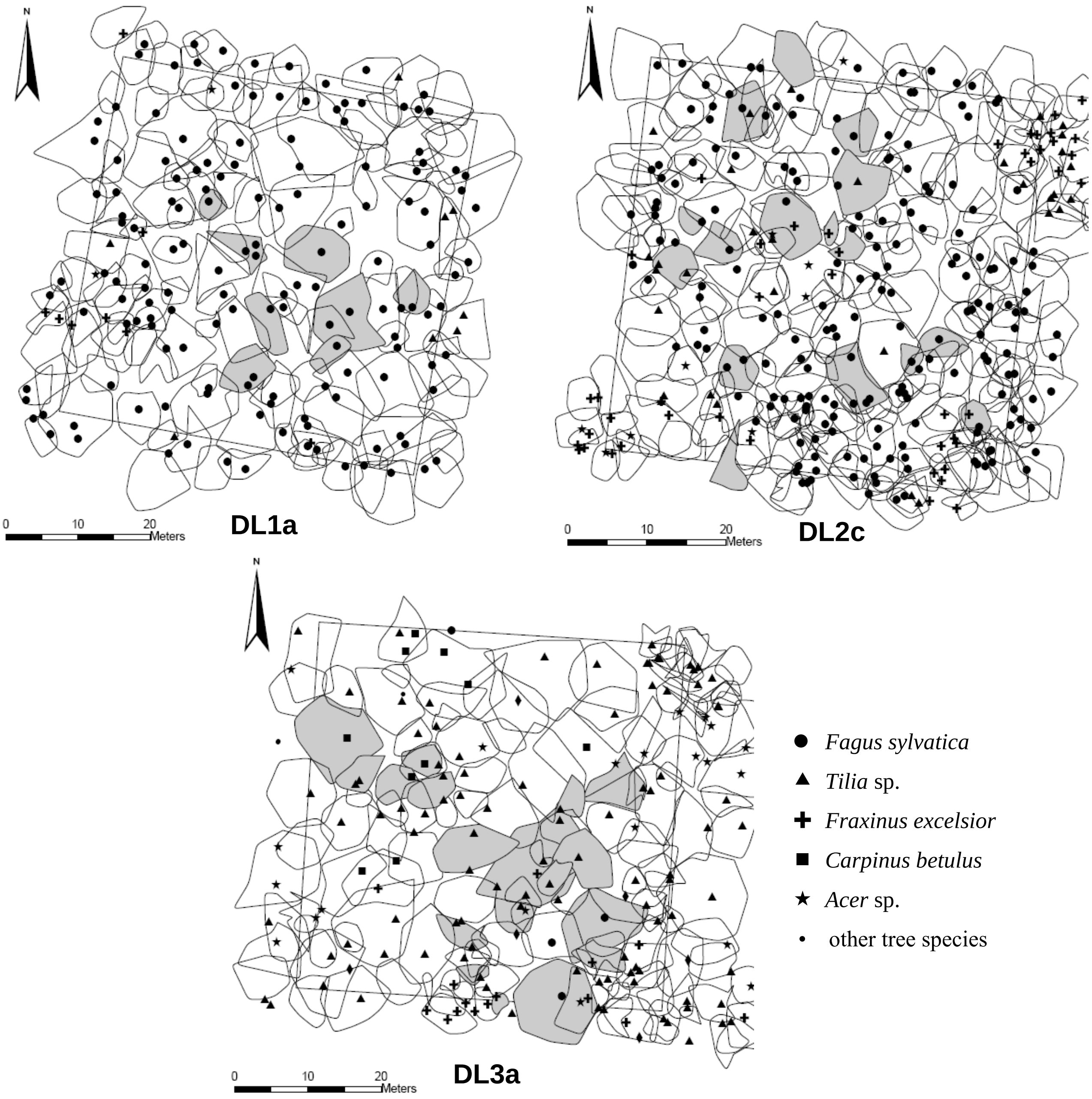

Figure 1. Maps of stem positions (dots) and projected crown areas of the trees in the study plots DL1a, DL2c and DL3a (GIS maps created by K.M. Daenner). Plot size was 50 m x 50 m. Shaded crowns are the trees instrumented with sap flux sensors.

Stand Structure

Diameter at breast height, basal area at 1.3 m height (A_B), and projected crown area (CA_p) of all trees in the 2500 m^2 plots were recorded by DBH measurements with dendrometer tapes and by determining the crown radii in 8 directions (8-point crown projections). LAI and tree height data was taken from Jacob et al. (in press). The LAI of the plots was calculated from the leaf biomass collected in each 10 litter traps per stand. The leaves were sorted by species and measured for size, dried and weighed. LAI was calculated by multiplying mean specific leaf area (SLA) with leaf mass for all species present. The hydroactive sapwood area (A_S) at breast height was calculated from relationships between DBH and A_S, that had been established earlier for the 5 most common tree species in the same stands by dyeing and wood coring (Gebauer and others, 2008). Basal area index (BAI), sapwood area index (SAI) and crown area index (CAI) (units: m^2 ha^{-1}) were calculated from stand- and species-specific A_B, A_S and CA_p values divided by ground area (A_G). The phenologies of the tree species were inspected regularly in both years for determining the exact length of the vegetation period in 2005 and 2006.

Sap flux measurements

We measured xylem sap flux density (J_s, unit: g m^{-2} s^{-1}) in the stem xylem using Granier-type heat dissipation sensors (Granier, 1985, 1987) in trees > 10 cm in diameter at 1.3 m height above ground. Pairs of 20 mm-long and 2.0 mm-wide heating probes were inserted in northern and southern trunk directions into the stem sapwood. For the ring-porous species ash, probes with 10 mm heating spiral length were used because of the smaller sapwood thickness compared to the diffuse-porous species. The probes were manufactured according to the original design protocol given by A. Granier (1996, and pers. communication). The two paired sensors were identical in construction. The upper probe was heated with constant current of 0.12 A and a heating power of 0.2 W. The lower probe was unheated and served as a reference to the upper probe. The distance between the two probes was about 15 cm whereby thermal interference especially at zero sap flux should be avoided. The temperature difference between the two probes was recorded with copper-constantan thermocouples placed at the centre of the heating spirals every 30 s with a data logger (CR10X; Campbell Scientific Ltd., UK) equipped with a 16/32-channel multiplexer (AM16/32, AM416; Campbell Scientific Ltd., UK). 30-min averages were calculated from the 30-s readings and stored in the data logger. The temperature difference was used to calculate sap flux density J_s (in g m^{-2} s^{-1}) according to the empirical calibration equation given by Granier (1985, 1987):

$$J_s = 119 \cdot K^{1.231} \qquad (1)$$

where $K = (\Delta T_M - \Delta T)/\Delta T$. ΔT_M is the maximum temperature difference when sap flux is assumed to be zero. In general, ΔT_M was calculated for every day from the predawn temperature readings, given that the VPD data indicated zero flux or very low flux in the night. When microclimatic data indicated significant nighttime flux to occur, ΔT_M was calculated by averaging the ΔT_M values of the days before and after that day (compare Lu et al., 2004).

In both summers (2005 and 2006), sap flux was measured at the same trees.

Canopy Transpiration

Up-scaling of sensor-level sap flux J_s to whole-tree sap flow requires information on the sapwood cross-sectional area (A_S) of the measured tree which was estimated from relationships between DBH and A_S established for 12 to 25 trees per species in these forest stands by Gebauer et al. (2008). Furthermore, the radial patterns of xylem sap flux density within the hydroactive xylem were obtained by analyzing species-specific radial flux profiles in the xylem of 1 to 3 stems each of the five species with sensors placed in four different depths of the sapwood (Gebauer et al., 2008). The flux data were expressed as relative flux density along the sapwood profile (scaled in relative terms) and applied to all stems where sap flux was only measured in the outermost xylem. The results of the dyeing experiments were used for estimating the sapwood depth of the studied trees. Based on this information, we calculated mean tree xylem flux density J_{st} as follows:

$$J_{st} = \frac{\sum_{n=1}^{n} J_s \cdot B_S(x_i) \cdot W(x_i)}{A_S} \qquad (2)$$

where J_{st} is the mean sap flux density in the entire sapwood of a tree (g m^{-2} sapwood s^{-1}), J_s is the mean sap flux density at the outermost sensor position (0-2 or 0-1 cm of xylem depth), B_S (x_i) is the area of concentric rings of 1 cm width between the cambium (x_i) and the heartwood boundary (x_{i+n}) where sap flux reaches zero (unit: m^2), n is the number of rings with index i, W (x_i) is a species-specific proportionality factor (unitless) which expresses flux density at a given sapwood depth (x_i) in relation to flux density at the outermost sensor position, and A_S is the cross-sectional sapwood area of the tree. W was obtained from 4-parametric Weibull functions fitted to the radial flux profile data of Gebauer et al. (2008).

Various methods are available for up-scaling from mean tree water flux to stand-level flow (Cermak et al., 2004). We used the sapwood area index (SAI) for extrapolation, which relates the cumulative sapwood area to ground area (unit: m^2 ha^{-1}), and did this separately for the major DBH classes and the different species. Before calculation, J_{st} was integrated over a day by multiplying the half-hour mean values by 1800 and adding them to obtain values in the unit g m^{-2} sapwood d^{-1}. The daily stand-level transpiration rate E_c (in mm d^{-1}) of a given species was then calculated for m DBH classes as

$$E_{cj} = \left(\frac{A_{Sj}}{A_G}\right) \cdot \frac{1}{m}\sum_{m=1}^{m} J_{st} \qquad (3)$$

with E_{cj} being the daily canopy transpiration of the DBH class j of a species, $\frac{1}{m}\sum_{m=1}^{m} J_{st}$ the daily mean tree sap flux (in g m^{-2} sapwood d^{-1}) of the DBH class j of a species in the stand, A_{Sj} the cumulative sapwood area of all stems of a species in the DBH class j, and A_G the ground area of the plot. The different DBH classes were summed to give the species-specific canopy transpiration of the stand. The total canopy transpiration of the stand (E_c) was then calculated as the sum of the E_{cj} values of all species being present in the plot (unit: mm d^{-1}). All E_c data were related to the length of the vegetation period which extended in the Hainich forest from about April 20 to October 31 (unit: mm or L m^{-2} per vegetation period).

In order to compare the species with respect to their water use, we related the canopy transpiration of a species to the respective species-specific CAI, BAI or SAI values in the stand.

Microclimatological and hydrological measurements

Micrometeorological (air temperature, relative air humidity (RH) and atmospheric vapor pressure deficit (VPD)) and precipitation data were obtained from the Weberstedt/Hainich meteorological station (Meteomedia AG, Germany) located 2 km northeast from our study plots. Incident shortwave radiation (R) data were taken from satellite measurements regionalized to the study region (Meteosat). All variables were recorded at hourly intervals.

Volumetric soil water content (θ) was recorded half-hourly in the three stands at depths of 10, 20, and 30 cm by I. Krämer (unpublished data) using EnviroSCAN FDR sensors (Sentek Pty Ltd., Stepney, Australia). The measurements started in June/July 2005 and were continued throughout the whole year 2006. These data were used to calculate the relative extractable water (REW) in the soil profiles of the three stands using equation (4) (Bréda et al., 1995, 2006, Granier et al., 1999):

$$\mathrm{REW} = \frac{(\theta - \theta_{\min})}{(\theta_{\max} - \theta_{\min})} \qquad (4)$$

where θ is the actual soil water content, $\theta_{\min}$ the minimum soil water content observed in the years 2005 and 2006, and $\theta_{\max}$ the soil water content at field capacity. Field capacity (FC) was estimated from laboratory desorption curves characterizing the water content – water potential relationship with -100 hPa being defined as FC (U. Talkner, unpublished data).

Data analysis

To test the first hypothesis (significant diversity effect on E_c) we applied a model II simple linear regression analysis combined with the major axis method using the *lmodel2* function of the statistical software R, version 2.8.1 (R Development Core Team) (Legendre and Legendre, 1998, Legendre, 2008, Warton et al., 2006) in order to obtain a quantitative measure of similarity or dissimilarity between the sets of E_c daily totals of the three plots. A model II regression was selected because both sets of variables (E_c values of two plots) are random. In the *lmodel2* function, a permutation test is included to determine the significance of the slopes of the major axis method. For the years 2005 and 2006, we analyzed the slopes of linear regression fits of daily E_c totals of one plot on the daily E_c totals of another plot and contrasted the slopes with the 1:1 line (45^{o}) which stands for complete congruity of the E_c time courses of the two plots. The analysis gave parametric 95% confidence intervals (C.I.) for the regression slopes in all six possible plot combinations and the *p*-values and coefficient of determination (R^2) of the respective regressions.

In a second analysis, we compared the patterns of temporal change in daily canopy transpiration in the first half of the vegetation period from early May (leaf flushing) to July 2006 (peak values of E_c) in more detail. Following Legendre (2008), we calculated in this model II regression analysis the inverse of the mean slope factor of the 3-month-period (unit: the inverse of $\frac{\mathrm{mm\,d^{-1}}}{\mathrm{d}} = \frac{1}{\mathrm{mm}}$) and compared their upper and lower 95% confidence intervals and R^2 values among the three plots in order to detect significant differences in the seasonal evolution of E_c in the plots. To obtain a quantitative measure of the size of species effects on E_c (second hypothesis), we partitioned the daily totals of canopy transpiration to the species level and analyzed the seasonal change in the contribution of the various species.

Results

Climatic conditions

The two study summers of 2005 and 2006 differed with respect to VPD, incident radiation and total amount of precipitation received in the vegetation period (363.5 and 314.5 mm in the period April 20 to October 31) (Figures 2 and 3, upper panels). 2005 was an average year with continuous precipitation during the whole vegetation period. VPD did never exceed 13 hPa. Rainfall was lower and rainfall distribution much more irregular in summer 2006 with pronounced rainless periods occurring in June, July and September. The dry spells were related to periods of elevated vapor pressure deficits with VPD maxima reaching 21 hPa in July 2006. In contrast, August 2006 received more rainfall than the long-term average. Volumetric soil water content decreased more or less continuously during the summer of 2005 on the three plots and reached seasonal minima of 13 to 20 vol.% in September and October. The more regular precipitation distribution during this year resulted in a less extreme depletion of the extractable water resources. In 2006, the moisture reduction was more rapid in the first half of the summer with minima of 11 to 20 vol.% already appearing in early August. High rainfall in August 2006 resulted in a temporal refilling of the soil water reserves that were depleted again in an extended rainless period in September. Throughout the summers of both years, the DL1a plot with the monospecific stand showed a higher soil water content than the DL2c and DL3a plots. The moisture decrease in rainless June 2006 was more pronounced under the species-richest stand DL3a than in the other two stands.

