Water use of a multigenotype poplar short-rotation coppice from tree to stand scale

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Abstract

Short-rotation coppice (SRC) has great potential for supplying biomass-based heat and energy, but little is known about SRC’s ecological footprint, particularly its impact on the water cycle. To this end, we quantified the water use of a commercial scale poplar (Populus) SRC plantation in East Flanders (Belgium) at tree and stand level, focusing primarily on the transpiration component. First, we used the AquaCrop model and eddy covariance flux data to analyse the different components of the stand-level water balance for one entire growing season. Transpiration represented 59% of evapotranspiration (ET) at stand scale over the whole year. Measured ET and modelled ET were lower as compared to the ET of reference grassland, suggesting that the SRC only used a limited amount of water. Secondly, we compared leaf area scaled and sapwood area scaled sap flow (F_s) measurements on individual plants vs. stand scale eddy covariance flux data during a 39-day intensive field campaign in late summer 2011. Daily stem diameter variation (∆D) was monitored simultaneously with F_s to understand water use strategies for three poplar genotypes. Canopy transpiration based on sapwood area or leaf area scaling was 43.5 and 50.3 mm, respectively, and accounted for 74%, respectively, 86%, of total ecosystem ET measured during the intensive field campaign. Besides differences in growth, the significant intergenotypic differences in daily ∆D (due to stem shrinkage and swelling) suggested different water use strategies among the three genotypes which were confirmed by the sap flow measurements. Future studies on the prediction of SRC water use, or efforts to enhance the biomass yield of SRC genotypes, should consider intergenotypic differences in transpiration water losses at tree level as well as the SRC water balance at stand level.

Keywords: bioenergy, evapotranspiration, poplar, sap flow, short-rotation coppice, stand water balance

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Introduction

Short-rotation coppice (SRC) of fast-growing and high-yielding hardwood species as poplar and willow offers an important and environmentally sustainable way of producing heat and electricity from a renewable energy source (Herrick & Brown, 1967; Graham et al., 1992; Gustavsson et al., 1995; Berndes et al., 2003; Kauter et al., 2003; Aylott et al., 2008). Poplar SRC showed high biomass production rates of 10–15 t ha⁻¹ yr⁻¹ (Heilman et al., 1996; Trnka et al., 2008; Broeckx et al., 2012). However, there have been conflicting observations about the water use of SRC or its impact on the local water cycle. High-yielding SRC has high water requirements (Hall & Allen, 1997; Hall et al., 1998; Allen et al., 1999; Meiresonne et al., 1999; Jassal et al., 2013; Navarro et al., 2014) potentially leading to negative effects on regional water resources (see references in Fischer et al., 2013). A number of – experimental and modelling – studies on evapotranspiration (ET, mm day⁻¹) have argued that the water use of SRC is substantially higher than that of conventional agricultural crops or grasslands (see references in Dimitriou et al., 2009; Petzold et al., 2011). In contrast, other studies have reported that the water use rates of SRC are similar to those from agricultural crops and grasslands (Fischer et al., 2013), that is comparable to or lower than the reference crop evapotranspiration (ET₀) (e.g. Meiresonne et al., 1999; Linderson et al., 2007; Migliavacca et al., 2009; Tricker et al., 2009). It is expected that the transpiration component of ET (E_T, mm day⁻¹) is large as poplar species have high transpiration rates (Hall & Allen, 1997; Hall et al., 1998; Meiresonne et al., 1999; Kim et al., 2008). Simulated transpiration was 71% of ET for a poplar SRC in the Czech Republic (Fischer et al., 2013) and 66% of ET on a seasonal basis for a willow SRC in southern Sweden (Persson & Lindroth, 1994). Measurements of sap flow...
(\(F_o\), kg h\(^{-1}\)) of individual trees scaled to the stand level are frequently used to quantify \(E_c\) for mature forest ecosystems (e.g., Oren et al., 1998; Schafer et al., 2002; Unsworth et al., 2004; Bovard et al., 2005; Tang et al., 2006; Oishi et al., 2008). Little is known, however, about the contribution of \(E_c\) to ET for SRC as only a limited number of studies combined plant-level measurements with stand-level water balance measurements or estimates of the water use of SRC. In addition, measurements of daily fluctuations in stem diameter (\(\Delta D\)) can provide complementary information on genotype-specific tree water use as short-term shrinkage and swelling are related to internal water storage dynamics (Zweifel et al., 2000, 2001; Larcher, 2003) and therefore changes in transpiration. As the first reports that stem dimensions change with changes in plant hydration (Fritts, 1961; Kozlowski & Winget, 1964; Impens & Schalck, 1965), short-term high temporal resolution dendrometer measurements have been made on different forest species (see references in Zweifel et al., 2000; De Swaef et al., 2015), including on poplar genotypes grown under controlled conditions (Giovannelli et al. 2007). Field measurements of daily \(\Delta D\) fluctuations, in combination with \(F_o\), might help to understand the dynamics in the contribution of \(E_c\) to ET for SRC and to identify unexplored intergenotypic differences in plant water use.

