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# Sap flux density and stomatal conductance of European beech and common oak trees in pure and mixed stands during the summer drought of 2003

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SUMMARY

Sap flux density of European beech and common oak trees was determined from sap flow measurements in pure and mixed stands during the summer drought of 2003. Eight trees per species and per stand were equipped with sap flow sensors. Soil water content was monitored in each stand at different depths by using time-domain reflectometry (TDR). Leaf area index and vertical root distribution were also investigated during the growing season. From sap flux density (*SFD*) data, mean stomatal conductance of individual trees ($G_s$) was calculated by inverting the Penman–Monteith equation. Linear mixed models were developed to analyse the effects of species and stand type (pure vs. mixed) on *SFD* and $G_s$ and on their sensitivity to environmental variables (vapour pressure deficit ($D$), incoming solar radiation ($R_G$), and relative extractable water (*REW*)). For reference environmental conditions, we did not find any tree species or stand type effects on *SFD*. The sensitivity of *SFD* to $D$ was higher for oak than for beech in the pure stands ($P < 0.0001$) but the mixing of species reduced it for oak and increased it for beech, so that the sensitivity of *SFD* to $D$ became higher for beech than for oak in the mixed stand ($P < 0.0001$). At reference conditions, $G_s$ was significantly higher for beech compared to oak (2.1 and 1.8 times in the pure and mixed stand, respectively). This was explained by a larger beech sapwood-to-leaf area ratio compared to oak. The sensitivity of $G_s$ to *REW* was higher for beech than for oak and was ascribed to a higher vulnerability of beech to air embolism and to a more sensitive stomatal regulation. The sensitivity of beech $G_s$ to *REW* was lower in the mixed than in the pure stand, which could be explained by a better sharing of the resources in the mixture, by facilitation processes (hydraulic lift), and by a rainfall partitioning in favour of beech.

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## 1. Introduction

Water transport in trees is required for a number of physiological processes. Among others, transpiration is coupled with photosynthesis through stomata functioning (Jarvis and Davies, 1998) and the water flux caused by transpiration is one of the processes involved in nutrient transport from soil to roots (Barber, 1995). In this context, canopy stomatal conductance for water vapour is defined as the mean value of the stomatal conductance of individual leaves added in parallel and weighted by leaf area (Baldocchi et al., 1991). This variable is particularly interesting since it reflects the stomatal control of transpiration. From transpiration measurements, canopy stomatal conductance can be derived by using the reverse form of the Penman–Monteith equation (Jarvis and McNaughton, 1986; Stewart, 1988). Several techniques have been developed to estimate transpiration, depending on the spatial and temporal scales (Smith and Allen, 1996; Köstner et al., 1998; Wullschleger et al., 1998). Common meteorological methods (e.g. eddy covariance) are suitable to measure transpiration at the stand level while the sap flux method is more adapted to estimate transpiration at the tree level (Granier and Bréda, 1996).

Stomatal conductance varies among individuals of a given tree species or of different tree species as a function of several tree characteristics depending on tree genetic, tree age, and growth conditions (site and competition): tree height, leaf area, sapwood area, root area, sapwood-to-leaf area ratio, and root-to-leaf area ratio (Addington et al., 2006). At the stand level, transpiration depends on the distribution of these tree characteristics that may vary greatly depending on species composition and stand structure. In multispecies stands, the spatial heterogeneity in water use is high and can partly be ascribed to physiological differences between tree species and to the variability in competition conditions (Hölscher et al., 2005). In addition, antagonistic or synergistic interactions between tree species may occur regarding water use in mixed stands; individuals of different species might reduce tree

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competition for water in partitioning water uptake, either at a temporal or at a spatial level or both. Temporal partitioning occurs when species have a different phenological timing resulting in staggered water needs. Spatial partitioning may happen vertically due to differences in root distribution with depth and horizontally in relation with stand density and composition (Meinzer et al., 2001).

Stomatal conductance is also controlled by climatic variables, both on daily and sub-daily scales (McNaughton and Jarvis, 1991). The response of stomatal conductance to increasing vapour pressure deficit generally follows a logarithmic decrease. However, the magnitude of the decrease reflecting the stomatal sensitivity varies considerably both between and within tree species (Oren et al., 1999). Stomatal conductance is also affected by the soil water availability and is known to decrease when soil relative extractable water drops below a threshold of 0.4 (Granier et al., 1999). Bréda et al. (2006) analysed the ecophysiological responses of temperate forest trees and stands under the drought conditions of 2003 and concluded that there is a large inter and intra-specific diversity of hydraulic and stomatal responses to soil water deficit.

Tree species effects on transpiration and stomatal conductance have generally been analysed by comparing pure stands or patch of different species (Granier et al., 2000a; Gartner et al., 2009) or by comparing different species in a mixed stand (Pataki et al., 2000; Oren and Pataki, 2001; Wullschleger et al., 2001; Raftoyannis and Radoglou, 2002; Leuzinger et al., 2005; Keel et al., 2007). When trees species are compared based on pure stands located at different sites, the species effects can be confounded with spatial effects. The inter-species comparisons within a mixed stand do not present this disadvantage but are only valid for the particular competition conditions occurring in this stand. Comparing tree species in pure and mixed stands on a same site would allow to evaluate the species effect in different competition conditions and to test for the mixture effect. To the best of our knowledge, it has never been done until now.

The objective of this study was (i) to compare European beech and common oak tree sap flux density (*SFD*) and mean stomatal conductance ($G_s$) in pure stands located at a same site and within a mixed stand and (ii) to evaluate the mixture effect by comparing tree *SFD* and $G_s$ of a same species in pure and mixed stands. Linear mixed models were developed to describe the response of *SFD* and $G_s$ to environmental variables, which allowed us to test for the species and mixture effects on a reference *SFD* and $G_s$ (at fixed environmental conditions) and on their sensitivity to the environmental variables. As the measurements were carried out during the 2003 vegetation period characterized by a severe drought, large ranges of atmospheric and soil moisture conditions were available.

## 2. Materials and methods

### 2.1. Study site

The study site is located in the western part of the Belgian Ardennes at 300 m elevation (50°01′N, 4°24′E). Mean annual rainfall is about 1044 mm with 411 mm falling during leaf cover period (May–September). Mean annual temperature is around 8 °C. However, in 2003, the year of concern for this study, rainfall was 836 mm with 344 mm during leaf cover period and mean annual temperature was 9.8 °C. The site consists of a 60 ha oak (*Quercus petraea* (Matt.) Liebl.) and beech (*Fagus sylvatica* L.) forest lying on an acid brown earth soil, classified as Dystrochrepts (USDA soil taxonomy), with a moder-type humus and a $A_hB_wC$ profile. The soil has been developed on a loamy and stony solifluxion sheet in which weathering products of the bedrock (Lower Devonian: sandstone and schist) were mixed with added periglacial loess.

By the end of the 19th century, the stand was probably an oak coppice with a few standards. Taking advantage of a massive oak regeneration in 1880, the stand was progressively converted to a high forest and then was invaded by beech. In 2003, the area was covered by even-aged (~120 years) oak trees and uneven-aged beech trees.

### 2.2. Experimental plots

Three experimental plots were installed in stands dominated either by oak (0.25 ha) or by beech (0.35 ha) and in a 1:1 mixture of both species (0.51 ha). These plots are all situated on the same tableland (305–312 m) and were selected in such a way that stand species composition was the main varying factor. The beech plot is located 600 m away from the oak plot and the mixed plot is located halfway between them. Soil homogeneity was evaluated on the

**Table 1**
Selected physical and chemical properties of a soil profile per experimental plot.

| Plot | Horizon | Depth (cm) | Stone content ($m^3$ 100 $m^{-3}$) | Sand (%) | Silt (%) | Clay (%) | MO[a] (g 100 $g^{-1}$) | pH ($H_2O$) |
|---|---|---|---|---|---|---|---|---|
| Oak stand | Ah | 0–6 | 5 | 10 | 62 | 28 | 21.43 | 3.96 |
| | Bw1 | 6–27 | 30 | 11 | 54 | 35 | 4.66 | 4.28 |
| | Bw2 | 27–42 | 30 | 11 | 56 | 33 | 4.02 | 4.38 |
| | 2Bw3 | 42–55 | 30 | 9 | 47 | 44 | 5.21 | 4.40 |
| | 2Bg1 | 55–75 | 30 | 10 | 47 | 43 | 3.43 | 4.49 |
| | 2Bg2 | 75–119 | 30 | 11 | 48 | 41 | 4.13 | 4.67 |
| | 2Bg3 | 119–160 | 30 | 6 | 51 | 42 | 4.25 | 4.76 |
| Mixed stand | Ah | 0–6 | 8 | 15 | 74 | 11 | 18.46 | 3.82 |
| | Bw1 | 6–20 | 8 | 14 | 61 | 25 | 4.71 | 4.37 |
| | Bw2 | 20–36 | 8 | 14 | 60 | 26 | 4.06 | 4.41 |
| | 2Bw3 | 36–50 | 8 | 10 | 49 | 40 | 4.39 | 4.33 |
| | 2Bg1 | 50–81 | 10 | 11 | 42 | 47 | 4.51 | 4.41 |
| | 2Bg2 | 81–110 | 23 | 16 | 37 | 47 | 4.32 | 4.53 |
| | 2Bg3 | 110–160 | 75 | 12 | 47 | 42 | 3.96 | 4.95 |
| Beech stand | Ah | 0–8 | 8 | 14 | 62 | 24 | 15.87 | 4.15 |
| | Bw1 | 8–20 | 8 | 15 | 60 | 25 | 5.69 | 4.27 |
| | 2Bw2 | 20–50 | 28 | 16 | 55 | 30 | 4.35 | 4.39 |
| | 2Bw3 | 50–80 | 60 | 18 | 61 | 21 | 3.78 | 4.46 |
| | 2Bw4 | 80–112 | 70 | NA | NA | NA | NA | NA |
| | BC | 112–160 | 80 | NA | NA | NA | NA | NA |

NA: not available.
[a] Organic matter determined by loss on ignition.