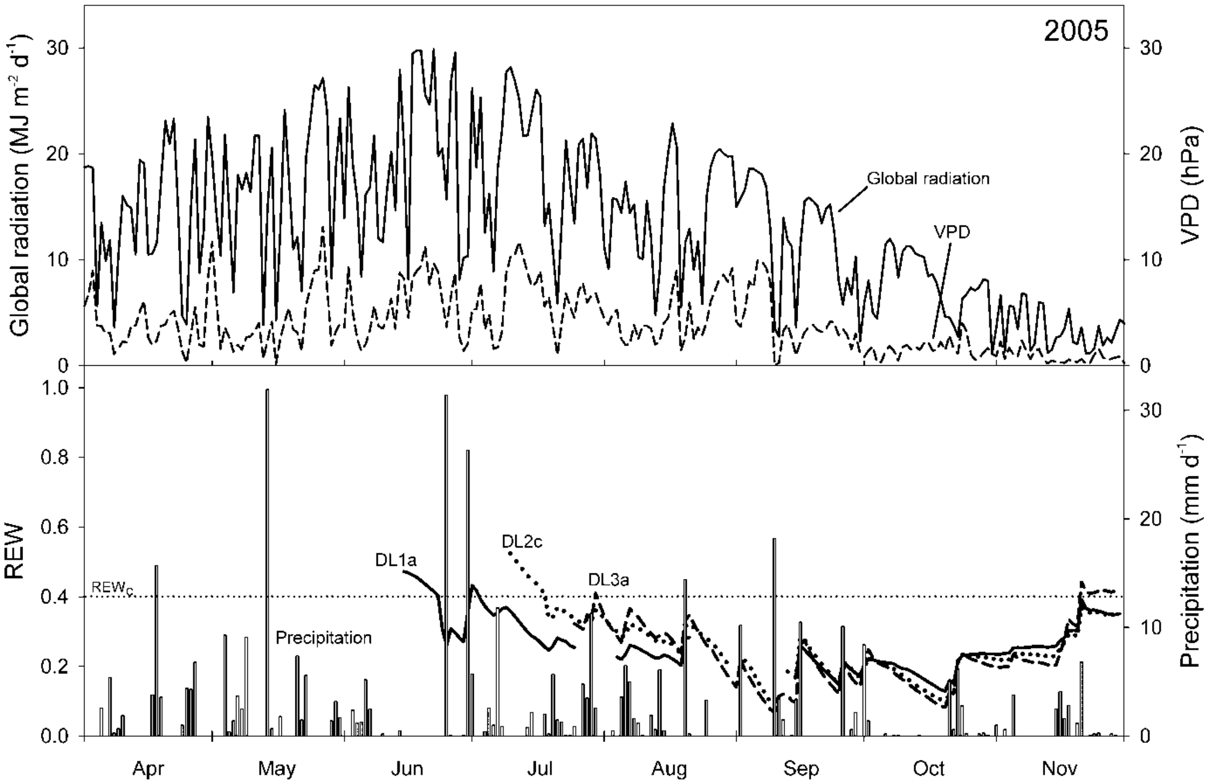

Figure 2. Seasonal course of incident global radiation (daily totals) and atmospheric water vapor pressure deficit (VPD, daily means) at the Weberstedt meteorological station (upper panel) and daily precipitation totals together with the seasonal course of relative extractable water (REW) in the 0-30 cm profile in the plots DL1a, DL2c and DL3a in the period April to November 2005 (lower panel). The dotted line indicates 0.4 x REW which is thought to represent a critical minimum threshold of soil water availability (REW_c) in temperate forests (Granier et al., 1999, 2007; Bernier et al., 2002). No soil water content data were available before mid of June 2005.

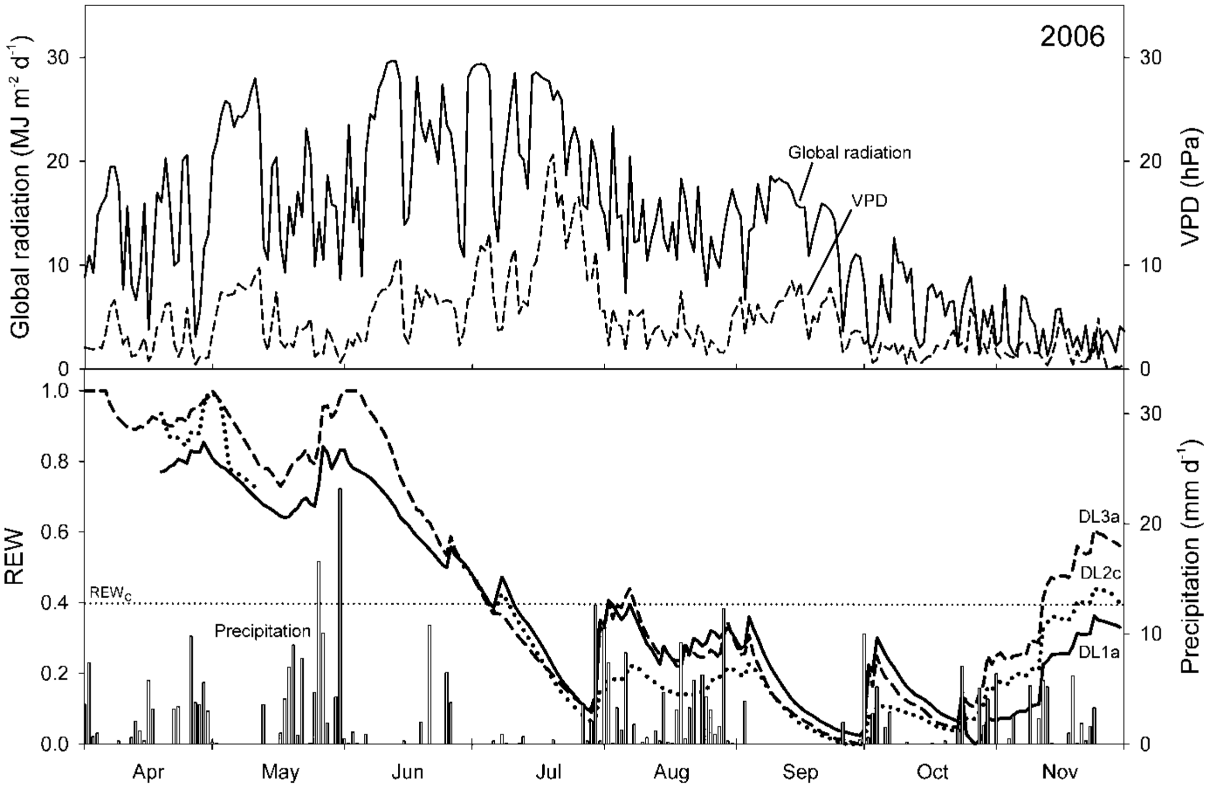

Figure 3. Seasonal course of incident global radiation (daily totals) and atmospheric water vapor pressure deficit (VPD, daily means) at the Weberstedt meteorological station (upper panel) and daily precipitation totals together with the seasonal course of relative extractable water (REW) in the 0-30 cm profile in the plots DL1a, DL2c and DL3a in the period April to November 2006 (lower panel). The dotted line indicates 0.4 x REW.

Canopy transpiration

Up-scaling from tree to stand level gave totals of canopy transpiration (E_c) for the vegetation periods 2005 and 2006 that ranged from 97 to 158 mm in the three stands (Table 2). With regard to our first hypothesis, we found no clear evidence of a general increase or decrease of E_c with an increase in tree species diversity from 1 to 5 abundant species (or genera). In the summer 2005 without a pronounced rainless period, E_c was by 50 % higher in the species-rich stand DL3a (158.4 mm) than in the less diverse stands DL1a and DL2c (97.3 and 100.6 mm). A similar difference between the species-richest stand and the DL1a and DL2c stands existed for mean daily E_c (0.89 mm d^{-1} vs. 0.52 and 0.54 mm d^{-1}) and maximum daily transpiration (2.45 mm d^{-1} vs. 1.14 and 1.25 mm d^{-1}). In comparison to 2005 (190 days), the vegetation period (bud burst to leaf fall) was 17 days longer in 2006. In this summer with several extended dry spells, we calculated similar transpiration rates in the vegetation period for all three stands

(128 to 139 mm). The beech-ash-linden stand (DL2c) showed the highest annual total (139.3 mm) of the three stands, even though the observed maximum daily transpiration rates were lower in this stand (1.52 mm d^{-1}) than in the two others (1.91 and 1.75 mm d^{-1}).

Highest daily transpiration occurred in the DL1a and DL2c stands in July and August 2005, while the peak occurred about 4 weeks earlier in June/July 2005 in the species-richest stand DL3a (Figure 4). Similarly in 2006, E_c peaked earlier in the DL3a stand (around end of June) than in the DL1a and DL2c stands (mid of July, Figure 5). Comparing the initial slopes (May to July) of the seasonal increase in daily transpiration rates in 2006 among the three plots revealed that the DL1a and DL2c stands had similar time courses of canopy transpiration with a slow but steady increase of E_c over time (lower and upper limits of the 95% confidence interval of daily E_c: 0.81-0.99 and 0.79-0.95 mm d^{-1}, respectively, Table 3b). In the species-rich DL3a stand, the increase in E_c was much steeper in early summer (confidence interval limits for E_c: 1.09-1.19 mm d^{-1}). In 2006, higher water losses early in summer were reflected by a more rapid drop of soil water content in late June and early July in stand DL3a as compared to the other stands: the critical threshold of 0.4 REW (Granier et al., 1999, 2007; Bernier et al., 2002) was reached about 10 days earlier (July 2 or 3) in DL3a than in the DL1a and DL2c stands (July 11 and 13) (Figure 3). Corresponding data for 2005 do not exist in the case of stand DL3a.

Table 2. Canopy transpiration (E_c) of all individuals of a species and of the whole stand in the years 2005 and 2006 in the plots DL1a, DL2c and DL3a. The transpiration rates are also expressed in relation to basal area index (BAI), sapwood area index (SAI) and crown area index (CAI) (units of indices: m^2 ha^{-1}). The last column gives stand transpiration as a proportion of precipitation during the vegetation period (P_v) for both years. The indices BAI, SAI and CAI were calculated from stand- and species-level A_B, A_S and CA_p values each divided by ground area (A_G).

Plot	**Tree species**	**E_c** (mm)	**Proportion of stand E_c** (%)	**E_c/BAI** ($x10^3$ L m^{-2})	**E_c/SAI** ($x10^3$ L m^{-2})	**E_c/CAI** (L m^{-2})	**E_c/P_v** (mm mm^{-1})	**E_c** (mm)	**Proportion of stand E_c** (%)	**E_c/BAI** ($x10^3$ L m^{-2})	**E_c/SAI** ($x10^3$ L m^{-2})	**E_c/CAI** (L m^{-2})	**E_c/P_v** (mm mm^{-1})
		2005						2006					
DL1a	**Stand**	**100.6**	**100.0**	**21.8**	**30.2**	**80.8**	**0.28**	**134.3**	**100.0**	**29.1**	**40.3**	**107.9**	**0.41**
	Fagus sylvatica	99.9	99.3	22.7	31.4	85.0		133.4	99.3	30.3	42.0	113.5	
DL2c	**Stand**	**97.3**	**100.0**	**21.6**	**33.5**	**65.4**	**0.28**	**139.3**	**100.0**	**31.0**	**48.0**	**93.7**	**0.42**
	Fagus sylvatica	61.7	63.5	20.5	27.5	57.0		66.6	47.8	22.1	29.7	61.5	
	Tilia sp.	22.4	23.1	39.4	50.0	109.3		59.5	42.7	104.8	132.8	290.2	
	Fraxinus excelsior	13.1	13.4	16.6	80.9	88.9		13.2	9.5	16.7	81.5	89.6	
DL3a	**Stand**	**158.4**	**100.0**	**44.3**	**67.0**	**126.1**	**0.47**	**128.0**	**100.0**	**35.8**	**54.1**	**101.9**	**0.41**
	Fagus sylvatica	15.6	9.8	41.5	58.4	178.2		15.7	12.3	41.8	58.8	179.3	
	Tilia sp.	105.3	66.5	53.8	77.5	153.7		78.1	61.0	39.9	57.5	114.0	
	Fraxinus excelsior	1.9	1.2	5.7	14.5	16.3		1.6	1.3	4.8	12.2	13.8	
	Carpinus betulus	18.4	11.6	51.4	76.0	103.9		17.3	13.5	48.3	71.5	97.7	
	Acer sp.	17.1	10.8	75.7	103.6	235.9		15.3	12.0	67.7	92.7	211.1	

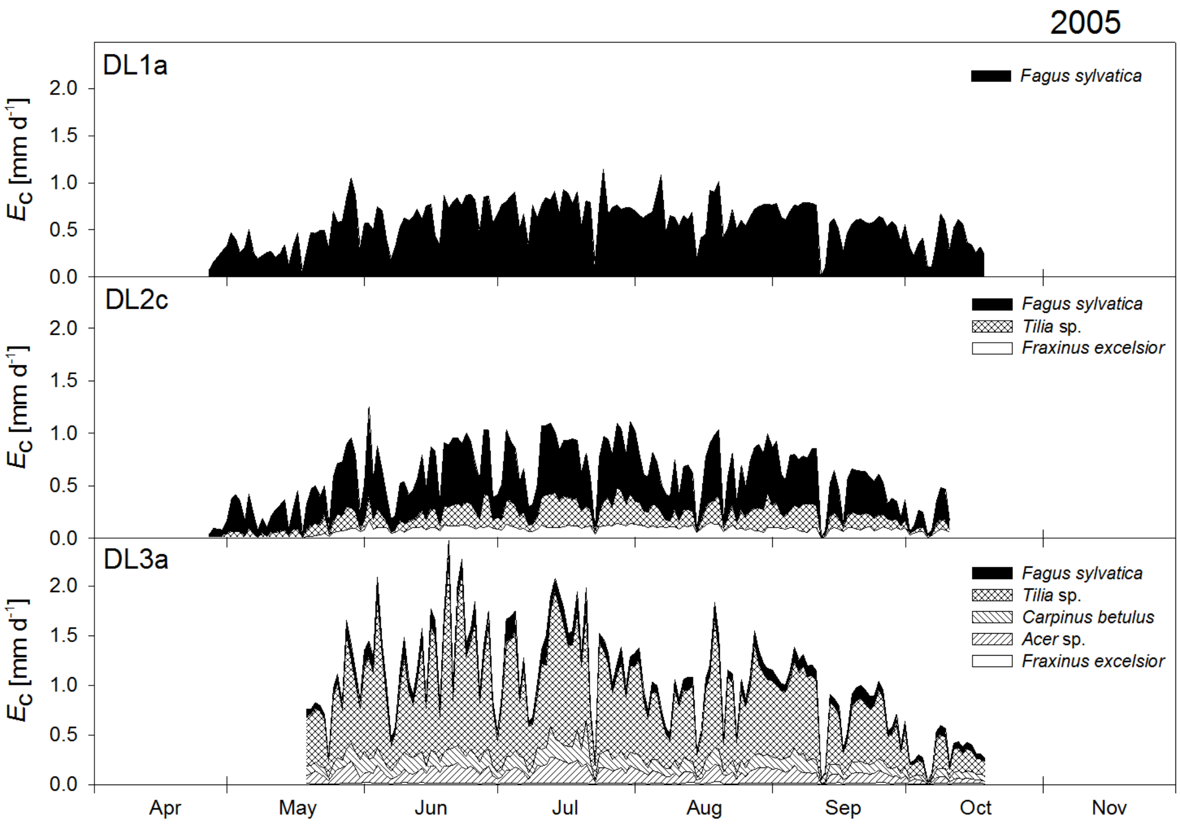

Figure 4. Annual course of canopy transpiration (E_c) in the three plots DL1a, DL2c and DL3a during 2005. Different hatching indicates the contribution of different species to stand E_c.