In this study, we monitored the water use of a poplar SRC in Flanders, Belgium, both at stand and at tree level. Our specific research hypotheses were as follows: (i) poplar SRC uses more water than a reference grassland under our specific conditions, (ii) \(E_c\) is the largest component of the stand water balance, and (iii) there are important intergenotypic differences in plant water use. For the entire growing season of 2011, we analysed the stand-level water balance of the poplar SRC using the AquaCrop model (Hsiao et al., 2009; Raes et al., 2009; Steduto et al., 2009) complemented with eddy covariance measurements of ET. We further focused on tree-level measurements of plant water use during an intensive field campaign performed during the same growing season. Using detailed tree-level measurements of \(F_o\) and \(\Delta D\), we quantified the contribution of \(E_c\) to ET across three genotypes and we identified intergenotypic differences in plant water use.

**Materials and methods**

**Study site and plant material**

Measurements were made in a commercial scale multigenotype SRC plantation, established in Lochristi, province East Flanders, Belgium (51°06′44″N, 3°57′02″E), at an elevation of 6.25 m above sea level. Long-term average annual temperature at the site is 9.5 °C and the average annual precipitation is 726 mm, evenly distributed over the year. The soil has a loamy sand texture (clay content of 11% between 30 and 60 cm depth) with deeper clay-enriched sand layers (~75 cm) and is classified as Anthrosol according to the World Reference Base for Soil Resources (Dondeyne et al., 2015). On 7–10 April 2010, large replicated mono-genotypic blocks were established over a total of 14.5 ha. Cuttings of 12 selected and commercially available poplar (Populus) genotypes (see Table 2 in Broeckx et al., 2012) were planted at a density of 8000 plants ha\(^{-1}\) (Fig. 1). Hardwood cuttings were planted in a double-row design with alternating distances of 0.75 and 1.50 m between the rows and 1.1 m between the individuals within each row. The site was neither fertilized, nor irrigated. More information on the site, on the management and on soil characteristics is provided by Broeckx et al. (2012) and Verlinden et al. (2015).

An extendable eddy covariance and meteorological mast was positioned in the north-eastern part of the plantation (Fig. 1) at the beginning of June 2010. Continuous ecosystem flux and microclimate measurements were then initiated (Zona et al., 2013a). The prevailing wind direction was from the south-west (Fig. 1). Tree-level sap flow (\(F_s\)) and stem diameter variation (\(\Delta D\)) measurements were therefore performed within the flux footprint on the upwind side of the mast. These measurements were confined to a subset of the three genotypes closest to the mast (~15 m) characterized by a different parentage, namely Skado (parentage *Populus trichocarpa* T & G. × *P. maximowiczi* A. Henry), Oudenberg (parentage *P. deltoides* Bartr. ex Marsh. × *P. nigra* L.) and Grimminge (parentage *P. deltoides* Bartr. ex Marsh. × *P. trichocarpa* T & G. × *P. deltoides* Bartr. ex Marsh.) (Fig. 1). More details on the origin, the selection and the gender of these species are given by Broeckx et al. (2012). Stand-level measurements were performed for the entire growing season of 2011, that is during the second growth year of the plantation and before the first coppice of the plantation (performed on 2–3 February 2012). Tree-level measurements were made during an intensive field campaign from 19 August 2011 (day of the year, DOY 231) until 27 September 2011 (DOY 270). All tree-level measurements were made on single stem trees as trees had not yet been coppiced.

**Stand-level measurements and modelling**

**Climate variables.** Climate variables were continuously recorded at the site: air temperature (\(T_{air}\)) and relative humidity were recorded on the extendable mast at 5.4 m above the ground surface using Vaisala probes (model HMP 45C; Vaisala, Helsinki, Finland); these data were used to calculate vapour pressure deficit (VPD). Incoming photosynthetically active radiation (PAR, 400–700 nm) was recorded at the same height using a quantum sensor (model LI-190; Li-COR, Lincoln, NE, USA). Precipitation was recorded using a tipping bucket rain gauge (model 3665 R; Spectrum Technologies Inc., Plainfield, IL, USA). Soil water content (SWC) was measured diagonally in the 0–10 cm soil layers and horizontally at a specific depth of 40 cm next to the extendable eddy covariance mast using moisture probes (model TDR CS616; Campbell Scientific, Logan, UT, USA). Water table depth was recorded with a
pressure transducer (model PDCR 1830; Campbell Scientific) installed in a pipe inserted into the ground to a depth of 1.85 m. Two data loggers (model CR5000 and CR1000; Campbell Scientific) recorded 30-min averages for each environmental variable. If an instrument occasionally failed, the missing environmental variable ($T_{air}$, relative humidity, or precipitation) was gap-filled using data from nearby standard meteorological stations at 10 and 14 km from the research site. More information on the logging and the gap-filling procedures for the environmental measurements has been published previously (Zona et al., 2013a,b).

Ecosystem evapotranspiration. Ecosystem level fluxes (of carbon, water and energy) were continuously monitored from the eddy covariance mast; in this study, only the water vapour fluxes are considered. High-frequency (10 Hz) measurements of the three-dimensional wind speed components were made using a sonic anemometer (model CSAT3; Campbell Scientific Inc.). Vertical wind velocity was combined with measurements from a closed-path, fast-response gas analyzer (model LI-7000; Li-COR) to measure the latent heat and to calculate evapotranspiration. Additionally, sensible heat fluxes were derived from vertical wind speed and sonic temperature measurements. The sonic anemometer and the inlets of the gas sample lines were positioned at 5.8 m above the ground for the period before 31 August 2011 (DOY 243) and afterwards raised to 6.6 m. Fluxes of latent heat (LE) were gap-filled using the marginal distribution sampling (MDS) method (implemented in www.bgc-jena.mpg.de/~MDIwork/eddyproc/). This method is adopted by the FLUXNET community as a standardized gap-filling technique. A detailed description of the ecosystem flux measurements at our site has been given by Zona et al. (2013a).

