



# Canopy transpiration of pure and mixed forest stands with variable abundance of European beech

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## ARTICLE INFO

### Article history:

Received 17 November 2010

Received in revised form 30 December 2011

Accepted 8 March 2012

Available online 28 March 2012

This manuscript was handled by Laurent Charlet, Editor-in-Chief, with the assistance of Jiin-Shuh Jean, Associate Editor

### Keywords:

Tree diversity

*Fagus*

*Fraxinus*

Sap flux

Hydraulic architecture

Seasonality

## SUMMARY

The importance of tree species identity and diversity for biogeochemical cycles in forests is not well understood. In the past, forestry has widely converted mixed forests to pure stands while contemporary forest policy often prefers mixed stands again. However, the hydrological consequences of these changes remain unclear. We tested the hypotheses (i) that significant differences in water use per ground area exist among the tree species of temperate mixed forests and that these differences are more relevant for the amount of stand-level canopy transpiration ( $E_c$ ) than putative complementarity effects of tree water use, and (ii) that the seasonal patterns of  $E_c$  in mixed stands are significantly influenced by the identity of the present tree species. We measured xylem sap flux during 2005 (average precipitation) and 2006 (relatively dry) synchronously in three nearby old-growth forest stands on similar soil differing in the abundance of European beech (pure beech stand, 3-species stand with 70% beech, 5-species stand with <10% beech). In summer 2005 with average rainfall,  $E_c$  was 50% higher in the beech-poor 5-species stand than in the two stands with moderate to high beech presence (158 vs. 97 and 101 mm yr<sup>-1</sup>); in the dry summer 2006, all stands converged toward similar  $E_c$  totals (128–139 mm yr<sup>-1</sup>). Species differences in  $E_c$  were large on a sapwood area basis, reflecting a considerable variation in hydraulic architecture and leaf conductance regulation among the co-existing species. Moreover, transpiration per crown projection area ( $E_{CA}$ ) also differed up to 5-fold among the different species in the mixed stands, probably reflecting contrasting sapwood/crown area ratios. We conclude that  $E_c$  is not principally higher in mixed forests than in pure beech stands. However, tree species-specific traits have an important influence on the height of  $E_c$  and affect its seasonal variation. Species with a relatively high  $E_{CA}$  (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.

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## 1. Introduction

In Central Europe, North America and elsewhere, large areas of natural forest have been replaced by monocultures of productive tree species, resulting not only in a reduction of tree species diversity, but also in a largely modified forest structure. Because monocultures are typically more threatened by herbivore damage and attack by pathogenic fungi (Jactel et al., 2005) and also harbor less diverse plant and animal communities than more species-rich stands, the forest policy of many industrialized countries has emphasized the establishment of mixed-species stands in the past decades (e.g. Otto, 1992). The large-scale establishment of monocultures replacing natural forests in the past and the recent

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conversion of monospecific to mixed stands may have had profound consequences for biogeochemical cycles and the diversity of various organism groups (Ellenberg and Leuschner, 2010).

Since more than 100 yr, foresters have been comparing the yield of pure and mixed stands, in most cases combinations of two species (e.g. Pretzsch, 2005; Kelty, 2006; Pretzsch et al., 2010). Another research focus exists on the susceptibility of pure and mixed stands to windthrow (review in Dhote (2005)) and nutritional interactions in mixed stands (e.g. Rothe and Binkley, 2001). In contrast, much less is known about the consequences of tree species mixing for the hydrological cycle in forests. Systematic comparisons between pure and two-species mixed stands with respect to tree water use have only been conducted in very few studies. We are aware of only two comparative hydrological investigations in temperate monospecific forests and the respective mixed stands (Anders et al., 2006; Schume et al., 2004). Baldocchi (2005) tackled the question by relating the normalized transpiration rates of six temperate forest stands to tree diversity. The first two investigations reported a higher water use of the mixed stands

as compared to the pure stands, while the latter one found a decrease of evapotranspiration with increasing tree species diversity. However, the analysis of Baldocchi (2005) included stands growing under contrasting edaphic conditions which make a direct comparison difficult. Thus, it remains unclear whether mixed stands differ systematically from the respective pure stands in water use and whether they consume more or less water. More recently, the water use of mixed and monospecific *Eucalyptus/Acacia*-plantations was compared in semiarid subtropical Australia by Forrester et al. (2010) showing a higher water use by the mixed plantation. The water use of multi-species stands composed of more than two species with contrasting hydraulic architecture (e.g. diffuse- vs. ring-porous) has not yet been compared to pure stands, neither in temperate nor in other climate regions.