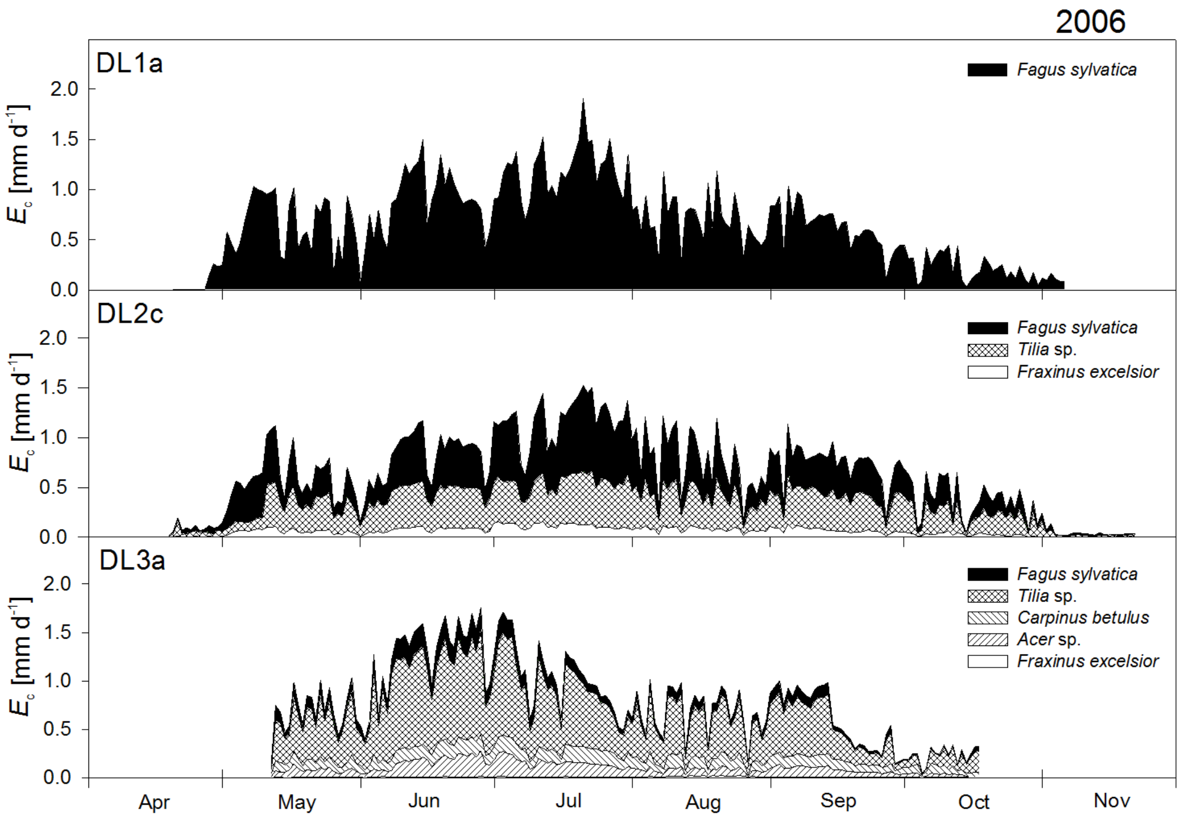

Figure 5. Annual course of canopy transpiration (E_c) in the three plots DL1a, DL2c and DL3a during 2006. Different hatching indicates the contribution of different species to stand E_c.

Table 3 summarizes the results of regression analyses conducted to compare the slopes of linear regressions of daily E_c totals of one stand on the $\mathrm{E_c}$ of another stand in order to compare the transpiration rates of the three stands. From the confidence intervals of the slopes, it is evident that the daily transpiration rates were significantly different between the three stands in both 2005 and 2006 (Table 3a). Only in 2006, the lower C.I. of the slope was close to 45 degrees (which is the 1:1 line of the relationship) indicating that the stands DL1a and DL2c had a rather similar canopy transpiration during the growing season. During the growing season in 2005, $\mathrm{E_c}$ was higher in the species-rich stand DL3 than in DL1 and DL2, while in 2006, the daily transpiration rates in the DL1 and DL2 stands were similar to each other but different to DL3. This difference is also visible during the first half of the vegetation period in 2006 (May to July, Table 3b).

Table 3 (a and b). Results of two statistical tests on differences between daily transpiration totals (E_c) in the three stands (DL1a, DL2c, DL3a). (a) Simple linear regression analysis, model II with major axis method, on the degree of similarity between E_c in the three plots (6 plot combinations in two years). Given are the lower and upper confidence intervals (C.I.) of the slopes of the regression lines between the E_c of one plot on the E_c of a second plot for the years 2005 and 2006 (in degrees, 45 degrees is the 1:1 line) together with the *p*-value and R^2 for the regressions. (b) Detailed regression analysis for the early-summer period 2006 in the three stands presenting the lower and upper C.I. of the regression slope (given as the inverse in $\frac{1}{\text{mm}}$) together with the *p*-value and R^2 of the regressions. The lower and upper C.I. of the E_c values itself is also presented (in mm d^{-1}).

a)

Plot combinations	**Lower and upper C.I. of regression slope (in degrees)**	**n**	***p*-value**	R^2
DL1a - DL2c (2005)	33.72 - 38.72	168	< 0.0001	0.74
DL1a - DL3a (2005)	13.14 - 21.40	154	< 0.0001	0.55
DL2c - DL3a (2005)	25.45 - 30.47	146	< 0.0001	0.71
DL1a - DL2c (2006)	45.08 - 48.38	206	< 0.0001	0.85
DL1a - DL3a (2006)	33.26 - 44.39	160	< 0.0001	0.39
DL2c - DL3a (2006)	24.64 - 38.35	160	< 0.0001	0.26

b)

Plots	**Lower and upper C.I. of regression slope (in $\frac{1}{\text{mm}}$)**	**n**	***p*-value**	R^2	**Lower and upper C.I. of E_c values (in mm d^{-1})**	
DL1a (May-July 2006)	0.0068 - 0.0132	72	< 0.0001	0.36	0.87	0.93
DL2c (May-July 2006)	0.0078 - 0.0133	73	< 0.0001	0.45	0.84	0.89
DL3a (May-July 2006)	0.0163 - 0.0253	56	< 0.0001	0.62	1.05	1.12

Relative contribution of different tree species to canopy transpiration

The relative contribution of the species to canopy transpiration in the mixed stands DL2c and DL3a deviated considerably from the relative importance of the species in the stands in terms of crown area index (CAI), sapwood area index (SAI) and basal area index (BAI) (Tables 1 and 2). Moreover, the E_c/CAI-, E_c/SAI- and E_c/BAI-quotients of the species differed markedly between the two hydrologically different years. *Tilia* sp., in particular, contributed more to canopy transpiration than would be expected from its (relative) crown, sapwood or basal area, as was evident in stand DL2c, and, to a lesser extent, also in stand DL3a (Table 2). Similarly, *Acer* sp. in stand DL3a had much higher E_c/CAI-, E_c/SAI- and E_c/BAI-values than the stand average. In contrast, *Fraxinus excelsior* tended to transpire less than the stand average in the mixed stands, as did *Fagus sylvatica* in stand DL2c in 2006. When normalized to the canopy projection area, the four diffuse-porous species varied in their water use during the vegetation period more than five-fold (57 to 290 L m^{-2}); ring-porous ash had an about ten times smaller E_c rate per canopy projection area than the average of the diffuse-porous species. The variation between the species was even larger when E_c was normalized to basal area (20.500 to 104.800 L m^{-2} yr^{-1} for the diffuse-porous species and 4.800 to 16.700 L m^{-2} yr^{-1} for *F. excelsior*). When related to hydroactive sapwood area, E_c varied more than fourfold among the diffuse-porous species, but the ranking among the species changed according to their sapwood area/basal area ratios.

Large interannual differences in the relative contribution of a species to stand E_c occurred in *Tilia*, which had a much higher transpiration per crown area in stand DL2c in the summer 2006 as compared to 2005, and in *F. sylvatica* and *F. excelsior*, which tended to transpire relatively less in 2006 than in 2005. However, when related to their contribution to stand crown area, sapwood or basal area, the interannual differences were small in these two species.

Discussion

Species diversity and canopy transpiration

The evidence in support of hypothesis 1, which postulates a diversity effect on E_c, was contradictory. In the summer of 2005 with average rainfall, the species-richest stand DL3a had a circa 50% higher transpiration than the less diverse DL1a and DL2c stands. In contrast, we calculated similar transpiration rates for all three stands in the relatively dry summer 2006.

Thus, the interannual variation in E_c was large indicating that directional changes in canopy transpiration, if they exist, are only visible in certain years. Data from many more summers would be needed to confirm a putative dependency of E_c on tree species diversity in the Hainich forest. The astonishing result of Baldocchi's (2005) meta-analysis of forest evapotranspiration data from the FLUXNET program (see Baldocchi et al., 2001, Baldocchi, 2005), which revealed a decrease in evapotranspiration with increasing number of tree species in a stand, was explained by him with an assumed greater proportion of ring-porous species in species-richer stands, or with a possible effect of the nitrogen economy of the stand on canopy conductance (Schulze et al., 1994), leading to a reduced stomatal conductance and leaf area index in the species-rich forests. However, the data base with six stands is probably too limited to draw firm conclusions on the forest diversity-canopy transpiration relationship. Moreover, the species-poor stand with the highest normalized evapotranspiration (Hesse in Eastern France) refers to a young beech forest of only 32 years in age. This factor might well explain the relatively high transpiration of this stand (Bush et al., 2008, Dunn and Connor, 1993, Granier et al., 2003, Köstner, 2001, Peck and Mayer, 1996) and probably not its low number of species. Further, the data set encompasses forest stands with different soil physical and chemical conditions, which could influence the diversity-transpiration relationship. Thus, unequivocal evidence for a diversity effect on E_c in temperate forest does not yet exist. Such an effect may be absent because complementarity in water use by different tree species is not a significant factor in temperate mixed forests, or the effect is masked by other factors influencing the variability of canopy transpiration.

What biotic factors have the largest influence on the transpiration of forest stands? First, transpiration varies with tree age and tree height (Köstner, 2001, Köstner et al., 1998, 2002, Mencuccini and Grace, 1996, Roberts, 2000, Ryan et al., 2000, Schäfer et al., 2000, Vertessy et al., 1994, 1995, 1997), but these factors were not that different between the DL1a, DL2c and DL3a stands in our study that they should have had a significant effect on E_c. Wullschleger et al. (1998, 2001) stated that E_c is largely dependent on sapwood area per unit ground area. In the Hainich forest, the quasi-monospecific DL1a stand had a larger cumulative sapwood area (33.4 $m^2\ ha^{-1}$) than the 3-species (29.0 $m^2\ ha^{-1}$) and the 5-species (23.6 $m^2\ ha^{-1}$) stands while the summed canopy projection areas of the trees in the stands were rather similar (1.26 – 1.49 $ha\ ha^{-1}$). Thus, the high transpiration rate of stand DL3a in 2005 is not explained by its sapwood area indicating that other factors must have been the drivers of high transpiration rates in this species-rich stand. Oren and Pataki (2001) arrived at the conclusion that forest stands composed largely of ring-porous species have a smaller stand sapwood area, a lower mean canopy conductance and, thus, a smaller canopy transpiration than stands composed primarily of diffuse-porous species with a larger sapwood area. The significant contribution of ring-porous *F. excelsior* in the DL2c and DL3a stands with 100 and 28 stems ha^{-1}, respectively, may partly explain the lower sapwood areas of these stands as compared to the *Fagus*-dominated DL1a stand. If the conclusion of Oren and Pataki (2001) is more generally valid, species-rich stands should exhibit higher sapwood areas and also transpiration rates in particular in those cases, where species-rich stands with many diffuse-porous trees are compared with species-poor stands of ring-porous trees. This would be a rare case. On the other hand, we are not aware of data which support the existence of a higher sapwood area in mixed stands as compared to the monospecific stands of the respective species. Bush et al. (2008) confirmed that the transpiration of trees is strongly dependent on xylem anatomy (ring-porous versus diffuse-porous). Ring-porous species reached maximum flow with increasing VPD at smaller saturation deficits than diffuse-porous species due to a generally higher vulnerability to cavitation of ring-porous species with larger vessel diameters than diffuse-porous species (Bush et al., 2008).

Species-rich stands could also transpire more than species-poor forests if tree species with high mean leaf conductances or species with particularly deep-reaching roots were included. In the first case, higher E_c rates in species-rich forests would be the consequence of a sampling effect, in the second case, complementarity of water use could be a reason. In the Hainich forest, we can rule out the latter situation, because we found no indication of a vertical segregation of the fine root systems of the coexisting species (Meinen et al., 2009), which makes the complementary use of soil water by different species unlikely. Species differences in water absorption, which could lead to elevated canopy transpiration rates, are discussed below.

Species effects on canopy transpiration

The different tree species in the mixed stands contributed not equally to canopy transpiration. *Acer* sp. and *Tilia* sp., in general, had a relatively high transpiration per projected crown area, *F. excelsior* relatively low E_c rates. In fact, not only diffuse- and ring-porous species, but also different diffuse-porous trees were found to differ largely in their water use on a sapwood area, basal area or canopy projection area basis, which is supporting our second hypothesis. Sap flux densities, related to the hydroactive sapwood area and measured with the same method in the Hainich forest in 2001 by Hölscher et al. (2005), also revealed large species differences in E_c.

However, the species contribution to canopy transpiration was not constant but apparently varied between the stands and years. For example, the canopy transpiration per sapwood area of *F. sylvatica* was higher in the species-rich DL3a stand than in the DL2c stand (58 vs. 27-30 x 10^3 L m^{-2} yr^{-1}) and reached much higher values for *Tilia* in the DL2c stand in 2006 than in 2005 (133 vs. 50 x 10^3 L m^{-2} yr^{-1}). Since available energy and soil moisture resources are not that different in the three stands, the variation in species-specific sapwood area-based sap flux density between the stands may partly reflect differences in the hydraulic conductance of the soil-to-leaf conducting pathway or in canopy conductance among different tree individuals of the same species, as they were reported by Köcher et al. (2009) in the Hainich forest. Another interpretation of differences in canopy transpiration of *F. sylvatica* between the DL2c and DL3a stands could be that the few beech trees in the DL3a stand possess a particularly large crown area with a high transpirative water loss caused by elevated fluxes of incident radiation. Alternatively, one may speculate about neighbourhood effects on water use in the mixed stands, by which water uptake and transpiration either could be promoted or suppressed by the specific nature of the surrounding tree individuals. Our data are not sufficient for proving such asymmetric interactions in mixed stands.

In our study, the *Acer* species (mostly *A. pseudoplatanus* and *A. platanoides*) and the *Tilia* species (*T. cordata* and *T. platyphyllos*) exhibited higher canopy transpiration rates than the stand average, whereas *Fraxinus excelsior* showed substantially smaller canopy transpiration, at least in stand DL3a. This highlights the role of functional plant traits, such as hydraulic architecture (e.g. ring- or diffuse-porous species, differences in sapwood area, micro- or macroporous xylem, vessel density, stem water storage capacity) and stomatal regulation, in determining the amount of canopy transpiration in mixed stands. Investigations by Köcher et al. (2009) in the Hainich forest showed that *A. pseudoplatanus* trees had a much higher hydraulic conductivity in the soil-to-leaf pathway than the other species which would explain the large relative contribution of maple to canopy transpiration in stand DL3a. The low sapwood area- or crown projection area-based transpiration rates of *F. excelsior* are easily explained by the small hydroactive sapwood area of ash with only the youngest annual rings (typically 3 to 10) being involved in water transport (Gebauer et al., 2008). On the other hand, *F. excelsior* reached higher maximum leaf conductances (~ 270 mmol m^{-2} s^{-1}) than most other tree species in this mixed stand (160-190 mmol m^{-2} s^{-1}) and showed no significant reduction in sap flux density between moist and dry periods. In contrast, such reductions were large in *T. cordata, F. sylvatica* and *A. pseudoplatanus*, and moderate in *C. betulus* in the stands (Köcher et al., 2009). Oren et al. (1999) found a greater sensitivity to VPD in species with high stomatal or leaf conductances which may reduce the risk of cavitation under high VPD. We assume that both the specific hydraulic architecture and the sensitivity of leaf conductance regulation are key functional traits being responsible for species differences in canopy transpiration in the Hainich forest.