Additionally, we calculated reference crop evapotranspiration (ET$_c$) for the site based on the Penman–Monteith method, as described by Allen et al. (1998). ET$_c$ was integrated either daily or annually and compared with measured and modelled ET to assess the SRC water use relative to a reference crop.

Modelling of the stand water balance. We used the AquaCrop model to determine soil evaporation (E$_{soil}$) as well as the $E_c$ and ET components of the stand water balance over the growing season. AquaCrop is a crop water productivity and yield response model developed by the FAO that simulates daily biomass production and final crop yield (Table 1, Vanuytrecht et al., 2014). Briefly, $E_c$ is calculated by multiplying ET$_{om}$ determined using the Penman–Monteith method, with a crop coefficient ($K_{C_T}$) and a water stress coefficient ($K_s$). $K_{C_T}$ is proportional to the fraction of the soil covered by the canopy (canopy cover, CC) and to $K_{Tr,x}$, the maximum crop transpiration coefficient for the specific crop relative to the grass reference surface. The $E_{soil}$ also depends on ET$_{om}$ and is further proportional to the fraction of the soil not covered by the canopy (1-CC), to $K_{om}$ which is the maximum soil evaporation coefficient for a fully wet and unshaded soil surface, and to $K_r$ which is the evaporation reduction coefficient that reduces transpiration when soil water content is low. In this study, we used the default value of 1 for both $K_s$ and $K_r$ as no water stress

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conditions were observed for the SRC plantation. All parameters relevant to the AquaCrop model, including the ones not mentioned above, are listed and explained in Table 1. Interception evaporation is not considered in the AquaCrop model. The ET is calculated as the sum of $E_{soil}$ and $E_c$ (Vanuytrecht et al., 2014). We performed a sensitivity analysis of the AquaCrop model for our site conditions. The results of this analysis were used to evaluate the effect of relative changes of a number of distributed parameters on the model outputs. Details on the simulated processes have been extensively documented in a set of publications at the model’s release (Hsiao et al., 2009; Raes et al., 2009; Steduto et al., 2009) as well as in the FAO irrigation and drainage paper # 66 (Steduto et al., 2012) and in the reference manual (Raes et al., 2012).

**Tree-level measurements**

*Sap flow measurements*. The sap flow rate ($F_s$, kg h$^{-1}$) of individual trees was measured using the heat balance principle established in previous studies of SRC trees (e.g. Hinckley...
Fₙ was monitored continuously during the entire field campaign, using three Dynamax sensors (model SG-EX 25; Dynamax Inc., Houston, TX, USA), one on a tree of each genotype. The sensors were mounted at a height of 50 cm above the base of the stem. The sensors were thermally insulated from the environment with an insulation sleeve and several layers of aluminium foil wrapped around the sensor. Fₙ was calculated according to the standard procedure for heat balance sensors, described in detail by Sakuratani (1981) and Baker & Van Bavel (1987). In this study, we additionally tested for the heat storage effect (Steppe et al., 2005), but we did not observe early morning spikes in the Fₙ data. As the poplars were fast growing, we accounted for the increase in stem surface area during the Fₙ measurements using the increase in stem diameter recorded by high-resolution dendrometers (see further below).

To validate the Fₙ measurements performed at 50 cm height and to account for variation in Fₙ among individuals, we also installed Fₙ sensors (models SG-EX 16 and model SG-EX 19; Dynamax Inc.) on four additional trees per genotype for the last twelve days of the intensive field campaign (15 September 2011–27 September 2011, DOY 258–270). Due to the limited number of sensors, these measurements were only performed on the Oudenberg and Grimminge genotypes and on a smaller number of sensors, these measurements were only performed with >5 μmol m⁻² s⁻¹) to determine different patterns in AD of trees of the different genotypes. We limited the combined analysis of Fₙ, ET and AD to the first week of the measurement campaign (DOY 231–236) to clarify the links between the different variables. This period was characterized by a strong variation in VPD, as large dynamics in T_air were observed, leading to strong dynamics in Fₙ, ET and AD.

### Stem diameter measurements

Stem diameter fluctuation (ΔD) was continuously measured using automatic point dendrometers (model ZN11-O-WP; Natkon, Hombrechtikon, Switzerland) installed with a ring-shaped carbon frame at a height of 22 cm. Sensors were installed on trees per genotype (12 sensors in total); one of these trees was also equipped with an Fₙ sensor as described above. Trees were selected to be representative of the whole range of stem diameters measured during an extensive inventory (n = 1742) performed in February 2011. Data from the dendrometers were collected at 30-s intervals with a data logger (model CR800; Campbell Scientific) and 30-min averages recorded. ΔD was expressed relative to the start of the measurement campaign, by setting the initial stem diameter to zero.