From a theoretical point of view, mixed stands could differ from the respective pure stands in water use due to at least three mechanisms. First, species mixing could introduce a tree species with particularly high (or low) water use per canopy projection area into the stand, thereby increasing (or decreasing) canopy transpiration ( $E_c$ ) in comparison to  $E_c$  of the focal species' pure stand. This would represent a simple sampling effect. Evidence for species differences in water use and water flow regulation among temperate broad-leaved trees is discussed below. Second, mixed stands could have a higher  $E_c$  than the corresponding pure stands if the different tree species would use soil water in a complementary way, for example by spatial stratification of their root systems or by a differing phenology of their foliage. Third, a tree species mixture could increase stand-level  $E_c$  through indirect effects such as a stimulation of nutrient cycling, thereby increasing foliar nutrient contents and consequently leaf conductance and transpiration rate of the species in the mixture.

Numerous hydrological studies provided evidence for the existence of significant tree species differences in canopy transpiration in temperate forests. Stand-level studies on canopy transpiration ( $E_c$ ) using xylem sap flux measurement, or investigations on stand evapotranspiration applying the eddy covariance technique, microclimatological gradient studies or soil moisture budgeting approaches, revealed a considerable variation in the water use of forest stands composed by different temperate broad-leaved or coniferous species growing under similar edaphic and climatic conditions. A well-studied example is the transpiration rate of mature European beech (*Fagus sylvatica* L.) stands which in most cases is higher than that of nearby planted Norway spruce (*Picea abies* Karst) stands when growing on similar soil (Benecke, 1984; Bücking and Krebs, 1986). In a literature survey for Central Europe, Ellenberg and Leuschner (2010) documented different  $E_c$  values for pure *Fagus*, *Quercus*, *Betula*, *Picea*, *Pinus* and *Larix* stands. Other authors reported up to fourfold differences in canopy transpiration per ground area of co-existing tree species in temperate and boreal forests 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. macro-porous), (iii) maximum rooting depth, (iv) leaf area index, (v) the sensitivity of stomatal regulation to vpd and leaf water status, 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). In addition, 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, the seasonal course of  $E_c$  may differ significantly between the species.

In this study, we measured canopy transpiration with the xylem sap flux method after Granier (1985, 1987) in three nearby temper-

ate broad-leaved forest stands that differed in the abundance of European beech (*Fagus sylvatica* L.) and the presence of other broad-leaved tree species with contrasting traits related to water use such as *Tilia*, *Fraxinus*, *Carpinus* and *Acer* species (Köcher et al., 2009). The three stands represent a series from a pure beech stand to a diverse five-species stand with *Fagus* being increasingly replaced by the other tree species (from 100% to 10% contribution of *Fagus* to stand basal area). The stands were selected in a forest area where a variety of forest patches with different tree species composition co-exist under more or less homogenous edaphic and climatic conditions, thus allowing to isolate the effect of tree species composition from other environmental factors that may influence  $E_c$ . The 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  $\geq 5$  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).

This study has the objectives (i) to compare a pure beech stand with two mixed stands with respect to annual totals of canopy transpiration and (ii) to quantify the contribution of *Fagus sylvatica* and of the other four tree species to stand transpiration in relation to their abundance in a species-rich temperate broad-leaved forest. Sap flux measurements were conducted in two consecutive years with contrasting precipitation amounts (average and relatively dry summer) covering 44 trees of the five species. We hypothesized (1) that significant differences in tree water use per ground area exist among the tree species in the mixed stands and that these differences are more relevant for the amount of stand-level  $E_c$  than putative complementarity effects of tree water use, and (2) that the seasonal patterns of  $E_c$  in the mixed stands are significantly influenced by the identity of the present tree species.

## 2. Materials and methods

### 2.1. Study sites and tree layer diversity

The study sites are located in the north-eastern part of Hainich National Park, Thuringia, Central Germany, between 295 and 355 m a.s.l. (51°04'N, 10°30'E). Hainich National Park is covered by 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 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 (601 mm), while 2006 was drier than the average (518 mm, Meteo-media 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%).

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