Interannual variability in canopy transpiration

Interannual differences in moisture supply had a profound effect on the seasonal course and total amount of canopy transpiration in the three stands. During the summer of 2005, rainfall was more evenly distributed throughout the growing season, while in the drier summer of 2006, two rainless periods in July and September caused a pronounced decrease in relative plant-extractable water (REW) in the soil. The species-poor and species-rich stands responded differently to this variation in soil moisture. Physiological measurements by Köcher et al. (2009) in the sun canopies of the trees indicated that a soil matrix potential of about -0.11 MPa represents a threshold in the drought response of most of the species (except for *F. excelsior*) in the Hainich forest, resulting in a pronounced reduction of leaf conductance and a marked decrease of sap flux. While contrasting rainfall regimes in the two years had a profound influence on canopy transpiration of all stands, it affected the three diversity levels differently. In the stands DL1a and DL2c, E_c increased from the moderately wet summer of 2005 to the drier summer of 2006 by 34 and 43%, respectively, which may be a consequence of extended periods with high radiation and VPD in 2006. A higher evaporative demand in 2006 is reflected by the larger transpiration rates of *Fagus* and *Tilia* in this summer compared to 2005 in the DL1a and DL2c stands. Another factor which may have contributed to the increase of E_c in the DL1a stand from 2005 to 2006 is the increase in LAI toward 2006 (Table 1). In contrast, the species-rich DL3a stand, which showed the highest canopy transpiration of all stands in 2005, responded to the drought periods in July and September 2006 with a reduction in transpiration, resulting in an 11% lower E_c total than in 2005. It appears that the species-rich DL3a stand was more sensitive in its transpiration regulation to the extended drought periods than the quasi-monospecific DL1a stand and the 3-species DL2c stand. A closer look on the seasonal course of soil water availability may explain the deviating behavior of E_c in the DL3a stand: in both summers, canopy transpiration increased more rapidly in the DL3a stand in May and June as compared to the DL1a and DL2c stands, reaching early peaks already in late June. This was mainly a consequence of a high water use of the *Tilia* trees early in summer. In the DL1a and DL2c stands with a higher *Fagus* and lower *Tilia* contribution, in contrast, E_c reached its peak later in summer in July or early August, which is probably a consequence of a more conservative water loss regulation of beech. This species is known for its sensitive regulation of leaf conductance to variations in VPD (e.g. Backes and Leuschner, 2000, Oren et al., 1999, Rennenberg et al., 2006, Köcher et al., 2009). Thus, it appears that the species-rich DL3a stand had extracted the bulk of plant-available water already in June 2006, mainly due to the high consumption of the dominant *Tilia* trees in this stand. Consequently, soil moisture dropped in DL3a to lower values in July, August and September than in the DL1a and DL2c stands, restricting canopy transpiration in the second half of the summer more severely in this linden-rich stand. This effect may have been enhanced by the somewhat smaller storage capacity for extractable water ($\theta_{\max} - \theta_{\min}$) in the DL3a stand (170 mm) as compared to the DL1a and DL2c stands (200 and 240 mm). In the wetter summer of 2005, soil water content remained at higher levels in the DL3a stand, thus supporting a high transpiration rate of *Tilia* throughout the summer. The lower VPD may have favoured *Tilia* by enabling this species with a relatively high maximum stomatal conductance to maintain higher photosynthesis and transpiration rates than in the other species. Species with larger leaf conductances in moist atmospheres (such as beech) may profit less from wet summers (cf. Oren et al., 1999). The abundant *Fraxinus* trees in the stand DL2c may have contributed to the fact that E_c did not pass through a low in mid-summer 2006, since ash was found to maintain high sap flux rates even beyond the -0.11 MPa threshold of soil matrix potential (Köcher et al., 2009).

Compared to other studies on canopy transpiration in temperate broad-leaved forests, we obtained low E_c totals for the vegetation periods of 2005 and 2006 (97 to 158 mm). For a set of Central European monospecific beech forests, Schipka et al. (2005) obtained a mean E_c value of 289 (± 58) mm in the vegetation period. Granier et al. (1996, 2000), Herbst et al. (2008), Peck and Mayer (1996), Vincke et al. (2005) and Wullschleger and Hanson (2006) reported E_c values for the vegetation period in stands dominated by beech, oak, maple or ash of 212 to 397 mm. On the other hand, Poyatos et al. (2007) observed in the very dry summer of 2003 in oak-dominated stands similarly low (or only slightly larger) E_c totals (118 and 164 mm) compared to our stands; their E_c values were low also in the year 2004 immediately after the drought. A possible explanation for the low canopy transpiration rates of the Hainich stands may be found in the specific edaphic situation of this forest with clay-rich soils that restrict root water uptake in summer by very low hydraulic conductivities of the soil matrix. Moreover, the extraordinary drought of 2003 resulted in a pronounced after-effect in 2004 and also in 2005 with higher canopy defoliation rates in many Central European broad-leaved forests as compared to average summers (Bréda et al., 2006, Ciais et al., 2005, Granier et al., 2007, ICP Forests Executive Report, 2007). Thus, we speculate that the specific edaphic conditions together with the consequences of an extreme drought event may be responsible for the low transpiration rates measured in the three stands in 2005 and 2006.

Conclusions

Even though our study used a comparative approach for investigating canopy transpiration in broad-leaved forests along a diversity gradient, several safe conclusions can be drawn. Canopy transpiration may increase or decrease with increasing tree species diversity, but a universal trend is unlikely to exist because complementarity in root water uptake in mixed stands seems not to be the rule. Thus, evidence in support of our first hypothesis is weak. We found large differences in the water use of coexisting tree species that can have a profound influence on canopy transpiration at the stand level. Substantial differences in canopy transpiration rate do not only exist between diffuse- and ring-porous tree species, but also within these functional groups, supporting our second hypothesis. This has the consequence that tree species identity and the related specific functional traits are much more important for canopy transpiration and its seasonal variabililty than is tree species diversity. We suggest that the sizes of sapwood area and leaf area as morphological attributes, and the hydraulic conductance in the root-to-leaf pathway and leaf conductance as physiological traits are main factors being responsible for different seasonal transpiration patterns of the tree species.

Since soil water is a preemptable resource that cannot be stored in large amounts, more diverse stands may suffer from a higher drought exposure when the tree mixture encompasses tree species such as linden that tend to exhaust the water reserves early in summer. If significant soil moisture preemption occurs in mixed stands, tree species diversity could enhance drought stress in dry years and may reduce ecosystem stability.

Acknowledgements

The authors are grateful to the management of the Hainich National Park, Thuringia, for the research permit and the good cooperation. We thank Heinz Coners for technical support and Karl Maximilian Daenner for help in statistical analysis. This study was conducted within the framework of the Graduiertenkolleg 1086 with funding from the German Research Foundation (DFG).

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Chapter
6

Atmospheric versus soil water control of sap flux-scaled transpiration in tree species co-occurring in species-poor and species-rich temperate broad-leaved forests

Gebauer T., V. Horna and C. Leuschner

Abstract

- How tree species diversity and tree identity influence ecosystem processes in forests is still poorly understood.
- We tested the hypotheses (i) that the functional attributes of different tree species are more influential on stand canopy transpiration than is tree species diversity, and (ii) that differences in the degree of atmospheric vs. edaphic control of tree water consumption are related to the xylem anatomy of the species.
- The five co-occurring species of the mixed stands differed considerably in leaf area-based canopy transpiration (E_L) with the four diffuse-porous species exhibiting higher E_L rates than ring-porous *Fraxinus excelsior*. vpd was the most influential factor explaining 75-87% of the variation in E_L on the stand level, while the influence of soil moisture was small (mostly < 5 %). Stands with low or high tree species diversity were not different with respect to their environmental control of E_L. On the species level, *F. excelsior* differed from the other species in being less vpd controlled, while soil moisture had a larger influence on E_L. Species diversity had a negligible effect on E_L at the species and stand levels with the exception of *F. excelsior*.
- We conclude that functional differences among tree species in mixed stands can result in large differences in the water consumption per leaf area which, however, disappeared at the stand level in the study year. Species differences in the environmental control of canopy transpiration may mostly relate to the diffuse- /ring-porous dichotomy.

Keywords: **tree diversity / saturation deficit / soil moisture / vpd sensitivity / canopy transpiration**

Introduction

The biodiversity-ecosystem functioning relationship is not well understood in forests (Scherer-Lorenzen et al. 2007), unlike grasslands where the bulk of studies were done (e.g. Loreau and Hector 2001, Hector et al. 1999, Tilman et al. 1996, Tilman et al. 1997).

Mixed forests can have a higher, or a lower, productivity than monospecific stands (Pretzsch 2005, Jacob et al., in revision). Resource utilization can be improved by 30 % by combining early and late successional species, ontogenetically early and late culminating species, shade-intolerant and -tolerant tree species (Pretzsch 2005). On the other hand, productivity can be reduced by up to 30 % due to competition for the same resources in crown and root systems of species with similar ecological niches and functional characteristics (Pretzsch 2005).

The existing evidence suggests that the identity of the species, and more important the specific functional traits of the species, present in a mixed forest is more important for productivity than is the number of species. Similarly, no clear positive relationship between tree diversity and ecosystem functioning emerged when the stability of pure and mixed forests against storm-induced damage was analyzed (Dhote 2005). On the other hand, species-rich stands seem to be less affected by insect herbivore attack than monospecific stands (Jactel et al. 2005). Thus, the diversity-function relationship in forests is complex and may be influenced more by the diversity of tree functional types than by species diversity or the number of species itself (e.g. Körner 1994, Naeem and Wright 2003). Keystone species may play an important role within a species mixture (e.g. Bond 1994, Hooper et al. 2005).

The amount of water consumed by forests through transpiration is an important function which determines the water loss through deep seepage and thus groundwater yield. Until recently, the dependence of forest transpiration on tree species diversity or tree functional diversity has not systematically been investigated. From a review of the relevant literature, Baldocchi (2005) postulated that the diversity effect on canopy transpiration should be small and might be even negative. Empirical data on the tree diversity-water consumption relationship may be expected from synthetic tree stands differing in species diversity as the recently planted BIOTREE experiment with 1 to 6 species per plot in Thuringia, Central Germany (Scherer-Lorenzen et al. 2007). However, it will take decades until data on canopy transpiration are to be expected, and the results may only partly be relevant for the situation in old-growth forests because of peculiarities in stand structure (e.g. small plot size with edge effects, systematic tree arrangement in the plot). In synthetic grasslands, which are more early accessed by experimental approaches, Verheyen et al. (2008) found a transregressive overyielding of evapotranspiration in polycultures with a reversed pattern at high intensities of drought stress so that highly diverse communities appear to be earlier affected by drought.

An alternative approach is to compare mature forest stands with different tree species diversities that are growing under sufficiently comparable edaphic and climatic conditions. It was practiced by Leuschner et al. (in revision) in the Hainich Tree Diversity Matrix, a species-rich temperate broad-leaved forest in Central Germany with a mosaic of species-poor and species-rich stands (1 to > 5 tree species) growing in close proximity to each other.

This forest structure is the consequence of a mosaic of different former ownerships and management practices that coexisted in the area for centuries (Leuschner et al. 2009). Leuschner et al. (in revision) employed the xylem sap flux measurement approach in neighboring stands with low, moderate and high tree species diversity and concluded that differences in canopy transpiration between the stands are mainly influenced by the species' functional attributes and the rainfall amount of the measuring year, while diversity *per se* plays a negligible role.

In this study, we conducted sap flux measurements in six stands differing in species diversity in the Hainich Tree Diversity Matrix and related sap flux-scaled transpiration to important atmospheric (vapor pressure deficit (vpd), radiation), edaphic (soil moisture, clay content) and stand structural variables (tree species diversity, stem density, fine root abundance) likely to influence canopy transpiration. With a large number of sensors installed in five different tree species (four diffuse-porous, one ring-porous), we were able to express sap flux to the stand level and also the species level and could analyze the canopy transpiration – environment relationship for the species separately. Study aim was to detect similarities and differences among the five species with respect to water flux control in mature trees for reaching at a functional classification of the species in terms of their hydrology. This would be a prerequisite of understanding possible complementarity and competition effects in tree water consumption of mixed stands. We tested the hypotheses that (i) the five co-existing species in the mixed stands consume water at different rates, (ii) the five species differ in the degree of atmospheric vs. edaphic control of sap flux, and (iii) tree species diversity plays a minor role in determining canopy transpiration rate of the stands.

Materials and Methods

Study sites, tree layer diversity and stand structure

The study was conducted in six forest stands of the Hainich Tree Diversity Matrix, a set of forest plots located in the north-eastern part of the Hainich National Park, Thuringia, Central Germany, between 295 and 355 m a.s.l. (51°04' N, 10°30' E). The Hainich National Park is a temperate mixed broad-leaved forest dominated by European beech (*Fagus sylvatica* L.). Linden (*Tilia cordata* Mill. and *T. platyphyllos* Scop.), common ash (*Fraxinus excelsior* L.), European hornbeam (*Carpinus betulus* L.) and 3 different maple species (*Acer pseudoplatanus* L., *Acer platanoides* L. and *Acer campestre* L.) also occurr in the stands in different densities. Other deciduous tree species like elm (*Ulmus glabra* L.), oak (*Quercus robur* L. and *Q. petraea* Liebl.), cherry (*Prunus avium* L.) and service tree (*Sorbus torminalis* L.) are present in lower numbers.

Tilia cordata and *T. platyphyllos* show a high degree of hybridization in the area, which made it difficult to differentiate at the species level. Thus, linden trees are referred to as *Tilia* sp.

The climate is sub-continental with a mean annual precipitation of 590 mm and 7.5 °C as mean annual air temperature (1973-2004, Deutscher Wetterdienst, Offenbach, Germany). The study year 2005 received 518 mm of rainfall. The soils developed from eolic loess which is underlain by Triassic limestone (Muschelkalk) showing stagnant properties during winter and spring, while the soils are drying out strongly during summer (Guckland et al., in press).