Changes in the stem water status were characterized by calculating the maximum daily shrinkage (MDS) as the difference between the maximum and minimum values of stem diameter during the day (Giovanelli et al., 2007). We also determined the day- and night-time increases in stem diameter over time (ΔD/Δt, with daytime defined as periods when PAR

\[ F_{c} = a(1 - e^{-l_{V P D}}) \times 24 \frac{h}{d} \]  

with \( a \) (kg day⁻¹) and \( b \) (kPa⁻¹) corresponding to the fitted coefficients, and 24 h day⁻¹ corresponding to a time conversion factor. The relationship between Fₙ and PAR was analysed using a linear regression. For both analyses, Fₙ was summed per day and expressed relative to the daytime-averaged VPD (with daytime defined as periods when PAR >5 μmol m⁻² s⁻¹) or the PAR summed per day.

### Scaling of sap flow from tree to stand level

Two approaches were applied to scale Fₙ to canopy Eₚ which was then compared to ET. In a first approach, Fₙ was scaled to Eₚ by multiplying it by the ratio of the genotype-specific leaf area index (LAI, m² m⁻²) of the whole canopy to the total leaf area (LA, m²) of the individual tree equipped with a sap flow sensor:

\[ E_{c,\text{leaf}} = F_{c} \frac{LAI}{LA} \frac{h}{24} \frac{d}{a} \]  

with \( E_{c,\text{leaf}} \) (mm day⁻¹) corresponding to the leaf area scaled Eₚ and 24 h day⁻¹ corresponding to a time conversion factor. LA was determined from genotype-specific regressions relating leaf area with leaf length \( \times \) leaf width (\( R^2 \geq 0.99 \) for all genotypes) for a minimum sample of 25 leaves spanning the whole leaf size range from trees neighbouring those equipped with sap flow sensors. Harvested leaves were scanned and analysed using ImageJ software (NIH, Bethesda, MD, USA). Leaf length and width of all leaves on the trees equipped with sap flow sensors were measured before (i.e. 10 August 2011, DOY 222) and after the intensive field campaign (i.e. 28 September 2011, DOY 271) to account for changes in LA (Table 2). LAI was monitored for different locations in the study site for three occasions during the period July–September 2011 on 22 July (DOY 203), on 2 September (DOY 245) and on 23 September (DOY 266) using cross-calibrated plant canopy analyzers (models LAI-2000 and LAI-2200; Li-COR). We selected data from the measurements performed closest to the Fₙ sensors, which we assumed to best represent the LAI in the footprint of the eddy covariance measurements (Table 2). More information on the LAI measurements has been published previously (Broeckx et al., 2012).

In a second approach Fₙ was scaled to Eₚ by multiplying it by the ratio of the average sapwood area for all trees equipped with dendrometers (\( A_{\text{avg},\text{sapwood}} \), m²) to the sapwood area of the sample tree (\( A_{s} \), m²) and per unit of average ground surface area per tree (SA, m²):

\[ E_{c,\text{sapwood}} = F_{c} \frac{A_{\text{avg},\text{sapwood}}}{A_{s} \cdot SA} \frac{h}{24} \frac{d}{a} \]  

where \( E_{c,\text{sapwood}} \) (mm day⁻¹) corresponding to the sapwood area scaled Eₚ and 24 h day⁻¹ corresponding to a time conversion factor. Both \( A_{s} \) and \( A_{\text{avg},\text{sapwood}} \) were estimated using the dendrometer data, assuming that for these young trees the entire stem consisted of functional sapwood except for a small fraction of bark tissue. SA was estimated for each genotype based on the...
Table 2 Parameters used for scaling sap flow rate to canopy transpiration during the field campaign from 19 August (DOY 231)–27 September (DOY 270) 2011, according to a leaf-based approach (leaf area (LA) or genotype-specific leaf area index (LAI)) and a stem-based approach (ground surface area per tree (SA)) for three poplar genotypes.

| Genotype | DOY 222 | LAI (m² m⁻²) | DOY 203 | DOY 245 | DOY 266 | SA (m²) |
|----------|---------|--------------|---------|---------|---------|---------|
| Skado    | 1.2     | 271          | 1.9     | 2.1     | 2.1     | 1.2     |
| Oudenberg| 1.2     | 1.5          | 1.6     | 1.9     | 2.1     | 1.3     |
| Grimminge| 1.8     | 2.0          | 1.6     | 2.4     | 2.2     | 1.4     |

DOY, day of the year. See Materials and Methods for additional description.

spatial and the consistent stocking of trees in the mono-genotypic block design of the site (Table 2). Finally, both $E_{c\text{-leaf}}$ and $E_{c\text{-sapwood}}$ were averaged for the three genotypes and summed per day for comparison with the daily sums of ecosystem ET.

Statistical analysis

For the stand-level measurements, we used Pearson correlation and linear regression analysis to determine correlations and regressions between measured and modelled data. For the intensive field campaign, the rate of change in diameter, $\Delta D$/$\Delta t$, was analysed using a repeated-measures ANOVA model with genotype ($n=3$) and night- or daytime period ($n=11$) as fixed factors and individual tree ($n=4$) treated as random factor. A similar model was used to analyse MDS; however, data were confined to the daytime period ($n=5$). The Akaike information criterion correcting for small sample sizes (AICc) was used to determine the covariance structure that best estimated the correlation among individual trees over time. Treatment means were compared using Fisher’s least significance difference test. ANOVA analyses were performed using the mixed model procedure (PROC MIXED) of SAS (Statistical Analysis System, Cary NC, USA) with $\alpha=0.05$.