**Table 2**
Mean stand characteristics of the three experimental plots in 2003 (standard deviation in parentheses).

| Plot | Species | No./ha | $C_{130}$[a] (cm) | Basal area ($m^2$/ha) | Height (m) | | $R$[c] | $LAI_{max}$[d] |
|---|---|---|---|---|---|---|---|---|
| | | | | | Top[b] | Mean | | |
| Oak stand (0.25 ha) | Oak | 244 | 99 (24) | 20.3 | 22.4 | 20.9 (2.8) | 19.9 (3.0) | 4.9 (1.2) |
| | Beech | 60 | 41 (27) | 1.1 | | 12.9 (4.9) | | |
| | Hornbeam | 164 | 34 (11) | 1.6 | | | | |
| Mixed stand (0.51 ha) | Oak | 133 | 120 (21) | 15.8 | 25.4 | 24.7 (1.6) | 17.9 (3.2) | 7.2 (0.7) |
| | Beech | 324 | 63 (35) | 13.4 | 25.0 | 17.9 (6.4) | | |
| | Hornbeam | 6 | 19 (7) | <0.1 | | | | |
| Beech stand (0.35 ha) | Oak | 51 | 92 (14) | 3.6 | | 22.2 (1.0) | 21.3 (3.4) | 6.4 (0.8) |
| | Beech | 309 | 80 (44) | 20.3 | 25.3 | 18.5 (7.4) | | |

[a] Stem circumference at a height of 1.3 m.
[b] Mean height of the hundred highest trees per hectare.
[c] Crown-to-stem diameter ratio (m $m^{-1}$), not presented for beech and hornbeam for which $R$ is varying with tree size.
[d] Maximum stand leaf area index.

**Table 3**
Dendrometric characteristics of the trees selected for sapflow measurements. Figures are means of two values per girth class.

| | Girth class (cm) | Pure stand | | | | Mixed stand | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | $C_{130}$[a] (cm) | $H_t$[b] (m) | $s$[c] ($m^2$) | $LAI_{ind}$[d] | $C_{130}$ (cm) | $H_t$ (m) | $s$ ($m^2$) | $LAI_{ind}$ |
| Oak | 0–90 | 83.4 | 20.8 | 26.6 | 2.7 | 87.8 | 23.9 | 22.0 | 3.2 |
| | 90–115 | 102.0 | 21.1 | 33.5 | 3.4 | 104.0 | 23.6 | 28.8 | 4.2 |
| | 115–140 | 126.7 | 21.2 | 54.3 | 3.9 | 125.9 | 25.4 | 51.5 | 5.7 |
| | >140 | 150.7 | 22.9 | 82.0 | 4.3 | 149.9 | 25.3 | 52.2 | 4.2 |
| Beech | 0–70 | 57.7 | 22.4 | 13.2 | 5.2 | 54.4 | 18.7 | 8.2 | 7.9 |
| | 70–105 | 83.3 | 22.7 | 24.6 | 6.2 | 89.2 | 23.7 | 19.5 | 10.5 |
| | 105–140 | 123.1 | 24.9 | 52.6 | 7.3 | 127.2 | 26.3 | 38.7 | 12.1 |
| | >140 | 158.0 | 25.7 | 96.1 | 7.5 | 153.4 | 27.3 | 55.8 | 12.9 |

[a] Stem circumference at a height of 1.3 m.
[b] Total height.
[c] Individual area associated to the tree (see Eq. (7)).
[d] Individual leaf area index (see Eq. (10)).

basis of a detailed characterisation of the soil profile of each plot (Table 1). In the three plots, the silt fraction dominates largely (60–70%) within the upper horizons and tends to decrease with increasing depth, contrary to the clay content which increases with depth as a result of schist weathering. The pH ($H_2O$) of the hemiorganic horizon is around 4.0 in the three stands and increases up to values of 4.5–5.0 below 1 m depth. The effective cation exchange capacity ($BaCl_2$ extraction; Hendershot and Duquette, 1986) of the three soil profiles is largely dominated by aluminium and the base saturation is generally lower than 20% (data not shown). The main soil difference is the stone content in deeper horizons which is higher in the beech and mixed stands. The soils of all stands are well drained: the ground water table is below 1.5 m depth during the growing season and rises up to 30–45 cm depth in winter. Rainfall interception in these plots is described in André et al. (2008a, 2011). In each stand, all trees were measured (stem circumference at a height of 1.3 m, total tree height) in 2003 (Table 2). The understorey vegetation is abundant in the oak stand and is dominated by *Rubus* sp. while in the beech and mixed stands the understorey is very sparse due to canopy closure.

### 2.3. Sap flow measurements

Sixteen trees of each species (oak and beech) were equipped with sap flow sensors: eight trees in each pure plot and eight oaks and eight beeches in the mixed plot. These trees were selected to be representative of stem circumference at 1.3 m and of crown class distributions in the corresponding plot. Two trees were chosen per class of circumference (4 classes), species (oak or beech) and stand type (pure or mixed). Dendrometric characteristics of the selected trees are given in Table 3.

#### 2.3.1. Sap flux density

Sap flux density ($SFD$ [l $m^{-2}$ $s^{-1}$]) of individual trees was measured between DOY 130 and DOY 273 with Granier type thermal dissipation sensors (UP GmbH, Cottbus, Germany). Each sensor consists of two metal probes with a diameter of 2 mm and a length of 20 mm. The probes were inserted above each other (approximately 15 cm apart) in a radial orientation behind the cambial zone and at a mean height of 1.5 m above the soil surface. Each probe contains a copper–constantan thermocouple. The upper probe contains a thermal heating element covering its entire length and the lower probe served as an unheated reference. All probes were installed on the north side of the trees and covered by a plastic protection and an aluminium shield to protect them from rain and direct solar heating. The output of the probes was recorded every 15 min by a data logger (Easylog 3000, GME, Incourt, Belgium).

A standard calibration is widely used for the thermal dissipation sensor method (Granier, 1985), relating $SFD$ to the difference in temperature between a pair of probes ($\Delta T$ [°C]):

$$SFD = 0.119K^{1.23} \quad (1)$$

where $K$ (dimensionless) is a parameter calculated as:

$$K = \frac{\Delta T_{max} - \Delta T}{\Delta T} \quad (2)$$

where $\Delta T_{max}$ is the value of $\Delta T$ when there is no sap flux, which corresponds to the nocturnal $\Delta T$ maximum over a 24 h period. It is worth noting that this calibration function (Eq. (1)) is valid for the two studied species; in fact, Granier (1985) showed that the sensor response is independent of the species.

*2.3.2. Tree sap flow and transpiration*

For oak, sap flow ($SF_{oak}$ [l h$^{-1}$]) was obtained by multiplying *SFD* values by sapwood area (*SA* [m$^2$]) and a constant for the time unit conversion:

$$SF_{oak} = SFD\,SA\,3600 \quad (3)$$

For this species, sapwood is clearly distinguishable from heartwood thanks to the difference in colour. Oak *SA* (cm$^2$) was estimated from *DBH* (cm) according to an allometric relationship established based on 16 oaks of the experimental site:

$$SA = 9.422\,DBH - 129.11 \quad R^2 = 0.73, \;\; n = 16 \quad (4)$$

A similar relationship has been reported by Herbst et al. (2008).

For beech, sapwood and heartwood are not clearly demarcated. Granier et al. (2003) observed that the sap flux density decreases from the cambial zone to the pit. The following relationship has been fitted to the data presented in Granier et al. (2003):

$$SFD_r = 104.36 - 1.019X_r \quad R^2 = 0.66, \;\; n = 100 \quad (5)$$

where $SFD_r$ is the relative sap flux density with respect to the maximum sap flux density (%), $X_r$ is the relative depth below cambium (%). The maximum sap flux density arises at the periphery of the wood, where the sensors are located. Beech *SF* ($SF_{beech}$ [l h$^{-1}$]) was calculated by integrating Eq. (5) over the trunk cross-section at the level of the sensors and multiplying the result by *SFD* and a constant for the time unit conversion:

$$SF_{beech} = SFD\,A\,3600 \quad (6)$$

where *A* (m$^2$), the equivalent sapwood area, results from the integration of Eq. (5) and is equal to $\frac{2.11\pi}{12}DBH^2$.

As there was only one probe per tree, we did not take into account the azimuthal variation of sap flux within the tree; we supposed that it was low.

At tree scale, the difficulty is to associate an area to each tree in order to express individual tree transpiration per unit area. We chose to determine it based on the proportion of the tree basal area in the total basal area measured within a radius of 15 m around the considered tree. Oak and beech individual tree transpiration (*T* [mm d$^{-1}$]) was therefore obtained by dividing the daily *SF* by the individual area associated to the tree (*s* [m$^2$]) calculated as follows:

$$s = \frac{BA}{BA_{15m}}\pi 15^2 \quad (7)$$

where *BA* is the basal area of the considered tree (m$^2$) and $BA_{15m}$ is the basal area measured within a 15 m radius around the considered tree (m$^2$).