Six 50 m x 50 m plots with low, medium or high tree species richness at a maximum distance to each other of 5 km and a minimum distance of 420 m (in two cases: 70 and 200 m) were selected for the study. We used the Shannon diversity index H' as a measure of canopy layer diversity with all tree individuals present in the upper canopy being considered. In the following, the six stands are referred to as diversity level 1 (DL1, plots No.: DL1a and DL1c), 2 (DL2, plots No.: DL2a and DL2c) and 3 (DL3, plots No.: DL3a and DL3c). Selection criteria for the stands were a markedly different tree species diversity and the fit to a pre-defined scheme of relative tree species abundances in the stands. The DL1a and DL1c stands were mainly composed of beech (93.5 % and 100 % of the stems) with Shannon diversity indices between 0 and 0.3. The DL2a and DL2c stands were dominated by beech, linden and ash and were characterized by H' values between 0.8 and 1.1. The species-richest DL3a and DL3c stands included all tree species of DL2 and, in addition, hornbeam and maple species (mainly *A. pseudoplatanus* and *A. platanoides*, *H*' values between 1.3 and 1.5 (Table 1)). All stands had a closed canopy (gap fraction < 0.1) and roughly comparable stand basal areas (35 to 46 m^2 ha^{-1}). Diameter at breast height and projected crown area (CA_p, in m^2) of the trees in the 2500 m^2 plots were obtained from DBH measurements with dendrometer tapes and by determining the crown radii in 8 directions (8-point crown projections). Mean tree ages ranged from 78 to 187 years (Schmidt et al. 2009). The leaf area index (LAI) of the six stands varied between 6.2 and 7.8 (M. Jacob, pers. communication).

The hydro-active sapwood area (A_S, in m^2) of the trees in the plots was estimated from the DBH measurements and empirically established DBH-A_S-relationships for the 5 most common tree species of the stands obtained in an earlier study by Gebauer et al. (2008) using dyeing and stem wood coring.

Table 1. Stand structural characteristics of the six study plots. Values are given at the stand and also at the species level. The number of sap flux sensors installed per tree species and for the whole stand is also indicated. Leaf area index and tree height data were obtained from M. Jacob (unpublished data). The DL1 stands are monospecific beech forests, the DL2 stands have three abundant tree species, and the DL3 stands five abundant species. *H*'- Shannon diversity index.

Stand no.	**Tree species**	**Mean stand age (years)**	**Stem density (no. ha^{-1})**	***H'* (crown area basis)**	**Mean tree height (m)**	**Cumulative basal area (m^2 ha^{-1})**	**Cumulative sapwood area (m^2 ha^{-1})**	**Cumulative crown area (projected) (m^2 ha^{-1})**	**Leaf area index (m^2 m^{-2})**	**No. of sensors**
DL1a	**Stand**	**109 (±12.0)**	**428**	**0.27**	**33.3 (±2.2)**	**46.13**	**33.35**	**12446.8**	**7.8**	**16**
	Fagus sylvatica		400			44.01	31.78	11753.2	7.5	16
DL1c	**Stand**	**187 (±15.8)**	**228**	**0.00**	**38.4 (±2.7)**	**35.23**	**24.83**	**12555.5**	**6.8**	**6**
	Fagus sylvatica		228			35.23	24.83	12555.5	6.6	6
DL2a	**Stand**	**78 (±20.8)**	**436**	**1.05**	**27.5 (±2.0)**	**35.00**	**24.00**	**14011.2**	**7.1**	**13**
	Fagus sylvatica		108			19.16	13.93	8572.2	4.6	6
	Tilia sp.		144			6.16	4.95	3089.3	1.2	4
	Fraxinus excelsior		60			4.30	0.75	1498.2	0.7	3
DL2c	**Stand**	**83 (±17.8)**	**776**	**0.85**	**29.2 (±2.1)**	**45.00**	**29.02**	**14874.0**	**6.5**	**32**
	Fagus sylvatica		572			30.12	22.45	10832.4	4.5	16
	Tilia sp.		84			5.68	4.48	2050.4	0.9	6
	Fraxinus excelsior		100			7.98	1.62	1473.2	0.8	10
DL3a	**Stand**	**116 (±16.8)**	**392**	**1.45**	**27.4 (±1.9)**	**35.73**	**23.64**	**12557.6**	**6.2**	**40**
	Fagus sylvatica		12			3.76	2.67	875.6	0.4	6
	Tilia sp.		264			19.59	13.58	6851.6	3.4	16
	Fraxinus excelsior		28			3.35	1.31	1163.6	0.5	6
	Carpinus betulus		36			3.58	2.42	1770.4	0.3	6
	Acer sp.		32			2.26	1.65	724.8	0.7	6
DL3c	**Stand**	**97 (±44.2)**	**468**	**1.36**	**26.2 (±2.3)**	**40.52**	**25.50**	**15855.7**	**6.8**	**36**
	Fagus sylvatica		196			16.40	12.06	7598.8	1.6	10
	Tilia sp.		160			6.01	4.90	951.5	0.8	8
	Fraxinus excelsior		76			12.75	4.28	2969.0	1.4	6
	Carpinus betulus		16			1.77	1.20	964.8	0.9	6
	Acer sp.		20			3.60	3.02	1427.3	1.7	6

Sap flux measurements and up-scaling to the tree and stand levels

We measured stem xylem sap flux density (J_s, in g m^{-2} s^{-1}) in the summer 2006 using Granier-type heat dissipation sensors (Granier 1985, 1987, see also Lu et al. 2004). The sensors were installed in the stems of trees > 10 cm in diameter at 1.3 m height above ground. Pairs of 20 mm-long and 2.0 mm-wide heating probes were inserted in northern and southern trunk directions into the stem sapwood. The numbers of sensors per species and per stand are given in Table 1. In the case of ring-porous ash, probes with a heating spiral length of 10 mm were used because of the smaller sapwood thickness of this species compared to diffuse-porous trees (Gebauer et al. 2008). We calculated the sapwood depth for every measured tree for being able to correct sap flux density values if sensors had been placed beyond the limits of active xylem (see Clearwater et al. 1999).

The probes were manufactured according to the protocol given by A. Granier (pers. communication). The two paired sensors were identical in construction. The upper probe was heated with a constant current of 0.12 A and a heating power of 0.2 W. The lower probe was unheated and served as a reference for the upper probe. The temperature difference between the two probes was recorded every 30 s with copper-constantan thermocouples placed at the centre of the heating spirals using a data logger (CR10X; Campbell Scientific Ltd., UK) equipped with a 16/32-channel multiplexer (AM16/32, AM416; Campbell Scientific Ltd., UK). 30-min averages were calculated from the 30-s readings and stored in the data logger. The distance between the two probes was about 15 cm whereby thermal interference especially at zero sap flux was avoided. The temperature difference was used to calculate J_s in the unit g m^{-2} s^{-1} according to the empirical calibration equation given by Granier (1985, 1987):

$$J_s = 119 \cdot K^{1.231} \qquad \text{(Eqn. 1)}$$

where $K = (\Delta T_M - \Delta T)/\Delta T$. ΔT_M is the maximum temperature difference when sap flux is assumed to be zero.

For up-scaling of sensor-level sap flux to mean tree sap flux we used information on the size of A_S of each measuring tree. A further independent estimation of the radial xylem flux density pattern within the hydroactive xylem was obtained in an earlier study by analyzing species-specific sap flux densities in different xylem depths. One to 3 stems of each of the five species were equipped with sensors placed in four different sapwood depths (0-8 cm) (Gebauer et al. 2008). Based on this information, we calculated mean tree water flux J_{st} as follows:

$$J_{st} = \frac{\sum_{n=1}^{n} J_s \cdot B_S(x_i) \cdot W(x_i)}{A_S} \qquad \text{(Eqn. 2)}$$

where J_{st} is mean tree sap flux (g m^{-2} of sapwood s^{-1}), J_s is the mean stem sap flux density at the outermost sensor position (at 0-2 or 0-1 cm xylem depth), B_S (x_i) is the area of concentric rings of 1 cm width between the cambium (x_i) and the heartwood boundary (x_{i+n})

where sap flux reaches zero, $W(x_i)$ is a species-specific proportionality factor which expresses flux density at a given sapwood depth (x_i) in relation to flux density at the outermost sensor position, and A_S is the cross-sectional sapwood area of the tree. W was obtained from 4-parametric Weibull functions fitted to the radial flux profile data of Gebauer et al. (2008).

Total canopy transpiration of the stands was obtained by using an up-scaling procedure from mean tree sap flux J_{st} of m trees with a DBH class i of a given species multiplied with the quotient of cumulative sapwood area to ground area (unit: $m^2\ ha^{-1}$) (Oren et al. 1999):

$$E_{cj} = \left(\frac{A_{Sj}}{A_G}\right) \cdot \frac{1}{m} \sum_{m=1}^{m} J_{st} \qquad \text{(Eqn. 3)}$$

with E_{cj} being the canopy transpiration (unit: $mm\ d^{-1}$) of the DBH class j of a species, $\frac{1}{m} \sum_{m=1}^{m} J_{st}$ the mean -tree sap flux (in $g\ m^{-2}$ of sapwood d^{-1}) of the DBH class j of a species in the stand, A_{Sj} the cumulative sapwood area of all stems of a species in the DBH class j, and A_G the ground area of the plot. The DBH classes j were summed to obtain the species-specific canopy transpiration (E_c in $mm\ d^{-1}$) of the stand.

Finally, total canopy transpiration of the stand was calculated as the sum of the E_c values of all species in the plot. To compare changes in canopy transpiration between species within a stand and between the stands differing in diversity, we normalized E_c (which is canopy transpiration per ground area) by the leaf area index of the respective species or stand. Thus, we obtained canopy transpiration per unit leaf area on the species or stand levels, i.e. $E_L = E_c \cdot \frac{\text{SAI}}{\text{LAI}}$ (Oren et al. 1999). SAI is the sapwood area index of the species (i.e. cumulative sapwood area per ground area, unit $m^2\ m^{-2}$). The leaf area data of the individual species in the mixed stands and the stand LAI data were collected by M. Jacob with litter traps and species-specific leaf area analysis.

Microclimatological and hydrological measurements

Micrometeorological data (air temperature, relative air humidity (RH), atmospheric vapor pressure deficit (vpd), and precipitation) were obtained from the Weberstedt/Hainich meteorological station located 2 km northeast of our study plots. Incident shortwave radiation (R) data were taken from satellite measurements regionalized to the study region (Meteosat). All values were registered at hourly intervals. In this study, we used the daily average vpd of the day-light hours and the daily totals of incident shortwave radiation to account for changes in day length over the growing season.

Volumetric soil water content (θ) of the uppermost 10 cm was continually monitored at 30-min intervals with EnviroSCAN FDR sensors (Sentek Pty Ltd., Stepney, Australia) in the stands DL1a, DL2c and DL3a (I. Krämer, unpublished data) or time domain reflectometry sensors (TDR) at 12-hour intervals in the DL1c, DL2a and DL3c stands. About 50 to 70 % of fine root biomass was found within the 0-10 cm layer (Meinen et al., in revision).

Statistical analysis

Most statistical analyses were conducted with the software R (Version 2.7.1, R Development Core Team, Vienna, 2008). Simple regression analyses were performed with the software SigmaPlot 10.0 (SysStat Software Inc., 2006). To minimize the influence of non-synchronic phenologies when comparing the five tree species we only considered sap flux and leaf area-specific canopy transpiration (E_L) data after all trees had been reached full leaf expansion (June 1st) and before leaf senescence commenced (September 30th) in the summer 2006. For the stands DL1c, DL2a and DL3c, only data from mid of July to end of September was available. The unpaired Student t-test was used to detect significant differences in mean daily stand sap flux density between species in the same stand and for a given species between the stands. Linear models accounting for the effects of repeated measures were used to evaluate the influence of several environmental variables on E_L. Since canopy transpiration showed a non-linear dependence on vpd, radiation and soil moisture, the E_L data were log-transformed prior to multiple regression analysis to achieve linearity.

We conducted multiple regression analyses with backward variable selection for identifying those abiotic (vpd, R, θ and soil clay content) or biotic variables (Shannon diversity index H') exerting the largest influence on E_L. First, we calculated a correlation matrix with all abiotic and biotic variables to be incorporated in the model. We detected interactions between vpd and R ($r^2 = 0.78$), and soil clay content and θ ($r^2 = 0.55$). Given the importance of R and clay content for water flux in the ecosystem, we nevertheless decided to keep these variables in the multiple linear models for explaining the variation of E_L. Subsequently, factors with no significant effect on E_L were successively deleted from the model. Finally, the appropriate numbers of variables to be included in the general models were determined by using Akaike's Information Criterion (AIC).

Results

Species differences in the environmental control of sap flux density

Synchronous measurement of sap flux density (J_s) in the first 20 mm of the stem sapwood (ring-porous *F. excelsior*: 10 mm) of five co-occurring broad-leaved tree species revealed large differences among the species in J_s maxima and diurnal flow patterns. Figure 1 shows daily courses for the five species in the species-rich stand DL3a on two clear days in July 2006 with either relatively moist or dry soil. Species differences were large on July 3rd under moist soil with *F. sylvatica* reaching more than five times higher J_s maxima at noon than *F. excelsior* (> 55 vs. 11 g m^{-2} s^{-1}), while *T. cordata*, *A. pseudoplatanus* and *C. betulus* had intermediate flux maxima (22 to 38 g m^{-2} s^{-1}). Species differences were much smaller on July 18th with a relatively dry soil when *F. sylvatica* had greatly reduced its flux density (maxima about 25 g m^{-2} s^{-1}), despite even larger vpd maxima on this day, while *F. excelsior* maintained mostly unchanged peak flows of about 8 g m^{-2} s^{-1} (Figure 1: right panel). Highest peak flows of all investigated *F. excelsior* trees did not exceed 20 g m^{-2} s^{-1} during the whole measuring period.

Largest reductions in sap flux density during dry periods were found in *F. sylvatica*, followed by *A. pseudoplatanus* and *T. cordata*, while the reduction was less pronounced in *C. betulus* and negligible in ring-porous *F. excelsior*.