Results

Environmental conditions during the measurement campaign

Variable weather conditions were experienced during the measurement campaign (Fig. 2a,b). For instance, VPD (Fig. 2a) varied strongly during the measurement period leading to a range of $E_c$ and ET rates (Fig. 2c). The maximum VPD of 3.6 kPa was observed on 27 June 2011 (DOY 178), which coincided with maximum modelled ET and $E_c$ and measured ET. Precipitation patterns were dynamic as relatively dry periods alternated with periods of rainfall (Fig. 2b). In response to precipitation events, SWC measured at 0–10 cm depth increased, together with a less pronounced increase in SWC at 40 cm depth and a rising water table (Fig. 2b).

Yearly stand water balance

Both modelled and measured daily ET showed similar dynamics (Pearson’s correlation coefficient: 0.861) that were strongly related to changes in VPD (Fig. 2c). Modelled daily $E_c$ started to increase from mid-April onwards up to a maximum of 3.9 mm day⁻¹ at 27 June 2011. At the end of the growing season, $E_c$ decreased from late September onwards, as leaf fall started around that period. The average modelled daily $E_c$ for the growing season was 1.3 mm day⁻¹.

Summed over 2011 modelled ET was 437 mm, which was 87 mm higher than measured ET (350 mm) but still 94 mm lower than ET₀ (531 mm, Fig. 2d). Cumulative $E_c$ was 259 mm, representing 59% of ET over the whole year, as derived from the modelled data. When considering the actual growing season (from mid-April to late September), $E_c$ represented 69% of ET. Total modelled $E_{soil}$ was smaller than $E_c$ (177 mm) and accounted for 41% of the total ET. Total cumulative measured precipitation was 669 mm, which was higher than the total ET and ET₀. Run-off at our site was negligible for the stand water balance. The remainder of the precipitation was lost to groundwater leaching. The results from the sensitivity analysis of the model parameters showed that CGC had the largest impact on modelled $E_{soil}$, $E_c$ and ET followed by $K_{CT,x}$ (Table 3). In contrast, CDC had a limited impact on modelled $E_{soil}$, $E_c$ and ET. Overall, the deviation in model output observed during the sensitivity analysis ranged from -22.4% to +14.1%. Changes in parameter values had the largest impact on $E_c$, except for the parameter $K_{soil}$, which only impacted $E_{soil}$.

Sap flow

The highest $F_s$ rates were observed for Oudenberg (Fig. 3b), as compared to Skado (Fig. 3a) and Grimminge (Fig. 3c), with a maximum $F_s$ rate of 0.3 kg h⁻¹ on DOY 247. Skado had the lowest $F_s$ rates with a maximum $F_s$ rate of 0.2 kg h⁻¹; this occurred on the same day as the maximum $F_s$ for Oudenberg. The additional $F_s$ measurements performed for both Oudenberg and Grimminge between 15 September (DOY 258) and 27 September (DOY 270) 2011 confirmed the higher $F_s$ rates of Oudenberg as compared to Grimminge (data not shown). $F_s$ measured with these sensors installed higher up the tree varied in synchrony with the observed patterns in $F_s$ obtained with sensors installed at the stem base. For Oudenberg, $F_s$ at the stem base was within the range of $F_s$ rates measured during the additional campaign. For Grimminge, the daytime $F_s$ measured...
higher up the stem was on average 0.04 kg h\(^{-1}\) lower as compared to the \(F_s\) measured at 50 cm.

Daily sums of \(F_s\) were significantly correlated with daytime-averaged VPD (Fig. 4a, \(P < 0.001\)). The maximum \(F_s\) rate, estimated by coefficient ‘\(a\)’ in Eqn (2), was higher for Oudenberg (3.2 kg h\(^{-1}\)) than for Grimminge (2.6 kg h\(^{-1}\)) and Skado (2.3 kg h\(^{-1}\)) (Fig. 4a). A similar genotypic difference was observed for the \(F_s – PAR\) regression (Fig. 4b).

**Daily stem diameter variation**

Growth during the 39-day measurement campaign significantly differed among the three genotypes. Average (±SE) stem diameter increase during the intensive field campaign was significantly higher (\(P < 0.01\)) for Skado (0.8 ± 0.1 mm) as compared to Oudenberg (0.4 ± 0.1 mm) and Grimminge (0.4 ± 0.1 mm). More interestingly, daily \(\Delta D\) variations were observed for all three genotypes (Fig. 5) as trees tended to shrink during daytime when \(F_s\) was high and swelled during the night when they replenished their water reserves. The Skado tree, equipped with both \(F_s\) and dendrometer sensors, did not show a significant shrinkage during the day (except at the onset of \(F_s\) during DOY 231, Fig. 5a). The Oudenberg tree, and to a lesser extent the Grimminge tree, significantly shrank during days with high \(F_s\) rates (Fig. 5b,c).
Similar patterns in ΔD were observed for the other trees equipped with dendrometers (Fig. 6). Regardless of the genotype, stem diameter growth was observed for all trees of the different genotypes (Fig. 6b–d), but differences in the day- and night-time ΔD were observed among genotypes (Fig. 6e). The change in ΔD/Δt for both day- and night-time confirmed the intergenotypic differences in tree water use as observed with Fs measurements. Oudenberg showed a consistently higher ΔD/Δt during the night as compared to the daytime (Fig. 6e). Genotypes Grimminge and in particular Skado showed a larger variability in the