*2.3.3. Stand sap flow and transpiration*

For each stand, total sap flow ($SF_S$ [l h$^{-1}$]) was calculated by summing the contributions of oak and beech trees (hornbeam being considered as beech) according to the following equation:

$$SF_S = \left(\sum_{i=1}^{4} SFD_{oak_i} TSA_i + \sum_{i=1}^{4} SFD_{beech_i} TA_i\right) 3600 \quad (8)$$

where $SFD_{oak_i}$ (l m$^{-2}$ s$^{-1}$) is the average sap flux density in the class *i* for oak trees, $SFD_{beech_i}$ (l m$^{-2}$ s$^{-1}$) is the average sap flux density in the class *i* for beech trees, $TSA_i$ (m$^2$) is the total sapwood area in the class *i* for oak trees and $TA_i$ (m$^2$) is the total equivalent sapwood area in the class *i* for beech trees. Daily stand transpiration ($T_S$ [mm d$^{-1}$]) was obtained by summing hourly $SF_S$ over each day and dividing the sum by the stand area.

*2.4. Soil water content*

From June 11th to December 3rd 2003, soil volumetric water content ($\theta$ [m$^3$ m$^{-3}$]) was measured hourly at four different depths in one profile per plot using time-domain reflectometry (TDR) sensors (CS616, Campbell Scientific, Shepshed, UK). The sensors were inserted horizontally into the major soils horizons (ca 3–3.5 cm; ca 9–23 cm; ca 30–52 cm, ca 76–117 cm) and were connected to a data logger (Easylog 3000, GME, Incourt, Belgium). The pulse output obtained with the sensors was converted into propagation time along the sensors rods and converted into relative dielectric permittivity ($\varepsilon_r$ [dimensionless]) thanks to a calibration carried out using different media (water, methyl alcohol, ethyl alcohol and air). We finally used the model of Jacobsen and Schjønning (1993) to relate the soil volumetric water content to the soil relative dielectric permittivity.

Based on $\theta$ data, extractable water (*EW* [mm]) was calculated over a 160 cm depth according to:

$$EW = \sum_{i=1}^{n} (\theta_i - \theta_{\min,i}) z_i (1 - v_i) \quad (9)$$

where $\theta_i$ (m$^3$ m$^{-3}$) is the daily average volumetric water content in horizon *i*, $\theta_{min,i}$ (m$^3$ m$^{-3}$) is the minimum water content measured in the horizon *i* during the summer 2003, $z_i$ (mm) is the thickness of horizon *i* and $v_i$ (m$^3$ m$^{-3}$) is its stone content.

The relative extractable water (*REW* [mm mm$^{-1}$]) was calculated as the ratio of actual extractable water to maximum extractable water (Black, 1979). The latter was estimated from Eq. (9) by considering $\theta_i = \theta_{FC,i}$ which is the volumetric water content at field capacity in horizon *i*. In addition, the temporal evolution of the water table level was monitored in each plot by means of a piezometer.

*2.5. Meteorological data and potential evapotranspiration*

Meteorological data were monitored with an automatic meteorological station located in an open field 300 m away from the forest site. Air temperature and air relative humidity were recorded at 1.5 m height to calculate daytime mean vapour pressure deficit (*D* [hPa]). To account for changes in daylength over the study period, *D* was normalised by daylength/24 h ($D_z$ [hPa]) (Oren and Pataki, 2001). Incident rainfall was measured at 1.5 m height with a tipping bucket while solar radiation and wind speed were measured at 2.5 m. These measurements were used to calculate daily potential evapotranspiration (*PET* [mm d$^{-1}$]) according to the FAO Penman–Monteith equation applied to a hypothetical clipped grass surface actively growing with adequate water supply and having 0.12 m height (Allen et al., 1994).

*2.6. Mean stomatal conductance of individual trees*

Mean stomatal conductance of individual trees ($G_s$) was calculated from daily tree transpiration and meteorological variables by inverting the Penman–Monteith equation (see Granier and Loustau, 1994). All values of $G_s$ were reported on a leaf area basis. Air temperature, air relative humidity and solar radiation at the top of the canopy were assumed to be the same as those measured at the meteorological station. Wind speed measured at 2.5 m height was corrected using the equation proposed by Jetten (1996). When *D* was below 6 hPa (wettest air conditions), values of $G_s$ were too imprecise (Ewers and Oren, 2000) and were therefore not considered.

### 2.7. Leaf area index and vertical root distribution

Leaf area index (*LAI* [$m^2$ projected leaf surface $m^{-2}$ ground]) measurements were performed monthly during the growing season using an optical analyser (LAI-2000, Li-Cor, Lincoln, NE, USA). The above-canopy readings were taken in an open field located 300 m away from the study site, and the below-canopy readings were taken within each plot, on a 12.5 by 12.5 m grid consisting of 16, 20, and 28 measurements points in the oak, beech, and mixed stand, respectively. Only the upper three rings (0–43°) of the sensors were taken into account for computation (Dufrêne and Bréda, 1995). Moreover, the individual tree *LAI* ($LAI_{ind}$) was estimated based on the following equation:

$$LAI_{ind} = \frac{Q\ SLA}{10000\ s} \quad (10)$$

where $Q$ (g) is the individual leaf litter production during the vegetation period predicted by allometric equations (Jonard et al., 2006), *SLA* ($cm^2\ g^{-1}$) is the specific leaf area (data available in Jonard et al. (2006)) and $s$ ($m^2$) is the individual area associated to the tree (see Eq. (7)).

The assessment of the spatial root distribution is essential to estimate the amount of soil water actually available for vegetation. Especially for this study, such information is fundamental to explain differences in water use by both species between stands of contrasted species composition. In mid-May 2003, a trench (180 cm deep × 150 cm large) was dug out in each plot, at a place with surrounding tree density and species composition representative of the stand. One face of each trench was subdivided into square zones of 10 cm side (Bréda et al., 1995). Exposed roots of each zone were counted and classified into five diameter classes: <3 mm, 3–5 mm, 5–10 mm, 10–20 mm, and >20 mm. However, visual characterisation of the root species was not possible for the mixed stand. Root diameter cannot be totally correlated to specific root functions but it is generally accepted that coarse roots are responsible for the anchorage and architecture of the root system, while fine roots are responsible for water uptake (Bréda et al., 2006).

### 2.8. Statistics and modelling

Mixed linear models were used to relate *SFD* and $G_s$ to environmental variables. *SFD* was related to $D_z$ and *REW* according to:

$$SFD = a_i + b_i(ln(D_z) - 1.2) + c_i(ln(REW) + 0.5) + \tau + \varepsilon \quad (11)$$

where $\tau$ is the 'tree' random effect and $\varepsilon$ is the residual term.

$G_s$ was related to $D_z$, incoming solar radiation $R_G$ ($W\ m^{-2}$), and *REW* as follows:

$$G_s = a_i + b_i(ln(D_z) - 1.8) + c_i(R_G - 232) + d_i(REW - 0.6) + \tau + \varepsilon \quad (12)$$

In these models, the inter-tree variability was taken into account by using a random effect (Brown and Prescott, 1999). The inter-tree variability was obtained from the inter-sensor variability. It is worth noting that the intra-tree variability was included in the inter-tree variability as only one probe per tree was used. Moreover, fixed effect parameters were estimated for each species in each stand type. The independent variables of the models were centred to obtain an intercept ($a_i$) located in the centre of the experimental domain and therefore independent from the other model parameters. The indices $i$ refer to each species × stand type population ($i$ = 1 and 3 for oak in the pure and mixed stand, respectively; $i$ = 2 and 4 for beech in the pure and mixed stand, respectively). For both models and each species x stand population, a regression analysis was performed to test if the intercept and the slope of the linear relationship between observations and predictions differed significantly from 0 and 1, respectively. It was never the case ($\alpha$ = 0.05). Q–Q plots were also carried out and showed that residuals were normally distributed. Contrasts were used to test the impact of species (oak vs. beech) and mixture (pure vs. mixed) on the model parameters. All analyses were carried out with the MIXED procedure of the SAS software (version 9.1; SAS Institute Inc., Cary, NC).

## 3. Results

### 3.1. Meteorological conditions

The year 2003 was particularly dry and hot. Gaussen's ombrothermic diagram shows a drought episode during August and September (Fig. 1). May and July were the wettest months of the growing season. However, rainfall was unequally distributed in July since more than half of the amount felt in one day (DOY 211: 59 mm) (Fig. 2). During the growing season, rainfall events were separated by six large dry periods of 10 to 16 days (DOY 169–DOY 180, DOY 186–DOY 197, DOY 213–DOY 228, DOY 256–DOY 265, DOY 286–DOY 296, and DOY 306–DOY 319).

Cumulative rainfall was 836 mm for the year 2003 and 312 mm for the study period (DOY 130–DOY 273). Daily potential evapotranspiration (*PET*) reached 6 mm $d^{-1}$ in July and August. Cumulative potential evapotranspiration was 676 mm for the year 2003 and 456 mm for the study period (data not shown). Daylength-normalised daytime mean vapour pressure deficit ($D_z$) exceeded

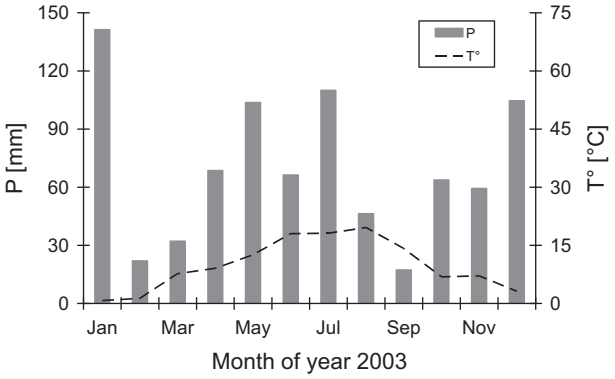


**Fig. 1.** Gaussen ombrothermic diagram for 2003 based on monthly rainfall ($P$) and mean monthly air temperature (T°) measured at the exposed meteorological station.