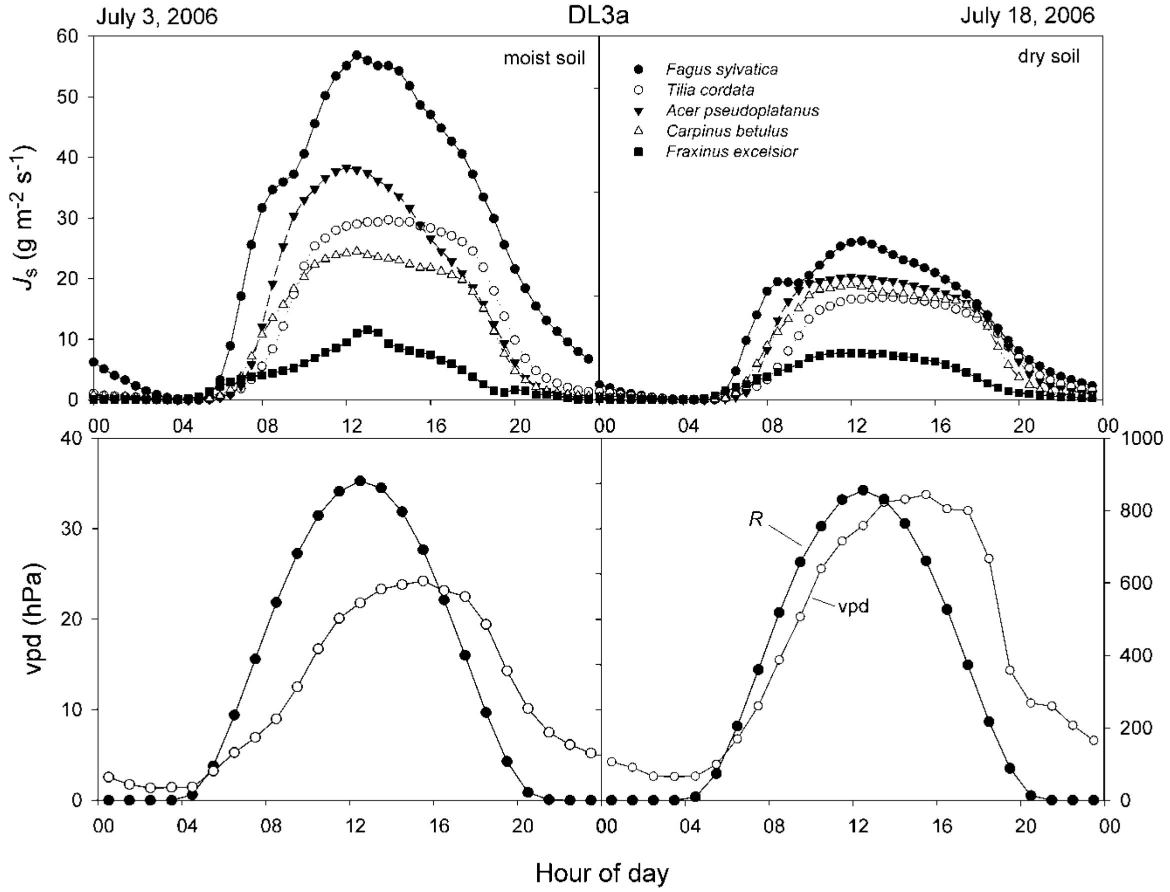

Figure 1. Diurnal course of sap flux density (J_s) in the outermost xylem of 5 co-occurring temperate broad-leaved tree species (diffuse-porous: *Fagus sylvatica*, *Tilia cordata*, *Acer pseudoplatanus*, *Carpinus betulus*, ring-porous: *Fraxinus excelsior*), incident shortwave radiation (*R*), and vapor pressure deficit (vpd) on a clear day with moist soil (July 3rd 2006, volumetric soil water content (θ): 22.5 vol. %) and a clear day with relatively dry soil (July 18th 2006, θ: 18.7 vol. %) in stand DL3a.

Environmental control of canopy transpiration – atmospheric vs. edaphic influences

To include the influence of soil moisture and to expand the analysis to a comparison of stands with contrasting tree species diversity, we calculated daily totals (or their monthly means) of canopy transpiration (E_C) by up-scaling of J_s to the tree and stand levels, and further expressed canopy transpiration on a leaf area basis (E_L) by multiplying E_c by the sapwood area to leaf area ratio (stand level or species level).

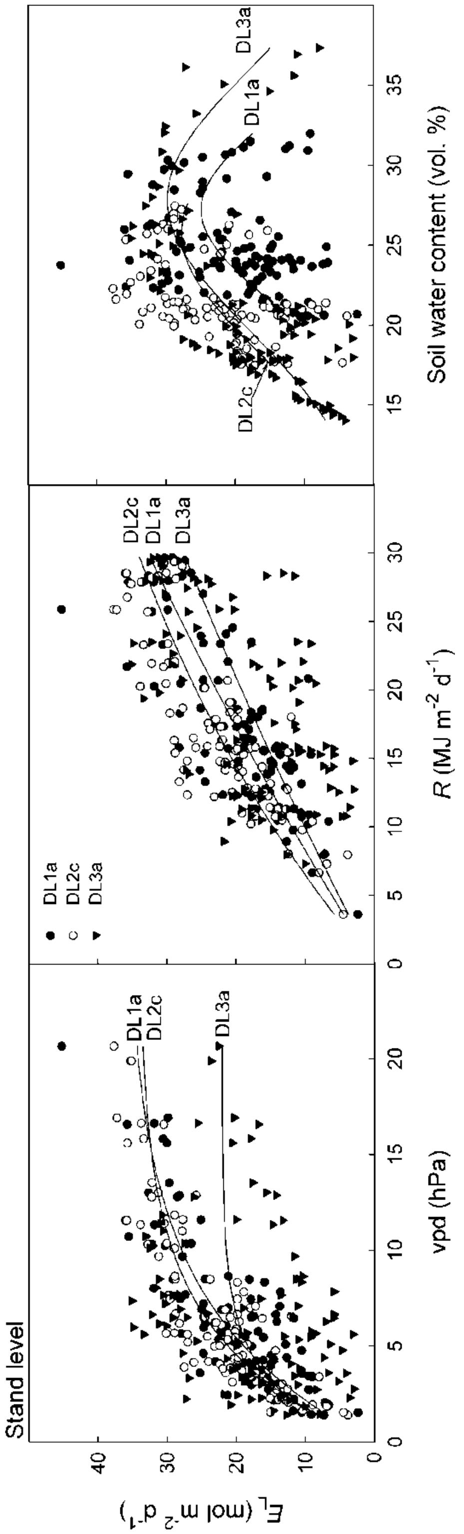

Figure 2. Daily totals of canopy transpiration per unit leaf area (E_L) regressed on a) average daily vapor pressure deficit (vpd) during the daylight hours, b) daily totals of incident shortwave radiation (*R*), and c) volumetric soil water content in the three stands DL1a, DL2c and DL3a.

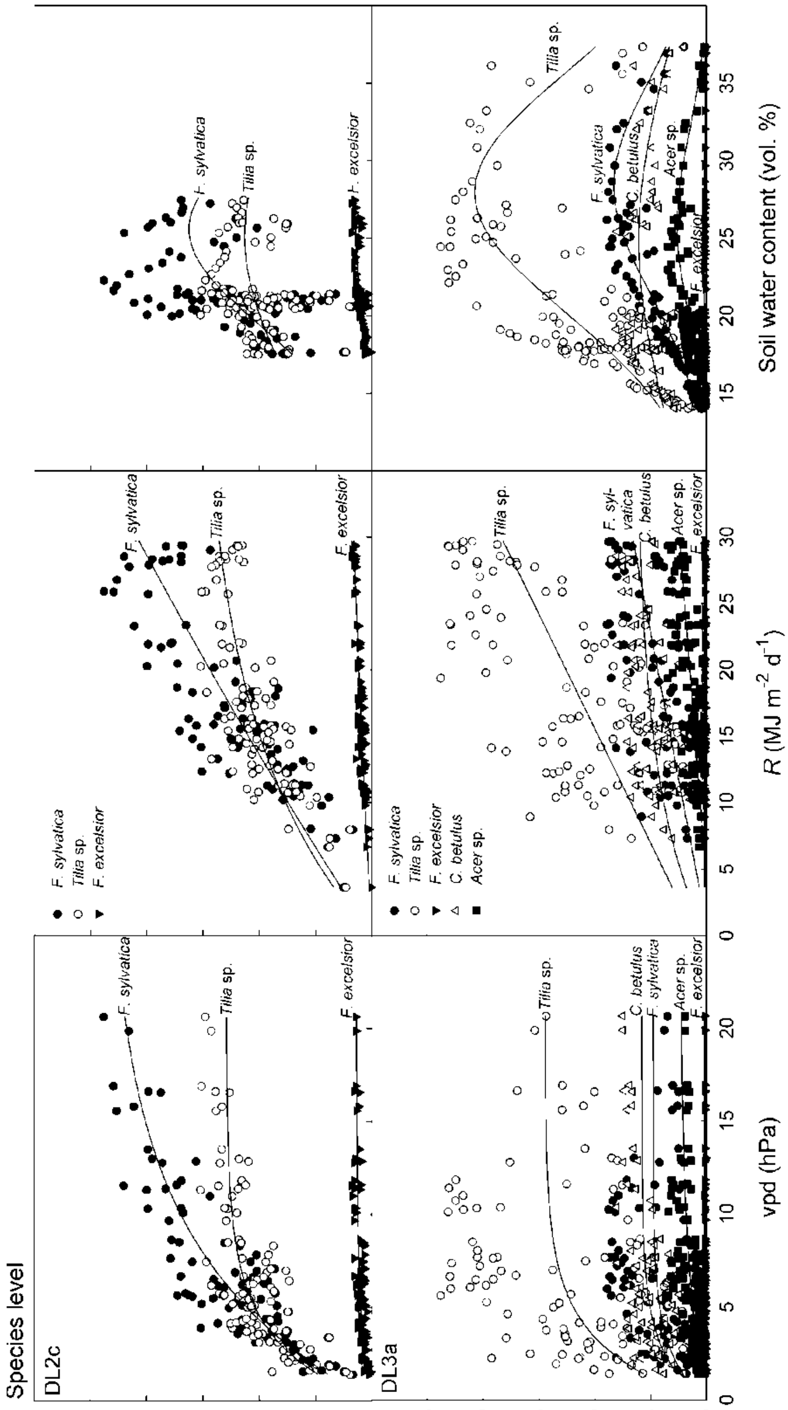

Figure 3. Daily totals of canopy transpiration per unit leaf area (E_L) regressed on a) average daily vapor pressure deficit (vpd) during the daylight hours, b) daily totals of incident shortwave radiation (R), and c) volumetric soil water content in the mixed stands DL2c and DL3a separately calculated for the tree species occurring in the two stands. The coefficients of the regression equations are given in Table 3.

This allowed to identify species differences in canopy transpiration on a leaf area basis and to compare different species and stands in their environmental control of sap flux and transpiration independently from contrasts in leaf area and relative abundance in the stand.

In a first step, we conducted a regression analysis of sap flux density on vapor pressure deficit and incident shortwave radiation (R) on an hourly basis. This analysis revealed the dominant role of vpd in the control of hourly sap flux density in all five tree species (Table 2), while the influence of R was small or negligible. Under conditions of a relatively moist (> 21 vol. % moisture) or relatively dry soil (< 21 vol. %), vpd explained 80 to 93 % of the diurnal variation in J_s. The influence of radiation seemed to increase under a drier soil in four of the five species.

Table 2. Percentage of variance in mean tree xylem sap flux (J_{st}) explained by the variables vpd and R according to multiple regression analyses employed for five co-occurring tree species reaching the upper sun canopy in the mixed stand DL3a. Hourly means of J_{st} were regressed on synchronously measured vpd and R for five consecutive days with relatively moist soil (July 1st to July 5th, 2006: $\theta > 21$ vol. %) and five days with relatively dry soil (July 16th to July 20th, 2006: $\theta < 21$ vol. %). The models had the general form $J_{st} = a \cdot x_1 + b \cdot x_2$, with x_1 being vpd and x_2 R. The coefficient of determination (r^2) for the regression models is also presented.

Species	**Moist soil**			**Dry soil**		
	vpd	***R***	***r*** **²**	**vpd**	***R***	***r*** **²**
Fagus sylvatica	88.2	4.6	0.93***	80.3	8.1	0.88***
Fraxinus excelsior	88.9	8.4	0.97***	83.0	12.7	0.96***
***Tilia* sp.**	92.7	0.1	0.93***	82.4	2.2	0.85***
Carpinus betulus	92.3	2.6	0.95***	88.0	5.0	0.93***
***Acer* sp.**	79.9	11.3	0.91***	84.5	6.1	0.91 *

In a second step, we regressed daily E_L totals on daily averages (or totals) of vpd, incident shortwave radiation or soil moisture content (θ), either on the stand level (Figure 2) or on the species level (mixed 3- and 5-tree species stands, Figure 3). Plotting stand-level E_L against vpd revealed saturation curves that differed between 1-species (DL1a), 3-species (DL2c) and 5-species (DL3a) stands. The species-rich DL3a stand with a low contribution of beech showed a similarly steep initial slope of the E_L/vpd curve, but the curve leveled off at lower E_L values and the scatter of the data was much greater than in the two other stands (Figure 2: left panel). In contrast, E_L increased more continuously with vpd in the pure beech stand (DL1a) and the 3-species stand (DL2c). Canopy transpiration per leaf area increased almost linearly with radiation but showed a clear optimum curve in its dependence of soil water content (Figure 2: centre and right panel). Maximum E_L values were observed at 25-30 vol. % in all three stands, but the species-rich DL3a stand reached somewhat higher transpiration rates at higher soil moisture in 2006 than the less species-rich stands. The differences in vpd, R and θ response of the three stands are reflected by different coefficients of the non-linear equations fitted to describe these relationships (Table 3).

The corresponding response analysis on the species level (covering the three dominant species in the DL2c stand and five species in the DL3a stand) revealed considerable species differences in the height of E_L (Figure 3). Based on species-specific sap flux data and leaf areas determined for each species separately in the mixed stands, we were able to quantify the contribution of each species to stand-level E_c and to express a species' canopy transpiration per unit leaf area. Accordingly, *F. sylvatica* transpired in 2006 in the three-species stand DL2c at nearly twice as high rates per unit leaf area as did *Tilia* sp. *F. excelsior* had by far smaller E_L rates than the other co-occurring species. This sequence was different in the five-species stand DL3a where *Tilia* sp. exceeded *C. betulus* and *F. sylvatica* by a factor of two. Again, *F. excelsior* (together with *Acer* sp.) reached very low canopy transpiration rates per unit leaf area.

Table 3. Coefficients a, b and c of exponential or Gaussian functions fitted to describe the relationship between canopy transpiration per unit leaf area (E_L) and vpd, incident shortwave radiation (R) or soil water content (θ) for the three stands DL1a, DL2c and DL3a, or the respective dominant species in these stands. a determines the height of the plateau in the exponential curves, b the shape of the curve. The coefficients of determination (r^2) are also given (* - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$). For vpd and R, the relationship to E_L was described by an exponential function of the form $E_\mathrm{L} = a \cdot e^{(-b \cdot x)}$. For θ, a Gaussian function of the form $E_\mathrm{L} = a \cdot e^{\left(-0.5 \cdot \left(\frac{x-c}{b}\right)^2\right)}$ was used. Data used in the analysis are daily totals of E_L and daily averages of vpd, θ or daily totals of R. ‡- linear regression functions of the form $E_L = a \cdot bx$ were used.

Plot type	**Tree species**	**vpd**			***R***			***θ***			
		a	*b*	r^2	*a*	*b*	r^2	*a*	*b*	*c*	r^2
DL1a	**Stand**	36.08	0.149	0.69***	133.18	0.009	0.68***	24.97	5.661	27.218	0.19***
	F. sylvatica	36.08	0.149	0.69***	133.18	0.009	0.68***	24.97	5.661	27.218	0.19***
DL2c	**Stand**	34.11	0.194	0.72***	60.56	0.028	0.72***	27.79	7.366	25.754	0.21***
	F. sylvatica	23.65	0.126	0.79***	113.75	0.007	0.71***	16.26	6.263	25.578	0.23***
	F. excelsior	1.38	0.245	0.48***	4.31	0.016	0.75***	1.44	6.118	26.297	0.53***
	***Tilia* sp.**	12.91	0.350	0.61***	15.72	0.067	0.61***	11.29	10.189	25.126	0.07*
DL3a	**Stand**	22.05	0.357	0.11***	114.48	0.009	0.35***	29.87	8.084	27.834	0.58***
	F. sylvatica	4.80	0.411	0.06*	‡-0.19	0.228	0.35***	8.28	6.956	28.374	0.82***
	F. excelsior	0.17	1.958	< 0.01	0.17	2.241	0	0.19	12.266	22.647	0.11**
	***Tilia* sp.**	14.45	0.350	0.08**	‡0.95	0.581	0.34**	20.73	7.748	27.935	0.63***
	C. betulus	5.80	0.414	0.13***	6.34	0.092	0.16***	6.07	11.353	24.873	0.18***
	***Acer* sp.**	2.34	0.151	0.28***	‡-0.39	0.093	0.46***	2.62	5.762	25.855	0.62***

In a third step, we applied multiple regression analyses to estimate the relative influence of vpd, R and θ on (log-transformed) E_L values comparing stands and species (Table 4). When analyzing daily totals of E_L and pooling all tree individuals per species in these stands, we in general found vpd to be the most important source of E_L variation, followed by radiation, while soil moisture was the least influential abiotic variable included in our model. While the three stands with contrasting tree species diversity showed a very similar environmental control of E_L in the day-to-day analysis, the co-occurring species were more different. Comparing the three most abundant tree species (*F. sylvatica*, *Tilia* sp., *F. excelsior*) indicated that the day-to-day variation in E_L showed lowest sensitivity to vpd in *F. excelsior* (31 % explained variation), because the low overall variation in sap flux density in this species (Table 4).