Table 3  Sensitivity analysis of the parameters used to model soil evaporation (Esoil), the transpiration component of evapotranspiration (Ec) and evapotranspiration (ET) for the multigenotype SRC over the 2011 growing season. The analysis evaluates the effect of changes in a range of site-specific realistic parameter values on the model output. Given are the % deviation at the minimum parameter value (min % deviation), the % of deviation at the maximum parameter value (max % deviation) and the total (total % deviation) deviation of modelled Esoil, Ec and ET relative to the base value used in the study

| Value used in study | CCmax | CC0 | Kex | KcTr,x | CGC | CDC |
|---------------------|-------|-----|-----|--------|-----|-----|
| Value used in study | 0.67  | 0.12| 1.1 | 1.2    | 0.058| 0.075|
| Minimum value       | 0.57  | 0.1 | 1   | 1      | 0.048| 0.065|
| Maximum value       | 0.77  | 0.4 | 1.2 | 1.3    | 0.068| 0.085|
| Min % deviation Esoil| +5.0  | +0.6| -6.3| +0.4   | +8.8 | -0.3 |
| Max % deviation Esoil| -4.9  | -4.5| +6.1| -0.2   | -5.7 | +0.3 |
| Min % deviation Ec   | -10.8 | -1.5| 0.0 | -16.7  | -22.4| +0.9 |
| Max % deviation Ec   | +9.8  | +11.3| 0.0 | +8.3   | +14.1| -0.7 |
| Min % deviation ET   | -4.2  | -0.6| -2.6| -9.6   | -9.4 | +0.4 |
| Max % deviation ET   | +3.7  | +4.7| +2.5| +4.7   | +5.9 | -0.3 |
| Total % deviation for Esoil | 9.9  | 5.1  | 12.4 | 0.7 | 14.4 | 0.6 |
| Total % deviation for Ec | 20.6 | 12.8 | 0.0  | 25.0  | 36.5 | 1.6 |
| Total % deviation for ET | 7.9  | 5.4  | 5.1  | 14.3  | 15.3 | 0.7 |

CCmax, maximum canopy cover; CC0, initial canopy cover at time = 0; Kex, maximum soil evaporation coefficient for fully wet and not shaded soil surface; KcTr,x, crop transpiration coefficient; CGC, increase in canopy cover; CDC, decrease in canopy cover.

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day- and night-time patterns of $\Delta D/\Delta t$, resulting in significant differences in daytime $\Delta D/\Delta t$ among genotypes on DOY 232 ($P = 0.0447$) and DOY 233 ($P = 0.0458$).

Significant differences in MDS ($P < 0.01$) were observed among the three genotypes (Fig. 6f). Oudenberg showed the highest MDS (maximum 10.5 mm), significantly higher than Skado (maximum 4.7 mm) and Grimminge (maximum 5.5 mm) on both DOY 231 ($P < 0.05$) and DOY 233 ($P < 0.05$). Small differences in MDS among the genotypes were observed during the days when lower ET (Fig. 6a) and $F_s$ (Fig. 5) occurred, that is DOY 234 and 235.

**Scaling of sap flow from tree to stand level**

Scaling of $F_s$ to $E_{c-sapwood}$ and $E_{c-leaf}$ resulted in daily average canopy transpiration rates of 1.1 and 1.3 mm day$^{-1}$, respectively (Fig. 7a). Total $E_{c-sapwood}$ and $E_{c-leaf}$ for the measurement campaign were 43.5 and 50.3 mm, respectively. Both values were lower than the total ET from eddy covariance, that is 59.9 mm. For most of the days during the field campaign, ET was higher than both $E_{c-sapwood}$ and $E_{c-leaf}$ resulting in a ratio of $E_c/ET$ lower than unity (Fig. 7b). Assuming that ET and $E_c$ were comparable, transpiration accounted for 74% and 86% of total ET, using average $E_{c-sapwood}/ET$ and $E_{c-leaf}/ET$ averaged over the period of the intensive field campaign as an estimate of the contribution of $E_c$ to ET, respectively. Overall, the leaf area-based approach tended to overestimate $E_c$ relative to ET (i.e. $E_c/ET > 1$) more than the sapwood area-based scaling of $F_s$ to $E_c$. The differences between ET and $E_c$ resulted from $E_{soil}$ and from the transpiration of understory weed vegetation, accounting for 26% and 14% of total ET when estimating $E_c$ using the sapwood and leaf area-based approach, respectively.

**Discussion**

**Stand water balance**

It has been argued that SRCs might have a strong impact on the regional water cycle. The stand water balance analysis at our site suggests that the impact of the SRC on the regional water cycle was not negative. First, our site was not water limited, as precipitation was around 53% and 26% higher than annual ET and $ET_0$, respectively. Secondly, for the year 2011, ET of our poplar SRC was around 18% lower as compared to $ET_0$, suggesting that the site used less water as compared to a reference grassland. Thirdly, an increase in the ecosystem water use efficiency over the year 2011 (reported earlier by Broeckx et al., 2014b) suggested that the poplars at our site could reduce the transpiration water loss per unit of fixed carbon by regulating stomatal opening. Caution is advised in generalizing these results to other SRCs. While studies on SRC water use in the Czech Republic (Fischer et al., 2013), in Mongolia (Hou et al., 2010) and in the USA (Nagler et al., 2007) showed similar results, almost a same number of studies (see references in Fischer et al., 2013) have shown that SRCs across the globe consume more water as compared to traditional agricultural crops or grasslands. Therefore, site location, local climatic conditions, species considered and the age of the plantation are important factors that determine the actual SRC water use and stand water balance (IEA-Bioenergy, 2011).