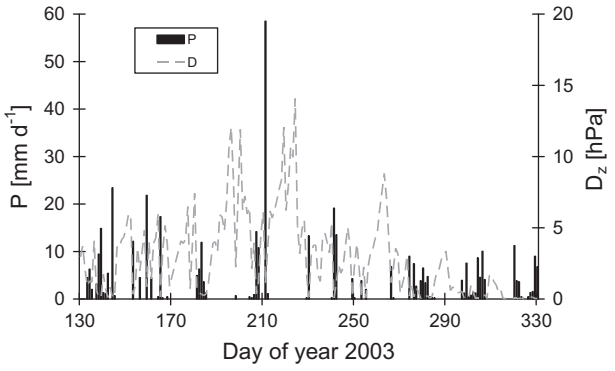


**Fig. 2.** Daily rainfall ($P$) and daylength-normalised daytime mean vapour pressure deficit ($D_z$) measured at the exposed meteorological station from May 10th to November 26th 2003.

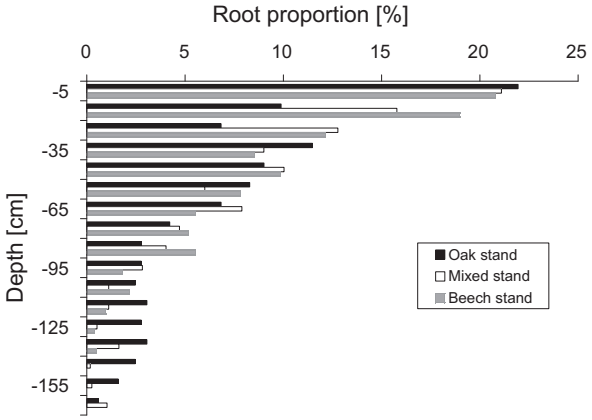


**Fig. 3.** Root ($\varnothing$ < 5 mm) distribution with depth based on root counts in the pure and mixed stands of oak and beech.

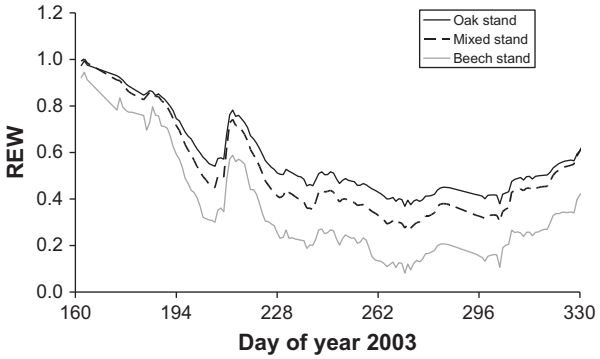


**Fig. 4.** Relative extractable water (*REW*) in the pure and mixed stands of oak and beech.

10 hPa during three days in July (DOY 195, DOY 196, and DOY 200) and three days in August (DOY 219, DOY 222, and DOY 224) (Fig. 2). Mean daytime air temperature ($T$°) exceeded 20 °C several days in June (3 days), July (7 days), August (12 days), and September (3 days) (data not shown).

### 3.2. Leaf area index and vertical root distribution

*LAI* in the three stands increased rapidly with budburst and leaf expansion from mid-April (DOY 104 to DOY 110 for oak; DOY 111 to DOY 117 for beech) until a maximum around mid-June. The maximum *LAI* was 4.9 in the oak stand, 7.2 in the mixed stand, and 6.4 in the beech stand (Table 2). By mid-October, *LAI* started to decrease due to leaf fall. During the whole growing season, *LAI* remained stable in all stands.

When considering only roots with a diameter less than 5 mm, we observed that the proportion of roots in the 0–30 cm horizon of the beech and mixed stands (52% and 50%, respectively) was larger than that of the oak stand (39%) (Fig. 3). Compared with the beech stand, a higher proportion of roots was observed in the deep horizons (>100 cm depth) of the oak stand, the mixed stand showing an intermediate proportion. Oak roots were still observed at 160 cm depth while no beech roots were counted below 140 cm depth. Root density (number of root $m^{-2}$) was significantly higher in the mixed stand than in the beech stand (between 0 and 160 cm depth) and than in the oak stand (between 0 and 100 cm depth) (data not shown). In the upper horizon (0–10 cm), root density amounted to 1007, 1153, and 1640 roots $m^{-2}$ in the oak, beech, and mixed stand, respectively.

### 3.3. Relative extractable water

The temporal variation of *REW* calculated in all cases on a 160 cm depth was similar in the three stands (Fig. 4). The maximum *REW* was observed in mid-June at the start of the measuring period (DOY 163) and reached 0.99, 1.00, and 0.95 in the oak, mixed, and beech stand, respectively. The values of *EW* measured during this day were 169 mm, 160 mm, and 90 mm in the oak, mixed, and beech stand, respectively. *REW* progressively decreased during the growing season, except around DOY 211 due to an important rainfall event that significantly increased *REW* in the three stands. The lowest value of *REW* was reached at the end of September (DOY 271) in each stand (0.37, 0.27 and 0.08 in the oak, mixed, and beech stand, respectively). During the whole measuring period, the oak and mixed stands presented similar *REW* while it was much smaller for the beech stand.

### 3.4. Sap flux density: model quality and description

The sap flux density model (Eq. (11)) explained 65% of the *SFD* variability ($n$ = 2925); the fixed effects and the 'tree' random effect accounted respectively for 48.5% and 18.5% of this variability. Fig. 5 shows the model results by representing the average and standard error *SFD* of each species x stand population as a function of the natural logarithm of $D_z$ (Fig. 5a) and as a function of the natural logarithm of *REW* (Fig. 5b).

The significance of the model parameters (Eq. (11)) was evaluated based on the 95% confidence interval (Table 4a). The parameters $b_i$ and $c_i$ describing respectively the sensitivity to the natural logarithm of $D_z$ and the sensitivity to the natural logarithm of *REW* were significantly different from zero for both species in the pure and mixed stands.

As revealed by the contrast analyses, the sap flux density (*SFD*) at $D_z$ = 3.3 hPa and *REW* = 0.6 (i.e. the model intercept, $a_i$) was not significantly different between the two species in the pure and mixed stands and, for both species, *SFD* was also not affected by stand type (Table 5a). The beech *SFD* was less sensitive to the natural logarithm of $D_z$ than that of oak in the pure stands while it was the opposite in the mixed stand (Table 5a). For beech, *SFD* was more sensitive to the natural logarithm of $D_z$ in the mixed than in the pure stand while the oak *SFD* sensitivity to the natural logarithm of $D_z$ was lower in the mixed than in the pure stand (Table 5a). The *SFD* sensitivity to the natural logarithm of *REW* was not significantly different between the two species in the pure stands. However, the beech *SFD* was more sensitive to the natural logarithm of *REW* than that of oak in the mixed stand (Table 5a). For beech, *SFD* was more sensitive to *REW* in the mixed stand than in the pure stand while the *SFD* sensitivity to *REW* was not significantly affected by stand type for oak (Table 5a).

### 3.5. Mean stomatal conductance: model quality and description

The model (Eq. (12)) explained 79.4% of the $G_s$ variability ($n$ = 1282); the fixed effects and the 'tree' random effect accounted respectively for 48.4% and 31.0% of this variability. The model results were illustrated separately for both species in the pure and mixed stands by representing $G_s$ as a function of the natural logarithm of $D_z$ (Fig. 6a) and of *REW* (Fig. 6b).