Table 4. Percentage of variance in canopy transpiration per unit leaf area (E_L) explained by the variables vpd, R or θ according to multiple regression analyses with backward variable selection employed at the stand level and at the species level (mean of all trees of a species in the three stands). The models had the general form $\log E_L = a \cdot x_1 + b \cdot x_2 + c \cdot x_3$ with x_1 being vpd, x_2 R and x_3 θ. The data refer to daily totals of E_L and daily totals or averages of vpd, R and θ. The coefficient of determination (r^2) for the regression models is also presented.

Species/stand no.	**vpd**	***R***	***θ***	***r*** ^{2}
DL1a	79.6	15.2	3.6	0.98***
DL2c	78.7	15.4	3.9	0.98***
DL3a	75.1	17.9	3.9	0.97***
Fagus sylvatica	69.5	13.6	3.7	0.87***
Fraxinus excelsior	31.2	12.5	12.7	0.56***
***Tilia* sp.**	75.2	17.1	3.4	0.96***

Differences in transpiration sensitivity to soil moisture variation between the three most abundant species became more evident when monthly means of E_L instead of daily totals were analyzed. In this regression model, we included as further possible sources of variation the clay content of the soil (which influences soil moisture) and the Shannon diversity index *H*' (Table 5). Additional variables tested were stem density and a measure of fine root abundance (root area index, data after Meinen et al., in press); neither of these two variables had a significant influence on E_L nor did they reduce the AIC value used to assess the quality of the model when included in it.

The explanatory power of this model with five variables was, in most cases, somewhat higher than the simpler 3-variable model used to explain the day-to-day variation (see Table 4). Diversity had only a very small or negligible influence on E_L, except in the case of *F. excelsior* (34 % of the variance explained). So did clay content, which explained more than 5 % of the E_L variance only in the case of *F. excelsior*. The dominant role of vpd as a controlling factor of E_L was similarly evident as in the 3-variable model (72 to 87 % of explained variance). Again, *F. excelsior* was an exception with a very low vpd effect. For soil moisture, a low sensitivity was confirmed for all three stands. In most studied cases was the soil moisture influence much smaller than the vpd effect and also less important than the radiation effect.

Table 5. Results of multiple regression analyses on the influence (percent of variance explained) of five abiotic (vpd, R, θ, soil clay content) and biotic variables (Shannon diversity index *H*’) on E_L. For explanations see Table 4, where the model included only three, and not five, variables. In contrast to Table 4, six stands (DL1a, DL1c, DL2a, DL2c, DL3a, DL3c) and monthly means of E_L (log-transformed) and monthly totals or averages of vpd, *R* and θ were used in the regression runs.

Species/stand no.	**vpd**	***R***	***θ***	**clay**	***H*'**	r^2
DL1	85.8	11.0	2.0	0.0	1.1	1.00 **
DL2	81.4	11.6	2.4	3.2	0.8	0.99 *
DL3	86.5	12.6	0.6	0.2	0.1	1.00 **
Fagus sylvatica	77.0	10.1	0.4	4.4	1.5	0.93***
Fraxinus excelsior	24.6	4.1	4.7	7.7	34.0	0.75 *
***Tilia* sp.**	72.3	13.4	1.4	0.8	0.0	0.88***

Discussion

Variable degrees of vpd, radiation and soil moisture control of transpiration at the species and stand level

Water flux in the soil-plant-atmosphere continuum of forests is driven by the soil-to-leaf water potential gradient and the leaf-to-air water vapor concentrations difference, while stomatal conductance and the hydraulic conductance in the soil-to-leaf pathway are controlling the flow rate. We employed multiple regression analyses to disentangle the influence of important atmospheric and edaphic factors (vpd, incident radiation, soil moisture, clay content), and also of stand structural attributes (stem density, fine root abundance, tree species diversity) on sap flux-scaled canopy transpiration. This analysis was conducted on different temporal and spatial scales, ranging from instantaneous flux variation (hourly values) to short-term (day-to-day) and long-term variation (monthly values) and focusing on species or stands. This multi-scale approach allowed us to differentiate between key variables with an immediate effect on canopy transpiration, and marginal factors that influence the magnitude of flux only on larger temporal and spatial scales.

The atmospheric moisture status was found to be the single most influential factor controlling transpiration across all investigated levels. Plotting measured flux against vpd yields a saturation curve with the shape of the curve being mostly dependent on maximal stomatal conductance, hydraulic conductance in the soil-to-leaf pathway, and stomatal sensitivity to vpd. Similar response curves have been reported from many other tree species and stands (Ewers et al. 2002, Ewers et al. 2005, Oren and Pataki 2001, Pataki et al. 2000, Zeppel et al. 2008). Variation in vpd explained more than 70 % of the variation in leaf area-related canopy transpiration in all species (except for ring-porous *F. excelsior*) and stand types, irrespective of the time integration selected. In certain species, instantaneous fluctuations in E_L could be explained to more than 90 % by vpd variation. Monospecific and species-rich stands did not differ with respect to the flux dependence on the atmospheric moisture status. It appears that species differences in the E_L-vpd relationship are lost at the stand level. In the species-rich stand DL3a, we observed a particularly high scatter of the transpiration data when plotted against vpd and radiation. A high variability in the relationship between E_L and vpd or R, which was caused by high soil moisture depletion, has also been observed by Oren and Pataki (2001), investigating subalpine tree species during periods of seasonal drought in the Rocky Mountains. Previous studies in the same mixed stand in the Hainich area have demonstrated a markedly shift in the sap flux-vpd relationship during periods of drought which are best explained by an increased sensitivity of stomatal conductance to vpd or leaf water status (Hölscher et al. 2005, Köcher et al. 2009).

The relative importance of vpd for sap flux regulation was different in *F. excelsior*, a species with a number of unique morphological and physiological properties (ring-porous, arbuscular mycorrhizal fungi, compound leaves, low leaf area index, relatedness to a family with tropical origin: Oleaceae). This species showed a low coupling of sap flux to vpd variation when longer time intervals (days to months) are considered, while the influence of soil moisture variation was larger than in the other species. Instantaneous variation in E_L, in contrast, was mostly explained by vpd which is similar to the other species.

The five tree species differed markedly with respect to the magnitude of leaf area-related canopy transpiration in the three- and five-species mixed stands. Moreover, certain species (e.g. *F. excelsior* and the *Acer* species) reached maximum E_L rates at small vpd values, while transpiration leveled off at much higher saturation deficits in *Tilia* sp. and *F. sylvatica*. Possible explanations for the species differences in the E_L-vpd relationship are that certain species appear to be more sensitive in their stomatal conductance to vpd than are others (Oren et al. 1999, Meinzer 2003). Indeed, porometer measurements of leaf conductance (g_L) conducted in the sun canopy of the Hainich forest by Köcher et al. (2009) indicated substantial differences in maximum g_L and in the vpd sensitivity of g_L among the five tree species. They identified *F. excelsior* and *T. cordata* as particularly vpd-sensitive species. However, it has to be kept in mind that our sap flux-scaled transpiration estimates represent the entire canopy and include trees from the upper and lower canopy, while the porometer data refer to the upper sun canopy leaves only. Low maximum E_L rates and a low vpd threshold, where the curve levels off, may indicate a large vpd influence on leaf conductance, but it may also result from a relatively small hydraulic conductance in the soil-to-leaf flow path. Based on sap flux measurements and corresponding leaf and soil water potential data, Köcher et al. (2009) calculated hydraulic conductances L_c that indeed differed by factors of two to four among the five species in the Hainich mixed stands. Finally, other factors such as soil moisture may influence the E_L-vpd relationship in the species because high saturation deficits are partly linked to low soil water contents which may have restricted the water flow from the soil to the roots.

For the dependence of sap flux on soil moisture, in most cases a linear relationship has been reported from trees (e.g. Pataki et al. 2000, Köcher et al. 2009). This was different in our study in the Hainich forest where the E_L-θ relationship for the tree species and also for the stands was best described by a hump-shaped curve with peak flow occurring at 25-30 vol. % of water. Köcher et al. (2009) found a rapid decrease of predawn leaf water potentials in several species of the Hainich forest when soil water potential dropped below -0.11 MPa (~ 21 vol. %). The clay-rich soils of the study region are temporarily unfavorable for tree growth since a large proportion of the soil water is bound by high matrical forces and thus are unavailable to plant roots. On the other hand, partial hypoxia is likely to occur under high moisture contents. Thus, the hump-shaped E_L-θ curve may be the consequence of both negative drought and water-logging effects on root water uptake. However, reduced E_L rates at soil moistures > 30 vol. % might also result from extended rainy periods that filled the soil water reserves, but also reduced vpd and available radiation. The effect of clay content, which has a large influence on soil hydrology at this site, was investigated in multiple regression models independently from the soil moisture effect on E_L. A notable effect was only detected in the case of *F. excelsior* (8 % of the variation explained).

As long as the boundary layer conductance exceeds stomatal conductance, radiation exerts only a minor effect on forest transpiration (Martin et al. 1997), because the canopy is well coupled to the atmosphere and the vpd effect is overwhelming (Jarvis and McNaughton 1986). Accordingly, we found incident radiation to explain not more than 18 percent, often less than 10 %, of the variation in E_L. Thus, the availability of energy controlled canopy transpiration to a much lesser extent than did vpd, but R was in most cases more important than soil moisture variation.

Effects of stand structure and tree diversity on canopy transpiration

Canopy transpiration of forests has been found to be influenced by several stand structural attributes, among them stem density (Schipka et al. 2005, Breda et al. 1995, Köstner et al. 2001), leaf area index (Granier et al. 2000, Oren et al. 1999, Vincke et al. 2005), stand age, and tree height (Ewers et al. 2005, Köstner 2001, Köstner et al. 1998, Köstner et al. 2002, Mencuccini and Grace 1996, Roberts 2000, Ryan et al. 2000, Schäfer et al. 2000, Zimmermann et al. 2000). A key trait with a large influence on canopy transpiration is the cumulative sapwood area of the stand (Oren and Pataki 2001, Wullschleger et al. 1998, Wullschleger et al. 2001), which is related to stem density and other stand structural attributes. In our sample of six stands, however, we could not detect significant effects of stem density, tree age, LAI, sapwood area and fine root abundance (root area index) on the annual totals of canopy transpiration in 2006. This may be due to the limited number of stands investigated and the rather small variability in stand structural attributes found among the stands (see Table 1). In agreement with this observation the annual totals of canopy transpiration in three structurally different stands (DL1a, DL2c, DL3a) were not different in 2006 (Leuschner et al., in revision).

Structural attributes of the species can influence canopy transpiration in mixed forests also by their specific canopy dimensions and their position within the canopy. In an *Abies amabilis* forest, Martin et al. (1997) observed that trees located in the upper canopy transpired for longer periods over the day than individuals of smaller size in the lower canopy. When sorted for stem diameter classes, it appeared that trees with > 25 cm stem diameter accounted for 70 % of total canopy transpiration. In the five-species stand DL3a, of our study, the few beech trees had very large canopies and thus dominated the upper canopy. As is clearly visible in Figure 1, these *F. sylvatica* trees started with their transpiration earlier in the morning and ended later in the evening than the other co-occurring species. Moreover, the daily course of J_s followed more closely the diurnal course of vpd and R than in other trees, which is an expression of their prominent position in the upper canopy.

By comparing 1-species, 3-species and 5-species stands, we hoped to get a better understanding of possible effects of tree diversity on canopy transpiration. In a review of the existing literature, Baldocchi (2005) concluded that diversity effects on transpiration in mixed forests should mainly be exerted through the structural and functional properties of the transpiring leaf surfaces. One should expect that the canopy transpiration of a mixed stand should mainly resemble the structural and functional properties of the foliage of the most dominant species, or to be a weighted average of the properties of all species composing the upper canopy. Our multiple regression analysis covering six stands with contrasting diversity indicated only a negligible diversity effect on E_L (less than 1.1 % of explained variation) when stand-level transpiration is considered. A remarkable exception existed in the case of *F. excelsior*: Shannon diversity index *H'* calculated for the respective stand explained 34 % of the variation in E_L of this species across the four mixed stands. This result could indicate that ash with its unique canopy morphology and physiology is in its transpiration to a considerable extent under the influence of its direct neighbors which often expand their crowns laterally, thereby suppressing *F. excelsior* (Frech 2006). Tree species diversity and identity in the neighborhood of ash trees could matter; for transpiration, however, this explanation must remain speculative.

Acknowledgments

The authors are grateful to the management of the Hainich National Park, Thuringia, for the research permit and the good cooperation. We thank Heinz Coners for technical support. This study was conducted within the framework of the Graduiertenkolleg 1086 with funding from the German Research Foundation (DFG).

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Chapter
7

Synopsis

The importance of plant diversity for ecosystem functioning has been one of the central research topics in ecology during the past 15 years. Much research has focused on the role of species diversity, or the diversity of plant functional types, for plant biomass and productivity in grasslands and old-field communities (e.g. Cardinale et al. 2007, Flombaum and Sala 2008, Hector et al. 1999, Loreau et al. 2001, 2002, Tilman et al. 1996, 1997, 2001, van Ruijven and Berendse 2005, Loreau and Hector 2001, Leps et al. 2001, 2004). Less is known about the biodiversity-ecosystem functioning relationship in forests (Scherer-Lorenzen et al. 2005, 2007). By establishing plantations, forestry recently changes from the planting of monospecific or species-poor stands to the establishment of mixed forest or more species-rich stands in certain regions such as Central Europe (Knoke et al. 2005). Those changes in tree diversity at large scales may have profound consequences for energy and matter fluxes and the diversity of organism groups being found above- and/or below-ground.

For example, Pretsch (2005) showed that resource utilization can be improved by 30 % by combining species with different structural and/or functional attributes (e.g. early and late successional species, ontogenetically early and late culminating, shade-tolerant and –intolerant). But, on the other hand, resource utilization may also be reduced by up to 30 % by competition of species with similar structural and functional attributes and ecological niches.

Beside their role in the global carbon cycle, forests have a large impact on regional and global hydrologic cycles by canopy interception, throughfall, canopy transpiration, and deep seepage, thereby affecting groundwater yields. Until recently, the significance of tree diversity on canopy transpiration has not systematically been investigated. Due to the acceleration of climate change and the expected increased number and intensity of drought periods in Central Europe and many other regions worldwide, the question if mixed forest systems could attenuate the direct and indirect drought effects arises.