In line with results from previous studies (e.g. Persson & Lindroth, 1994; Fischer et al., 2013), both the modelling approach of $E_c$ and the scaling approach of $F_s$ measurements to stand level showed that $E_c$ represented the largest component of ET. The average daily

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$E_c$ values for our site (1.3, 1.1 and 1.3 mm day$^{-1}$, for modelled, sapwood and leaf area scaled $E_c$, respectively) were within the lower end of the range of 1–8 mm day$^{-1}$ reported for poplar stands of different genotypes, stand age and geographic locations in temperate climate zones (Meiresonne et al., 1999). For an
irrigated *P. trichocarpa* × *P. deltoides* plantation in the Pacific Northwest of the USA, an average $E_c$ of 4 mm day$^{-1}$ was observed (Kim et al., 2008). Sap flow—measured with the same heat balance principle as in the present study—provided a growing season average $E_c$ of 2.2 mm day$^{-1}$ for a *P. maximowiczii* × *P. nigra*
A number of uncertainties may arise when scaling up data from the individual tree to the stand and levels or when modelling stand water balance components. These uncertainties were, however, considered to be minimized in our case for the following reasons. Uncertainties can be associated with the eddy covariance measurements of ecosystem fluxes (e.g. Baldocchi, 2003). However, for our site, the energy balance closure (based on the assessment of net radiation, latent and sensible heat flux densities, soil heat flux density and energy storage) was 93% in 2011 (Zona et al., 2013a). This value therefore shows the good performance of the eddy covariance system in measuring fluxes at our site during the year 2011 when our measurements were performed. In addition, potential mismatches between spatial footprints of F_s and ET measurements, which depend on the wind direction, were minimized by

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measuring $F_s$ close to the mast and on the upwind side for the prevailing wind direction.

Uncertainties are also associated with the methods used for scaling $F_s$. On the one hand, for the sapwood area-based scaling of $F_s$, we assumed that the whole stem cross section consisted of conducting sap wood; however, this approach was successfully used for scaling $F_s$ to stand level for a $P. \ nigra \times P. \ maximowiczii$ SRC in Wisconsin, USA (Zalesny et al., 2006) such that uncertainties were probably limited for this approach. On the other hand, uncertainties were clearly associated with the LA scaling of $E_c$, leading to a more frequent overestimation of $E_c$ than the sapwood area scaling approach (i.e. $E_c/ET$ frequently higher than 1). These uncertainties likely resulted from both the genotype-specific allometric reconstruction of LA and the heterogeneity in LAI around the mast. Therefore, at our site, a sapwood area scaling approach was preferable for scaling $F_s$ to $E_c$. Future studies should combine different techniques across different spatial and temporal scales and a range of environmental conditions (Fischer et al., 2013).

In addition to the uncertainties depending on the approach used for scaling $F_s$, $F_s$ can also vary considerably among individuals of a given genotype, which means that replicates are needed to give an accurate estimate of the mean flux (Oren et al., 1998; Oishi et al., 2008). As $F_s$ measurements in our study were limited to only 39 days, we used the AquaCrop model to estimate $E_c$ for the whole growing season. However, the choice of the model parameter values to determine the yearly stand water balance was also prone to uncertainty. For instance, model parameters used to describe canopy development will have an impact on both the transpiration and the soil evaporation component of the stand water balance. To this end, an additional model sensitivity analysis could be used to evaluate the effect of parameter changes on the model outputs, as performed for the AquaCrop model in our study.

### Intergenotypic differences in tree water use

Previously reported measurements at this site, made in the same year 2011 (Broeckx et al., 2014a), revealed differences in stomatal conductance among genotypes to be strongly related to differences in $F_s$ observed during our study. According to Broeckx et al. (2014a), Oudenberg showed the highest average stomatal conductance ($459 \text{ mmol s}^{-1} \text{ m}^{-2}$), while Grimminge showed the lowest ($319 \text{ mmol s}^{-1} \text{ m}^{-2}$) and in particular Skado showed substantially lower average stomatal conductances for the period of the intensive field campaign. Therefore, genetic differences in the control of stomatal opening were an important factor that determined different $F_s$ rates among genotypes. Once stomata are open, VPD is the driving force for $F_s$, as illustrated by the strong $F_s – \text{VPD}$ relationships for all genotypes.