The significance of the model parameters (Eq. (12)) was evaluated based on the 95% confidence interval (Table 4b). The parameter $b_i$ describing the sensitivity to the natural logarithm of $D_z$ was significantly different from zero for both species in the pure and mixed stands. The parameter $c_i$ describing the sensitivity to $R_G$ was significantly different from zero for both species only in the pure stands and the parameter $d_i$ describing the sensitivity to

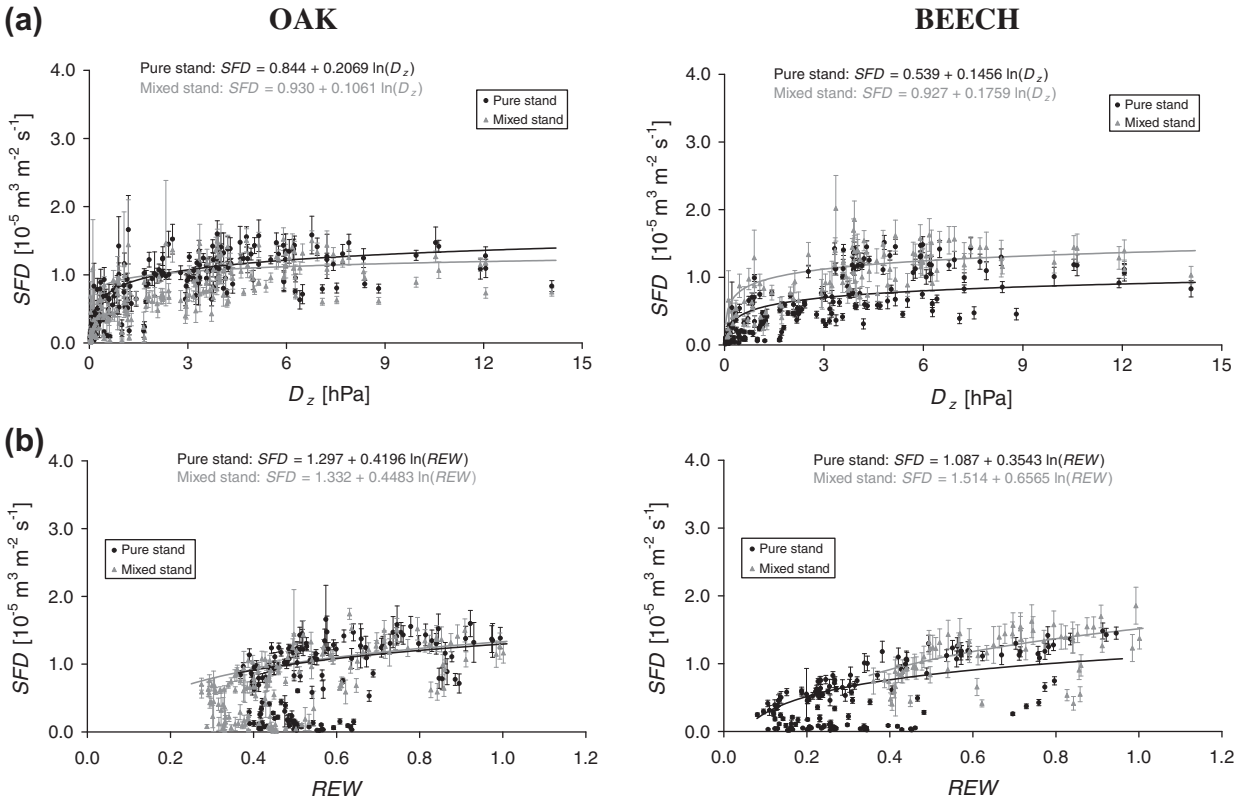


**Fig. 5.** (a) Average sap flux density (*SFD*) as a function of daylength-normalised daytime mean vapour pressure deficit ($D_z$) and (b) relative extractable water (*REW*) for both species in pure and mixed stands. Bar errors represent the standard error between the $n$ ($n$ = 1–8) replications in each species x stand population. The curves represent the model predictions as a function of $D_z$ or *REW*; they were calculated for each species and stand type by using the *SFD* model (Eq. (11)) and by fixing the other environmental variables to their mean value.

**Table 4**
Parameter estimates of the sap flux density model (A) and the mean stomatal conductance model (B). Confidence intervals are presented in parentheses ($\alpha$ = 0.05).

| Effect | Pure stand | | | | Mixed stand | | | |
|---|---|---|---|---|---|---|---|---|
| | Oak | | Beech | | Oak | | Beech | |
| *A. SFD model*[a]: $SFD = a_i + b_i\,(\ln(D_z) - 1.2) + c_i\,(\ln(REW) + 0.5) + \tau + \varepsilon$ | | | | | | | | |
| $a_i$ | 1.1089 | (0.1861) | 0.9423 | (0.1845) | 1.0928 | (0.1822) | 1.1325 | (0.1825) |
| $b_i$ | 0.2069 | (0.0158) | 0.1456 | (0.0113) | 0.1061 | (0.0162) | 0.1759 | (0.0222) |
| $c_i$ | 0.4196 | (0.1220) | 0.3543 | (0.0419) | 0.4483 | (0.0823) | 0.6565 | (0.0995) |
| *B. $G_s$ model*[b]: $G_s = a_i + b_i\,(\ln(D_z) - 1.8) + c_i\,(R_G - 232) + d_i\,(REW - 0.6) + \tau + \varepsilon$ | | | | | | | | |
| $a_i$ | 0.2412 | (0.0889) | 0.5181 | (0.0889) | 0.2795 | (0.0874) | 0.4894 | (0.0878) |
| $b_i$ | −0.2769 | (0.0396) | −0.2682 | (0.0321) | −0.2486 | (0.0322) | −0.3933 | (0.0349) |
| $c_i$ | 0.00044 | (0.00041) | −0.00048 | (0.00030) | 0.00017 | (0.00033) | 0.00018 | (0.00037) |
| $d_i$ | 0.1693 | (0.1088) | 0.7732 | (0.0729) | 0.1658 | (0.0751) | 0.5396 | (0.0792) |

[a] $D_z$ ranging from 0.03 to 14.07 hPa and *REW* ranging from 0.08 to 1.00.
[b] $D_z$ ranging from 3.05 to 14.07 hPa; $R_G$ ranging from 78.20 to 340.86 W m$^{-2}$; and *REW* ranging from 0.10 to 1.00.

**Table 5**
*P*-values of the contrasts used to evaluate the species and mixture effects on the response of sap flux density to vapour pressure deficit and relative extractable water (A) and the response of mean stomatal conductance to vapour pressure deficit, incoming solar radiation, and relative extractable water (B). Significant contrasts are shown in italics ($P < 0.05$).

| Effect | Pure vs. mixed | | Oak vs. beech | |
|---|---|---|---|---|
| | Oak | Beech | Pure | Mixed |
| *A. SFD model:* $SFD = a_i + b_i\,(\ln(D_z) - 1.2) + c_i\,(\ln(REW) + 0.5) + \tau + \varepsilon$ | | | | |
| $a_i$ | 0.9036 | 0.1509 | 0.2127 | 0.7630 |
| $b_i$ | *<0.0001* | *0.0174* | *<0.0001* | *<0.0001* |
| $c_i$ | 0.7022 | *<0.0001* | 0.3210 | *0.0016* |
| *B. $G_s$ model:* $G_s = a_i + b_i\,(\ln(D_z) - 1.8) + c_i\,(R_G - 232) + d_i\,(REW - 0.6) + \tau + \varepsilon$ | | | | |
| $a_i$ | 0.5367 | 0.6427 | *<0.0001* | *0.0016* |
| $b_i$ | 0.2762 | *<0.0001* | 0.7382 | *<0.0001* |
| $c_i$ | 0.2955 | *0.0062* | *0.0004* | 0.9535 |
| $d_i$ | 0.9587 | *<0.0001* | *<0.0001* | *<0.0001* |

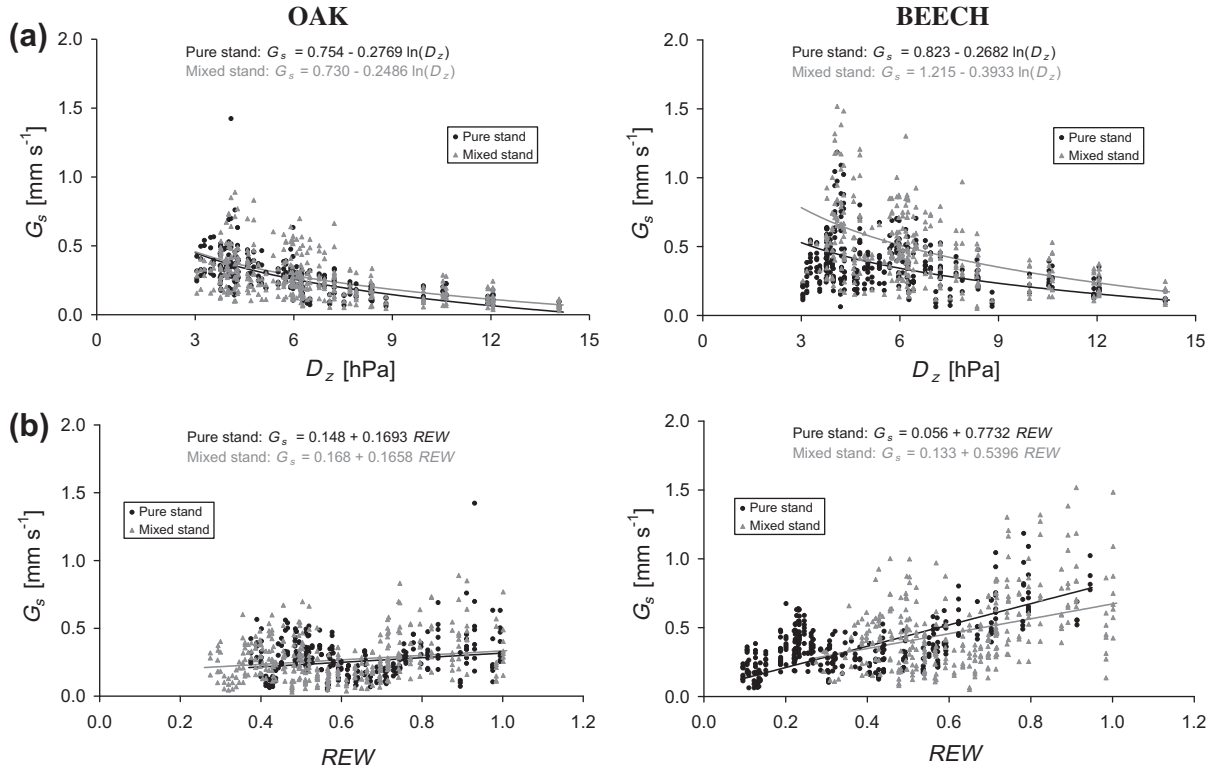


**Fig. 6.** (a) Mean stomatal conductance of individual trees ($G_s$) as a function of daylength-normalised daytime mean vapour pressure deficit ($D_z$) and (b) relative extractable water (*REW*) for both species in pure and mixed stands. The curves represent the model predictions as a function of $D_z$ or *REW*; they were calculated for each species and stand type by using the $G_s$ model (Eq. (12)) and by fixing the other environmental variables to their mean value.