We selected stands with one, three and five abundant tree species, which grew under similar edaphic and climatic conditions, and which are part of the Hainich Tree Diversity Matrix (Leuschner et al. 2008) established in 2005, to investigate the water consumption of these forest stands differing in tree species diversity. Most abundant tree species occurring in all stands was European beech (*Fagus sylvatica* L.). The moderately diverse stands comprised European beech, linden (*Tilia* sp.: *Tilia cordata* Mill. and *T. platyphyllos* Scop.) and European ash (*Fraxinus excelsior* L.) and the species-richest stands comprised additionally hornbeam (*Carpinus betulus* L.) and maple species (*Acer* sp.: *Acer pseudoplatanus* L. and *A. platanoides* L.).

This study quantified canopy transpiration of temperate broad-leaved forest stands of low, moderate or high tree species diversity using the constant-heating method after Granier (1985, 1987) to measure the stem xylem sap flux with the aim to investigate the relationship between tree species diversity, or tree species identity, and canopy transpiration.

To reach this goal, it is essential to reduce bias in the up-scaling from the sensor to the tree and stand level, and more precise information has to be obtained of the hydraulic properties of the species including radial patterns of xylem sap flux density and species-specific patterns of the hydro-active xylem area (sapwood area).

Supplementary to the continuous xylem sap flux measurements in the outer xylem, sensors at various depths were implemented to analyze the radial patterns of sap flux density in the sapwood of seven broad-leaved tree species, which differed in wood density and xylem structure. All studied tree species were diffuse-porous in their xylem anatomy, except for *F. excelsior*, which is ring-porous. The extent of the cross-sectional hydro-active xylem area (sapwood area) was estimated by injection of dye (0.1 % indigo carmine solution) into the transpiration stream. Furthermore, an allometric relationship between stem diameter at breast height (DBH) and functional sapwood for seven tree species was established.

F. sylvatica was the only species showing an exponential decrease in xylem sap flux density (J_s) with sapwood depth; thus, maximum J_s occurred in the youngest xylem elements. No evidence of a difference in the radial decrease in J_s for beech trees differing in stem size was found. In the case of ring-porous *F. excelsior*, the regression model (four-parametric Weibull function) revealed a peak in J_s close to the cambium, i.e., in the second or third annual ring, which is similar to diffuse-porous beech.

In contrast, stems of diffuse-porous *C. betulus*, *Tilia* sp., *Acer campestre* and *A. pseudoplatanus* showed an initial increase in J_s from the youngest xylem elements toward the older annual rings (at about 3 cm depth), which corresponds to a growth ring age of about 15 to 30 years. The dye injection experiments revealed that the hydro-active xylem occupied 70 to 90 % of the stem cross-sectional area in mature trees of the diffuse-porous tree species, whereas it occupied only about 21 % in stems of mature ring-porous *F. excelsior*.

In the diffuse-porous tree species, vessels in the older sapwood remain functional for 100 years or more and for up to 27 years in ring-porous *F. excelsior*, indicated by dendrochronological analyses. Ring-porous ash maintains the water conducting function in certain vessels much longer than one or two years as is expected from general theory. Even if most of the vessels lose their functionality because of embolism after one or two years, a minority of xylem elements still remain active for several years, even though they may be of marginal importance for mass flow.

Several steps for up-scaling of stem sap flux density to the tree- and canopy-level were done in order to compare the different stands in their water consumption. Also the influence of environmental and edaphic factors controlling sap flux in the different stands and tree species at different scales was analyzed.

In two study years (2005: average precipitation, 2006: relative dry), marked differences in canopy transpiration (E_c) were found, mainly as a result of differences in vapor pressure deficit (vpd), incident radiation, precipitation and soil water availability between the two years. In the average summer 2005, E_c was by 50 % higher in the species-rich DL3a stand than in the monospecific DL1a and moderately diverse DL2c stands (annual totals: 158 vs. 97 and 101 mm). In contrast, in the relatively dry summer 2006, all three stands had similar E_c rates (annual totals: 128 to 139 mm). In both summers, the species-rich stand DL3a showed a higher water consumption early in summer in May and June, reaching an early peak in late June, as compared to the species-poorer stands DL1a and DL2c. This was mainly a consequence of a higher water consumption of the *Tilia* sp. trees early in the summer. Consequently, soil moisture in DL3a dropped to lower values in July, August and September than in the DL1a and DL2c stands, restricting canopy transpiration in the second half of the vegetation period more severely in the linden-rich DL3a stand. The stands with a higher proportion of *Fagus* than *Tilia* showed a, in contrast, their peak of E_c later in the summer in July or early August. This is probably a consequence of a more conservative water use regulation in *F. sylvatica*.

Compared to other studies on E_c in temperate broad-leaved forests, low E_c totals were obtained for the vegetation periods of 2005 and 2006. For Central European monospecific beech stands, Schipka et al. (2005) obtained from a literature survey a mean E_c value of 258 (± 58) mm (annual totals). A possible explanation for the relatively low E_c values of the Hainich stands may be found in the specific edaphic situation of this forest with clay-rich soils that may restrict root water uptake in summer. The extraordinary drought of 2003 and a pronounced after-effect in 2004 and 2005 (which sometimes may hold on for up to 10 years) with reduced biomass increment, exceptional mast events, and higher defoliation rates could also be responsible for lower transpiration rates in 2005 and 2006.

Water consumption per projected crown area differed up to five-fold among the five tree species probably due to the contrasting sapwood/crown area ratios. The *Acer* and *Tilia* species exhibited higher water consumption rates than the stand average, whereas ring-porous *F. excelsior* showed s substantially smaller canopy transpiration.

The low transpiration rates on a sapwood area- and crown projection area-basis of *F. excelsior* are explained by the small hydro-active sapwood area of ash with only the youngest annual rings (typically 3 to 10) being involved in water transport.

Further, sap-flux-scaled transpiration was related to important atmospheric (vpd, radiation), edaphic (soil moisture (θ), clay content), and structural variables (tree species diversity (Shannon diversity index *H*'), stem density, basal area, fine root abundance). In order to compare the species on the physiological level, E_c was normalized by the leaf area (E_L). Single-factor and multiple regression analyses were used to identify key variables controlling E_L of the five species and this stands differing in *H*'.

The five co-existing tree species of the mixed stands differed considerably in J_s and E_L. The diffuse-porous tree species showed higher E_L rates than ring-porous *F. excelsior*. The most influencing variable was vpd, explaining 75 to 87 % of the variation in E_L on the stand level. The influence of soil moisture was small (mostly < 5 %). Stands differing in tree diversity were not different with respect to their environmental control of E_L.

On the species level, the diffuse-porous tree species again showed strongest control of E_L by vpd. Ring-porous *F. excelsior* was less vpd controlled, while θ had a larger influence on E_L. At the species level and stand level, *H*' had a small or even negligible effect on E_L, except in the case of *F. excelsior*. Thus, species differences in the environmental control of canopy transpiration as revealed by multiple regression analyses may mostly be explained by the dichotomy of diffuse- and ring-porous hydraulic architecture.

Furthermore, the water use regulation mechanisms at the leaf and whole-tree level of the five co-occurring tree species were investigated to improve the understanding of short-term regulation strategies in the control of water transport in the SPAC (soil-plant-atmosphere-continuum). This could help to predict more precisely how these tree species will respond to a predicted drier climate.

A canopy lifter allowing access to the upper canopy (up to 30 m height) was used in the Hainich forest. Synchronous measurement of leaf conductance for water vapor (g_L), stem xylem sap flux density (J_s), and leaf water potential (predawn: Ψ_{pd}, noon: Ψ_{noon}) in relation to climatic conditions (vpd, θ) allowed for a characterization of the water consumption strategies of the five tree species under ample and limited soil water supply.

Measurements in sun canopy leaves of mature trees revealed differences in maximum g_L among the five co-existing tree species. High peak g_L values (up to 280 mmol m^{-2} s^{-1}) were recorded in *C. betulus*, *F. excelsior* and *T. cordata*. In contrast, *F. sylvatica* and *A. pseudoplatanus* reached lower g_L maxima not higher than 160 to 180 mmol m^{-2} s^{-1}.

Ψ_{pd} values as a meaningful indicator of longer-term plant water deficits showed that *F. sylvatica* experienced considerable drought stress (Ψ_{pd}: -1.76 MPa) in summer 2006. This conclusion is also supported by the Ψ_{noon} values for beech providing evidence that *F. sylvatica* operated near the point of catastrophic xylem dysfunction in the twigs (-2.5 MPa for beech). *F. sylvatica* and also *A. pseudoplatanus* showed a strong reduction in J_s and leaf transpiration with increasing drought intensity. High leaf water potentials with low daily and seasonal amplitudes and a high apparent hydraulic conductance characterize *A. pseudoplatanus* as a drought avoiding species. Low Ψ_{noon} values were measured in *F. excelsior* (-3 MPa), indicating that cavitation in shoots may have occurred in this species in 2006, given the minimum threshold values of leaf water potential between -1.5 and 2.8 MPa in *F. excelsior* (Lemoine et al. 2001). However, *F. excelsior* reveals an ample and remarkable plasticity in its adaptation to wet and dry environments (Marigo et al. 2000), which showed up in a high variability in Ψ_{noon} from -5.54 to -1.94 MPa as recorded by Carlier et al. (1992) under different conditions.

T. cordata and *C. betulus* did not reach their physiological drought limit in the Hainich forest. Minimum predawn leaf water potentials did not drop below -1.0 MPa. Ψ_{noon} minima of -2.09 MPa indicated that *T. cordata* was above the threshold of -2.1 MPa detected by Pigott and Pigott (1993) for the onset of wilting, leaf shedding and growth reduction. *C. betulus* showed Ψ_{pd} minima of only -0.7 MPa.

The following tree responses were used as criteria of low or high drought sensitivity: (i) the capacity to maintain Ψ_{pd} at a high level during drought periods, (ii) to reach high leaf conductances in periods with not too dry soils, (iii) and to reduce sap flux upon soil drought only moderately.

European ash is the species which can deal best with prolonged drought periods; its ability to withstand drought is remarkable. Elements of a drought-tolerating strategy are a high maximum g_L and the maintenance of sap flux in a drying soil. These elements could not been detected in *F. sylvatica* and *A. pseudoplatanus*, which must be classified as drought-sensitive. Less clear is the grouping of *C. betulus* and *T. cordata* with respect to their drought sensitivity. Both species showed a high maximum g_L. This trait would suggest the species are drought tolerators. However, the sensitivity of g_L to vpd and decreased θ contains elements of a drought-avoiding strategy.

As a result, the five species can be arranged with respect to their drought sensitivity at the leaf and canopy levels of mature trees in the sequence *F. excelsior* < *C. betulus* < *T. cordata* < *A. pseudoplatanus* < *F. sylvatica*.

In the two study years, canopy transpiration increased (2005) or slightly decreased (2006) with increasing tree species diversity; thus, a universal trend is unlikely to exist in the Hainich forest. Complementarity in root water uptake and crown positioning in mixed stands seems not to be the rule in our study. Large differences in water consumption of the co-existing tree species were found, that had a profound impact on canopy transpiration in the mixed stands. Differences in canopy transpiration did not only exist between diffuse- and ring-porous tree species, but also within these functional groups. The consequence is that tree species identity and the specific functional traits are more important for water turnover than is tree species diversity *per se*.

If significant soil moisture depletion occurs in mixed stands, higher tree species diversity could increase drought stress in relatively dry years, thereby possibly reducing ecosystem stability. For example, *Tilia* tends to exhaust water reserves early in summer, thus increasing drought stress if present in the stand.

The sizes of sapwood area and leaf area as morphological traits, together with the apparent hydraulic conductance in the root-to-leaf pathway, leaf conductance and associated stomatal control as physiological traits were identified as main factors determining the transpiration rates of the tree species.

These traits are important for the success of the tree species to cope with changing climatic conditions such as increasing frequencies of heat waves and drought period as is predicted for parts of Central Europe. Tree species like *F. excelsior* and *C. betulus* (and the moderately drought-sensitive/-tolerant tree species *T. cordata*) will be in advantage over *F. sylvatica*, which dominates many deciduous forests in Central Europe nowadays. However, the vitality and productivity of the tree species do not only depend on the regulation strategies of plant water status in mature trees, but also on the success of rejuvenation under a changing climate.

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Acknowledgements

This work would not be possible without a lot of helping hands and minds.

First of all, I would like to thank my supervisor and advisor Prof. Dr. Christoph Leuschner for offering me working in this highly interesting field of ecological and ecophysiological sciences, and his trust, support, and discussions.

Special thanks go to Dr. Viviana Horna for her reliable support during all stages of my dissertation.

I thank Prof. Dr. Dirk Hölscher and Prof. Frank Thomas for being part of my PhD- and defense committee and supporting me whenever necessary (as Prof. Dr. Christoph Leuschner as supervisor). I also acknowledge Prof. Dr. Heiner Flessa, PD Dr. Dirk Gansert and Prof. Dr. Wolfgang Schmidt for being part of my defense committee.

I would also thank all my colleagues within the Research Training Group 1086 “The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests” for extraordinary teamwork and good times (Graduiertenkolleg 1086; http://www.forest-diversity.uni-goettingen.de). Prof. Dr. Frank Thomas, Dr. Hermann F. Jungkunst and Dr. Stefan Fleck were responsible for coordination and organization of the Grako 1086. The management of Hainich National Park is acknowledged for a very good cooperation and giving the opportunity and support for scientific research in this beautiful forest. I am very grateful for the financial support of these studies by the German Research Foundation (Deutsche Forschungsgemeinschaft; DFG).

I am deeply thankful for the chance working within such a nice, cooperative and wonderful research group as the Department of Plant Ecology is/was. Thank you very much for the wonderful atmosphere! Special thanks go to my roommates Mascha Jacob and Inga Mölder. I also thank for help during field work, technical help, discussion or just necessary distractions: Dr. Heinz Coners, Rene Eickhoff, Matthias Fleischner, Dr. Dirk Gaul, Sarah Haverstock, Paul Köcher, Dr. Sandra Korn, Dr. Matthias Kraul, Dr. Jasmin Lendzion, Florian Lovis, Dr. Catharina Meinen, Stefan Meyer, Hilmar Müller, Dr. Boris Rewald, Arek Rusin, Oliver Schaper, Dr. Stephi Sobek, Mechthild Stange, Katharina von Baggo, Dr. Alexandra Zach, Bernhard Schuldt and many, many others. Thank you all also for nice wine and dine times!

I also thank the members of the New Botanical Garden especially Dirk Deilke and Ulrich Werder for support in canopy lifter transportation to and from the study sites.

My deepest thank goes to my family. Thank you all for your love and support. I thank my mom for her fortitude. I thank my father for the inspiration, the strong interest in ecology and nature conservation and showing me the diversity of life. You have gone too early. I would like to thank my sister and brother.

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1 Mixed deciduous forest in the Hainich region (Central Germany)
2 Different insect taxa on the flowers of a thistle (*Cirsium* sp.)
3 *Glomeris* sp., a member of the decomposing soil fauna in forest ecosystems
4 *Pleodorina californica* (Chlorophyceae), colony-forming freshwater phytoplankton species
5 Grasshopper *Tettigonia cantans*, distributed from the Pyrenees to Northeastern China
6 *Microcebus berthae* (Cheirogaleidae), the smallest extant Primate species (Madagascar)
7 Tropical rain forest (Greater Daintree, Australia)
8 *Lethocolea glossophylla* (Acrobolbaceae), a liverwort of alpine mountain ranges in South America
9 Part of a coral reef in the Red Sea

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