*REW* was significantly different from zero for oak and beech in both stand types.

Compared to oak, the beech $G_s$ at $D_z$ = 6 hPa, $R_G$ = 232 W m$^{-2}$ and *REW* = 0.6 (i.e. the model intercept, $a_i$) was 2.1 times higher in the pure stands and 1.8 times higher in the mixed stand. For both species, it was not affected by stand type (Table 5b). The beech $G_s$ was more sensitive to the natural logarithm of $D_z$ than that of oak in the mixed stand but not in the pure stands. For beech, $G_s$ was more sensitive to the natural logarithm of $D_z$ in the mixed than in the pure stand while the $G_s$ sensitivity to the natural logarithm of $D_z$ was not significantly affected by stand type for oak (Table 5b). The beech $G_s$ was negatively affected by $R_G$ while that of oak was positively affected by $R_G$ in the pure stand (Table 4b); these effects were however at the limit of the significance. The beech $G_s$ was more sensitive to *REW* than that of oak in the pure and mixed stands (Table 5b). For beech, $G_s$ was more sensitive to *REW* in the pure stand than in the mixed stand while the $G_s$ sensitivity to *REW* was not significantly affected by stand type for oak (Table 5b).

## 4. Discussion

### 4.1. Drought conditions

The summer 2003 was particularly dry (312 mm of rain during the studied period) and hot (mean daytime $T^\circ$ > 20 °C several days per month). While the soil was progressively drying during the vegetation period, *REW* decreased more quickly in the beech stand due to the lower maximum extractable water (higher stone content) and dropped below the threshold of 0.4 from early August to the end of the growing season. Below this threshold, trees are known to suffer from water stress (Granier et al., 1999; Bernier et al., 2002). In the oak stand, *REW* dropped below 0.4 only few days at the end of September. In the mixed stand, it was intermediate between the pure stands and reached 0.4 from early September to the end of the growing season. Given the limited soil water supply in the beech stand during the growing season, we can assume that trees in the beech stand have been severely affected by drought during summer. This summer drought of 2003 has also been observed in many other regions of Europe (Rebetez et al., 2006).

### 4.2. Effects of species and mixture

The species and mixture effects on tree transpiration may be ascribed to (i) structural (tree height, leaf area, sapwood area) and/or (ii) functional (hydraulic architecture, stomatal regulation) differences between oak and beech trees or between trees that have grown in pure or mixed stands. In this study, the structural differences among trees, which were marked on individual *LAI* and on sapwood area but not on tree height (Table 3), account for a large part of the variability in tree transpiration. In order to focus more on the species and mixture effects on hydraulic functioning of trees, the structural effects were partly removed by considering either the sap flux density (expressed per unit sapwood area) or the mean stomatal conductance (expressed per unit leaf area).

#### 4.2.1. Sap flux density

The sap flux density (*SFD*) at reference conditions ($D_z$ = 3.3 hPa, *REW* = 0.6) was independent of tree species and stand type. The sensitivity of *SFD* to $D_z$ was higher for oak than for beech in the pure stands but the mixing of species reduced it for oak and increased it for beech, so that the sensitivity of *SFD* to $D_z$ became higher for beech than for oak in the mixed stand. These differences in sensitivity to $D_z$ can be explained by differential crown

exposition to atmospheric conditions. *SFD* sensitivity to $D_z$ seems to decrease with increasing foliage density, which can be explained by the fact that denser canopies buffer more climate variations than sparse ones. In the oak stand, tree crowns were well developed, individualised and exposed to sunlight (shade intolerant species) while the tree crowns were intermixed in the beech stand (shade tolerant species). The foliage density was lower in the oak stand than in the beech stand as indicated by their respective *LAI* (Table 2). In addition, part of the *LAI* in the oak stand can be ascribed to the understory (composed of beech and hornbeam) which limited foliage density in the upper story. The fact that the species effect on the sensitivity to $D_z$ changed direction in the mixed stand can be explained by the competition between oak and beech. In the mixed stand compared to the corresponding pure stands, individual leaf area of oak ($LAI_{ind} \times s$; Table 3) as well as exposition of oak crown to atmospheric conditions was decreased while the opposite was observed for beech. As mentioned in the site description, oak was pre-existing as standards in the mixed stand and beech developed progressively beneath the oak canopy. Even if most of the oak trees in the mixed stand had their crown in the upper story, beech trees were progressively outcompeting them, reducing oak crown development and their foliar biomass (Jonard et al., 2006). These observations are consistent with previous studies of Büttner and Leuschner (1994) and Leuschner et al. (2001a, 2001b) who found that beech is competitively superior in mixture with oak under non-limiting soil water conditions: the competitive superiority of beech is ascribed to its high potential for space occupation at low investment costs in carbon, nitrogen and magnesium.

The sensitivity of *SFD* to *REW* was similar in all species x stand populations, except for beech in mixed stand for which it was significantly higher. This higher sensitivity of beech *SFD* to *REW* in the mixture could be due to the fact that beech developed a larger individual leaf area (greater evaporative surface) given its competitive superiority on oak (Leuschner et al., 2001b).

#### 4.2.2. Transpiration

At the stand level, total transpiration measured during the studied period amounted to 73, 138, and 142 mm in the oak, mixed, and beech stand, respectively. These differences were due to contrasted sapwood area per unit ground area (oak stand: 6.1 $m^2\ ha^{-1}$, mixture: 12.5 $m^2\ ha^{-1}$, beech stand: 15.1 $m^2\ ha^{-1}$) and to differences in soil water conditions (*REW* in the beech stand lower than in the two other stands). In the oak stand, the lower tree transpiration was probably partly compensated by the contribution of the abundant ground vegetation. By contrast, ground vegetation development was very limited in the two other stands due to the high degree of canopy closure. Roberts (1983) observed compensation between understory and overstory in a series of forest stands, leading to a constant total transpiration at stand scale. Comparing two heterogeneous broad-leaved stands in southern England, Herbst et al. (2008) did not find any differences in annual water use despite variations in canopy stomatal conductance and stomatal sensitivity between both stands.

Within the mixed stand, the species effect on transpiration can be analysed by comparing the species contributions to total transpiration with their basal area, *LAI*, and sapwood proportions. While it accounted for 54.1% of the total basal area, oak trees contributed only to 26.3% of the transpiration measured during the studied period. In contrast, beech trees contributed to 45.9% of the basal area and 73.7% of the total transpiration. This apparent discrepancy can be explained based on the contribution of oak and beech to the total sapwood area (25% and 75%, respectively) or to the total *LAI* (31% and 69%, respectively) of the mixed stand. These results are consistent with the findings of Wullschleger et al. (2001) in a multi-species deciduous forest that relative contribution of each species to stand transpiration was driven largely by sapwood area per unit ground area and to a lesser extent by species-specific differences in daily water use. Similarly, Granier et al. (2000b) observed that the effects of species composition on tree transpiration are partly indirect effects of species composition on *LAI*.

#### 4.2.3. Mean stomatal conductance

Based on the mean stomatal conductance of individual trees ($G_s$), we analysed the species and mixture effects on hydraulic functioning of trees with a linear mixed model that described $G_s$ as a function of environmental variables ($D_z$, $R_G$, *REW*). Although the range of soil water conditions differed between stands, the parameter $a_i$ of the $G_s$ model (Eq. (12)) allowed us to compare oak and beech reference $G_s$ in pure and mixed stands for a fixed level of $D_z$, $R_G$, and *REW*. For the mixed stand, the species comparison was however straightforward since trees of both species were subjected to identical climate and soil conditions. The fixed effects of the $G_s$ model explained 48.4% of the variability, which is in the range of proportions reported in the literature for similar models (Granier and Bréda, 1996; Granier et al., 2000a). In addition, the inter-tree variability ('tree' random effect) accounted for 31.0% of the variability that could be ascribed to variations in tree characteristics not taken into account in the model (e.g. tree height, azimutal flux variations); the remaining variability amounted to 20.6%.

The beech reference $G_s$ (at $D_z = 6.0$ hPa, $R_G = 232\ W\ m^{-2}$, and *REW* = 0.6) was 2.1 and 1.8 times higher than that of oak in the pure and mixed stand, respectively. This species effect on reference $G_s$ could possibly be related to inter-specific differences in sapwood-to-leaf area ratio and/or in root-to-leaf area ratio (Addington et al., 2006). As beech sapwood area was not measured in this study, it was estimated based on the *DBH* of the sampled trees by using the allometric equation provided in Schmidt (2007). The mean sapwood-to-leaf area ratio amounted to 1.4 for oak and 2.6 for beech (1.9 times higher for beech). There was no significant effect of stand type on this ratio. The difference in oak and beech reference $G_s$ can therefore be explained in the framework of the simple hydraulic model of Schäfer et al. (2000), the reference $G_s$ of both species being roughly proportional to their sapwood-to-leaf area ratio. It means that the higher reference $G_s$ of beech compared to oak could be due to the larger conductive area (sapwood area) of the beech trunk per unit leaf area. Leuschner et al. (2001b) measured the root-to-leaf ratio in an old-growth mixed forest of oak and beech; this ratio amounted to 1.7 for oak and 3.9 for beech (2.3 times higher for beech). As for the sapwood-to-leaf ratio, if beech had a higher root-to-leaf ratio than oak, it could have promoted its higher reference $G_s$. At our study site, we observed that oak contributed to 34% and 28% of fine root (<2 mm) biomass in the hemiorganic horizon and in the forest floor of the mixed stand, respectively (Jonard et al., 2007). As these proportions were in accordance with the oak contribution to *LAI* (31%), the oak and beech root-to-leaf area ratio could therefore have been similar provided oak and beech had the same specific root area (Ostonen et al., 2007). However, our data concerned just the fine roots in the upper horizons.

As reference $G_s$ was two times higher for beech than for oak, the sensitivity of $G_s$ to $D_z$ of the two tree species can not be compared as such. Based on empirical analysis of stomatal sensitivity and on hydraulic theory, Oren et al. (1999) showed that the absolute sensitivity to $D_z$ of isohydric species increase proportionally with stomatal conductance at reference conditions. We therefore normalised $G_s$ sensitivity to $D_z$ by dividing it by reference $G_s$ in order to analyse oak and beech $G_s$ sensitivity to $D_z$ on comparable basis.

The normalised $G_s$ sensitivity to $D_z$ was higher for oak (1.1) than for beech (0.5) in pure stands and was intermediate for oak and

beech in mixture (0.9 and 0.8, respectively). Overall, this is in accordance with the tree species and mixture effects observed on *SFD* sensitivity to $D_z$ and could be explained by the same reasons. Normalised $G_s$ sensitivity to $D_z$ seems to decrease in canopies that better buffer climate variations due to higher foliage density in the upper story. *LAI* was indeed higher in the beech than in the oak stand (Table 2). Despite a higher *LAI* in the mixture than in the beech stand (Table 2), we believe that the foliage density of the mixture was intermediate between that of the pure stands as its canopy thickness was much larger. According to Oren et al. (1999), the higher normalised $G_s$ sensitivity to $D_z$ of oak could also be ascribed to the fact that it is a ring-porous species.

The normalised $G_s$ sensitivity to $D_z$ of oak trees in the mixed stand was intermediate between that of the pure stands while their *SFD* sensitivity to $D_z$ was the lowest of all tree populations. This low *SFD* sensitivity to $D_z$ was probably due to the small individual leaf area of oak trees in the mixed stand. This effect disappeared when considering $G_s$ sensitivity to $D_z$ as $G_s$ is expressed per unit leaf area.

Similarly, the $G_s$ sensitivity to *REW* can not be analysed independently of the reference conductance. We therefore divided it by reference $G_s$. The normalised $G_s$ sensitivity to *REW* amounted to 0.7 and 0.6 for oak trees in pure and mixed stand and to 1.5 and 1.1 for beech trees in pure and mixed stand, respectively. The normalised sensitivity of beech $G_s$ to *REW* was about two times larger than that of oak. Zapater et al. (2011) observed a much larger decrease in sap flow with increasing soil drought for beech than for oak and explained it by the shallower root system of beech. In this study, vertical root distribution was found to be globally similar for both species, with however a higher root proportion below 1 m in the oak stand. In the beech stand, the root depth could have been limited due to the higher stone content compared to the oak and mixed stands (Table 1). The higher normalised sensitivity of beech $G_s$ to *REW* could also be ascribed to the higher vulnerability of beech to air embolism (Cochard et al., 1992, 1999). As both tree species control hydraulic failure by stomatal closure (Cruiziat et al., 2002), it is logical that the stomatal regulation of beech is more sensitive to soil conditions than that of oak. The greater tolerance to drought of oak compared to beech has been reported by several authors (Backes and Leuschner, 2000; Leuschner et al., 2001a; Raftoyannis and Radoglou, 2002; Aranda et al., 2005; Leuzinger et al., 2005; Keel et al., 2007).

After the summer drought of 2003, beech crown condition deteriorated significantly during two years in the Belgian Ardennes while oak crown condition was much less affected (Jonard et al., 2010). This decline in beech tree vitality may be related to the fact that beech is a species whose stomatal regulation is quite sensitive to soil drying which therefore limits its carbon assimilation under drought conditions.

The lower normalised sensitivity of beech $G_s$ to *REW* in the mixed stand compared to the pure beech stand is surprising since the mixing effect is opposite when *SFD* is considered. The higher sensitivity of beech *SFD* to *REW* in the mixed stand was most probably due to the higher $LAI_{ind}$ of beech in the mixture. Since $G_s$ is expressed per unit leaf area, the effect of $LAI_{ind}$ on the sensitivity to *REW* is removed when $G_s$ is considered and this sensitivity to *REW* becomes lower in the mixture, probably because of a better sharing of the water resources and/or because of facilitation processes for water acquisition (hydraulic lift). In mixed stands, spatial partitioning may happen vertically due to differences in root distribution with depth and horizontally in relation with stand density and composition (Meinzer et al. 2001). We noticed that the root system of oak was somewhat deeper than that of beech. Competition for water is therefore probably reduced for beech when mixed with oak since the latter could take up water in deeper horizons (Zapater et al. 2011). In addition, a higher proportion of water is redirected towards the beech trunks and produces larger stemflow volumes under beech when rainfall is passing through the mixed canopy (André et al. 2008b, 2011). Zapater et al. (2011) demonstrated the occurrence of water lift under oak but they did not observe that the superficial enrichment in water around oak trees was beneficial for beech trees.

## 5. Conclusion

This study confirms that the high spatial variability in tree transpiration observed in a temperate mixed forest is mainly due to inter-specific differences in sapwood area and leaf area index. The variability of the sap flux density (*SFD*) between species and stand type is much lower. For reference conditions, we did not find any tree species or stand type effects on *SFD*. The sensitivity of *SFD* to daylength-normalised daytime mean vapour pressure deficit ($D_z$) was influenced by tree species and stand type and seems to be dependent on crown exposure to atmospheric conditions which varies according to the competition level encountered by the different species x stand populations.

A species effect was observed on mean stomatal conductance of individual trees ($G_s$) and was explained based on the sapwood-to-leaf area ratio. The higher reference $G_s$ of beech compared to oak was probably due to the larger conductive area (sapwood area) of the beech trunk per unit leaf area. The normalised sensitivity of $G_s$ to soil water conditions was higher for beech than for oak and was ascribed to a higher vulnerability of beech to air embolism and to a more sensitive stomatal regulation. The lower sensitivity of beech $G_s$ to soil relative extractable water (*REW*) in the mixed stand compared with the pure stand could be explained by a better sharing of the resources in the mixture, by facilitation processes (hydraulic lift), and by a rainfall partitioning in favour of beech; however, further researches are needed to confirm this.

Our study confirms the interest of analysing factors influencing sap flux density and stomatal conductance in heterogeneous stands. Such information help foresters to define which species composition and stand structure will be best adapted to the predicted climate changes.

Mixing tree species with different tolerance to drought presents the advantage to maintain carbon assimilation during drought conditions thanks to the drought-tolerant species (such as common oak) while benefiting from the good growth conditions with the drought-sensitive species which are generally more productive (such as beech).

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## References

Addington, R.N., Donovan, L.A., Mitchell, R.J., Vose, J.M., Pecot, S.D., Jack, S.B., Hacke, U.G., Sperry, J.S., Oren, R., 2006. Adjustments in hydraulic architecture of *Pinus palustris* maintain similar stomatal conductance in xeric and mesic habitats. Plant, Cell Environ. 29 (4), 535–545.

Allen, R.G., Smith, M., Pereira, L.S., Perrier, A., 1994. An update for the calculation of reference evapotranspiration. ICID Bull. 43 (2), 35–87.

André, F., Jonard, M., Ponette, Q., 2008a. Precipitation water storage capacity in a temperate mixed oak–beech canopy. Hydrol. Process. 22, 4130–4141.

André, F., Jonard, M., Ponette, Q., 2008b. Influence of species and rain event characteristics on stemflow volume in a temperate mixed oak–beech stand. Hydrol. Process. 22, 4455–4466.
André, F., Jonard, M., Jonard, F., Ponette, Q., 2011. Spatial and temporal patterns of throughfall volume in a deciduous mixed-species stand. J. Hydrol. 400, 244–254.
Aranda, I., Gil, L., Pardos, J.A., 2005. Seasonal changes in apparent hydraulic conductance and their implications for water use of European beech (*Fagus sylvatica* L.) and sessile oak [*Quercus petraea* (Matt.) Liebl] in South Europe. Plant Ecol. 179 (2), 155–167.
Backes, K., Leuschner, C., 2000. Leaf water relations of competitive *Fagus sylvatica* and *Quercus petraea* trees during 4 years differing in soil drought. Can. J. For. Res. 30 (3), 335–346.
Baldocchi, D.D., Luxmoore, R.J., Hatfield, J.L., 1991. Discerning the forest from trees: an essay on scaling canopy stomatal conductance. Agric. For. Meteorol. 54 (2–4), 197–226.
Barber, S.A., 1995. Soil Nutrient Bioavailability: A Mechanistic Approach. John Wiley & Sons, New York, 398 pp.
Bernier, P.Y., Bréda, N., Granier, A., Raulier, F., Mathieu, F., 2002. Validation of a canopy gas exchange model and derivation of a soil water modifier for transpiration for sugar maple (*Acer saccharum* Marsh.) using sap flow density measurements. For. Ecol. Manag. 163 (1–3), 185–196.
Black, T.A., 1979. Evapotranspiration from Douglas-fir stands exposed to soil-water deficits. Water Resour. Res. 15 (1), 164–170.
Bréda, N., Granier, A., Barataud, F., Moyne, C., 1995. Soil-water dynamics in an oak stand. 1. Soil-moisture, water potentials and water-uptake by roots. Plant Soil 172 (1), 17–27.
Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann. For. Sci. 63 (6), 625–644.
Brown, H., Prescott, R., 1999. Applied Mixed Models in Medicine. John Wiley & Sons, New York, 408 pp..
Büttner, V., Leuschner, C., 1994. Spatial and temporal patterns of fine-root abundance in a mixed oak beech forest. For. Ecol. Manag. 70 (1–3), 11–21.
Cochard, H., Breda, N., Granier, A., Aussenac, G., 1992. Vulnerability to air-embolism of 3 European oak species (Quercus-Petraea (Matt) Liebl, Quercus-Pubescens Willd, Quercus-Robur L). Ann. Sci. For. 49 (3), 225–233.
Cochard, H., Lemoine, D., Dreyer, E., 1999. The effects of acclimation to sunlight on the xylem vulnerability to embolism in *Fagus sylvatica* L. Plant, Cell Environ. 22 (1), 101–108.
Cruiziat, P., Cochard, H., Ameglio, T., 2002. Hydraulic architecture of trees: main concepts and results. Ann. For. Sci. 59 (7), 723–752.
Dufrêne, E., Bréda, N., 1995. Estimation of deciduous forest leaf-area index using direct and indirect methods. Oecologia 104 (2), 156–162.
Ewers, B.E., Oren, R., 2000. Analyses of assumptions and errors in the calculation of stomatal conductance from sap flux measurements. Tree Physiol. 20 (9), 579–589.
Gartner, K., Nadezhdina, N., Englisch, M., Čermák, J., Leitgeb, E., 2009. Sap flow of birch and Norway spruce during the European heat and drought in summer 2003. For. Ecol. Manag. 258 (5), 590–599.
Granier, A., 1985. A new method of sap flow measurement in tree stems. Ann. Sci. For. 42 (2), 193–200.
Granier, A., Loustau, D., 1994. Measuring and modelling the transpiration of a maritime pine canopy from sap-flow data. Agric. For. Meteorol. 71 (1–2), 61–81.
Granier, A., Bréda, N., 1996. Modelling canopy conductance and stand transpiration of an oak forest from sap flow measurements. Ann. Sci. For. 53, 537–546.
Granier, A., Bréda, N., Biron, P., Villette, S., 1999. A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. Ecol. Modell. 116 (2–3), 269–283.
Granier, A., Loustau, D., Bréda, N., 2000a. A generic model of forest canopy conductance dependent on climate, soil water availability and leaf area index. Ann. For. Sci. 57 (8), 755–765.
Granier, A., Biron, P., Lemoine, D., 2000b. Water balance, transpiration and canopy conductance in two beech stands. Agric. For. Meteorol. 100 (4), 291–308.
Granier, A., Aubinet, M., Epron, D., Falge, E., Gudmundsson, J., Jensen, N.O., Kostner, B., Matteucci, G., Pilegaard, K., Schmidt, M., Tenhunen, J., 2003. Deciduous forests: carbon and water fluxes, balances and ecophysiological determinants. Fluxes of Carbon, Water and Energy of European Forests. Ecological Studies: Analysis and Synthesis. Springer-Verlag, Berlin, pp. 55–70.
Hendershot, W.H., Duquette, M., 1986. A simple barium-chloride method for determining cation-exchange capacity and exchangeable cations. Soil Sci. Soc. Am. J. 50 (3), 605–608.
Herbst, M., Rosier, P.T.W., Morecroft, M.D., Gowing, D.J., 2008. Comparative measurements of transpiration and canopy conductance in two mixed deciduous woodlands differing in structure and species composition. Tree Physiol. 28 (6), 959–970.
Hölscher, D., Koch, O., Korn, S., Leuschner, C., 2005. Sap flux of five co-occurring tree species in a temperate broad-leaved forest during seasonal soil drought. Trees-Struct. Funct. 19 (6), 628–637.
Jacobsen, O.H., Schjønning, P., 1993. A laboratory calibration of time-domain reflectometry for soil-water measurement including effects of bulk-density and texture. J. Hydrol. 151 (2–4), 147–157.
Jarvis, P.G., McNaughton, K.G., 1986. Stomatal control of transpiration – scaling up from leaf to region. Adv. Ecol. Res. 15, 1–49.
Jarvis, A.J., Davies, W.J., 1998. The coupled response of stomatal conductance to photosynthesis and transpiration. J. Exp. Bot. 49, 399–406.
Jetten, V.G., 1996. Interception of tropical rain forest: performance of a canopy water balance model. Hydrol. Process. 10 (5), 671–685.
Jonard, M., André, F., Ponette, Q., 2006. Modeling leaf dispersal in mixed hardwood forests using a ballistic approach. Ecology 87 (9), 2306–2318.
Jonard, M., André, F., Jonard, F., Mouton, N., Procès, P., Ponette, Q., 2007. Soil carbon dioxide efflux in pure and mixed stands of oak and beech. Ann. For. Sci. 64, 141–150.
Jonard, M., André, F., Giot, P., Weissen, F., Van der Perre, R., Ponette, Q., 2010. Thirteen-year monitoring of liming and PK fertilization effects on tree vitality in Norway spruce and European beech stands. Eur. J. For. Res. 129, 1203–1211.
Keel, S.G., Pepin, S., Leuzinger, S., Koerner, C., 2007. Stomatal conductance in mature deciduous forest trees exposed to elevated $CO_2$. Trees 21 (2), 151–159.
Köstner, B., Granier, A., Čermák, J., 1998. Sap flow measurements in forest stands: methods and uncertainties. Ann. For. Sci. 55 (1–2), 13–27.
Leuschner, C., Backes, K., Hertel, D., Schipka, F., Schmitt, U., Terborg, O., Runge, M., 2001a. Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. Trees in dry and wet years. For. Ecol. Manage. 149 (1–3), 33–46.
Leuschner, C., Hertel, D., Coners, H., Büttner, V., 2001b. Root competition between beech and oak: a hypothesis. Oecologia 126 (2), 276–284.
Leuzinger, S., Zotz, G., Asshoff, R., Korner, C., 2005. Responses of deciduous forest trees to severe drought in Central Europe. Tree Physiology 25 (6), 641–650.
McNaughton, K.G., Jarvis, P.G., 1991. Effects of spatial scale on stomatal control of transpiration. Agric. For. Meteorol. 54 (2–4), 279–302.
Meinzer, F.C., Clearwater, M.J., Goldstein, G., 2001. Water transport in trees: current perspectives, new insights and some controversies. Environ. Exp. Bot. 45 (3), 239–262.
Oren, R., Pataki, D.E., 2001. Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. Oecologia 127 (4), 549–559.
Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N., Schafer, K.V.R., 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. Plant, Cell Environ. 22 (12), 1515–1526.
Ostonen, I., Puttsepp, U., Biel, C., Alberton, O., Bakker, M.R., Lohmus, K., Majdi, H., Metcalfe, D., Olsthoorn, A.F.M., Pronk, A., Vanguelova, E., Weih, M., Brunner, I., 2007. Specific root length as an indicator of environmental change. Plant Biosyst. 141 (3), 426–442.
Pataki, D.E., Oren, R., Smith, W.K., 2000. Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought. Ecology 81 (9), 2557–2566.
Raftoyannis, Y., Radoglou, K., 2002. Physiological responses of beech and sessile oak in a natural mixed stand during a dry summer. Ann. Bot. 89 (6), 723–730.
Rebetez, M., Mayer, H., Dupont, O., Schindler, D., Gartner, K., Kropp, J.P., Menzel, A., 2006. Heat and drought 2003 in Europe: a climate synthesis. Ann. For. Sci. 63 (6), 569–577.
Roberts, J., 1983. Forest transpiration: a conservative hydrological process? J. Hydrol. 66 (1–4), 133–141.
Schäfer, K.V.R., Oren, R., Tenhunen, J.D., 2000. The effect of tree height on crown level stomatal conductance. Plant, Cell Environ. 23 (4), 365–375.
Schmidt, M.W.T., 2007. Canopy transpiration of beech forests in Northern Bavaria – Structure and function in pure and mixed stands with oak at colline and montane sites. Ph.D. Thesis, Bayreuth, 252 pp.
Smith, D.M., Allen, S.J., 1996. Measurement of sap flow in plant stems. J. Exp. Bot. 47 (305), 1833–1844.
Stewart, J.B., 1988. Modeling surface conductance of pine forest. Agric. For. Meteorol. 43 (1), 19–35.
Wullschleger, S.D., Meinzer, F.C., Vertessy, R.A., 1998. A review of whole-plant water use studies in trees. Tree Physiol. 18, 499–512.
Wullschleger, S.D., Hanson, P.J., Todd, D.E., 2001. Transpiration from a multi-species deciduous forest as estimated by xylem sap flow techniques. For. Ecol. Manag. 143, 205–213.
Zapater, M., Hossann, C., Bréda, N., Bréchet, C., Bonal, D., Granier, A., 2011. Evidence of hydraulic lift in a young beech and oak mixed forest using $^{18}O$ soil water labelling. Trees – Struct. Funct. 68, 433–442.