In addition to root water uptake and $F_s$, stem tissue water storage is an important factor in tree water relations (Zweifel et al., 2000). The pattern of stem diameter variation in response to the replenishment of water storage has been previously observed for poplars under controlled conditions (Giovanelli et al., 2007) and for other species (e.g. Zweifel et al., 2000, 2001; Conejero et al., 2007; Kocher et al., 2012). At our site, the highest shrinking and swelling were observed for the genotype with the highest $F_s$ (Oudenberg), showing that this genotype used an important fraction of its stem water storage to meet its transpiration demand. Skado had lower $F_s$ than the other genotypes, while it was the highest yielding genotype of those considered in our study (Broeckx et al., 2012). This was consistent with previous measurements of leaf gas exchange and intrinsic leaf water use efficiency (Broeckx et al., 2014a) and of carbon isotope discrimination (Verlinden et al., 2015) performed during the same period in 2011. Therefore, at our site, Skado had the highest water use efficiency as compared to Oudenberg and Grimminge. In addition, carbon isotope discrimination techniques already showed that $P. \ deltoides$ and $P. \ nigra$ (both male and female parental species of Oudenberg) were less water use efficient than $P. \ trichocarpa$ (female parent of Skado) at an experimental poplar plantation in central France (Dillen et al., 2008). During a summer drought at a freely draining site in the United Kingdom, genotype Beaupré ($P. \ trichocarpa \times P. \ deltoides$) was able to maintain its transpiration rate for a longer period than genotype Dorschkamp ($P. \ deltoides \times P. \ nigra$) (Hall & Allen, 1997).

In response to prolonged drought, stems of SRC poplar genotypes shrank as trees were unable to refill their stem water storage reserves (Giovanelli et al., 2007).

In conclusion, we observed that the SRC poplar of our study, which was not water limited in the year 2011, consumed less water as compared to a reference grassland. Moreover, $E_c$ contributed for 69% to the total growing season ET. The $F_s$ scaling approach for the intensive field campaign yielded similar results as the modelling exercise. At tree level, we observed important intergenotypic differences in both $F_s$ and $\Delta D$ showing different water use strategies associated with different growth strategies among the three genotypes. For our site, Skado had the highest water use efficiency as compared to Oudenberg and Grimminge. Besides harvestable yield, tree water use should be considered as a key criterion in SRC management through careful genotype selection. More large-scale experiments combining
measurements at leaf, plant and stand level under different rotations are necessary to better understand and quantify the water use of SRC at different scales.

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References

Albaugh JM, Domec JC, Maier CA, Sucre EB, Leggetti ZH, King JS (2014) Gas exchange and stand-level estimates of water use and gross primary productivity in an experimental pine and switchgrass intercrop forestry system on the Lower Coastal Plain of North Carolina, USA. Agricultural and Forest Meteorology, 192–193, 27–40.

Allen RC, Pereira LS, Raes D, Smith M (1998) Crop evapotranspiration – guidelines for computing crop water requirements. In: FAO Irrigation and Drainage Paper 56 (ed. FAO). FAO, Rome, Italy.

Allen SJ, Hall RL, Rosier PTW, Hopkins R (1998) Transpiration from coppiced poplar leaves in a short-rotation plantation. Tree Physiology, 18, 34–51.

Aylott MJ, Casella E, Tubby I, Street NR, Smith P, Taylor G (2008) Yield and spatial supply of bioenergy poplar and willow short-rotation coppice in the UK. Agricultural and Forest Meteorology, 148, 353–370.

Baker JM, Van Bavel CHM (1987) Measurement of mass flow of water in the stems of herbaceous plants. Plant, Cell & Environment, 10, 777–782.

Baldocchi DD (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. Global Change Biology, 9, 479–492.

Berndes G, Hoogwijk M, Van Den Broek R (2003) The contribution of biomass in the future global energy supply: a review of 17 studies. Biomass and Bioenergy, 25, 1–28.

Bovard BD, Curtis PS, Vogel CS, Su HB, Schmid HP (2005) Environmental controls on seasonality and stable isotope composition of photosynthesis, intrinsic water-use efficiency and stable isotope composition of plant carbon. Tree Physiology, 34, 701–715.

Broeckx LS, Verlinden MS, Ceulemans R (2014a) Seasonal variations in photosynthesis, intrinsic water-use efficiency and stable isotope composition of poplar leaves in a short-rotation plantation. Tree Physiology, 34, 701–715.

Budinsky G, Hoogwijk M, Van Den Broek R (2003) The contribution of biomass in the future global energy supply: a review of 17 studies. Biomass and Bioenergy, 25, 1–28.

Bridges LG, De Wit AJ, Coleman CA (2013) Effects of drought on productivity and carbon balance of temperate and tropical forest ecosystems. Agriculture, Ecosystems and Environment, 157, 64–75.

Brown JS, Ceulemans R, Albahm JM et al. (2013) The challenge of lignocellulosic bioenergy in a water-limited world. BioScience, 63, 102–117.

Bucheli TD, Zanganeh-Bani H, Riechers D, Dugas M (2013) Evaluation of drought response of two poplar clones (Populus × euramericana ‘M 101’ and P. deltoides Marsh. ‘Drina’) through high resolution analysis of stem growth. Journal of Experimental Botany, 58, 2673–2683.

Cormie RM, McVicar TR (2009) Evapotranspiration and water balance simulations of a grassland system. Agricultural and Forest Meteorology, 149, 885–891.

Dimitriou I, Busch G, Jacobs S, Schmidt-Walter P, Lammersdorf N (2009) A review of the impacts of Short Rotation Coppice cultivation on water issues. Landbeauf- forschung Volkenrode, 59, 197–206.

Dondesyn S, Vaniercht J, Langohr R, Van Ranst E, Deckers J (2013) – The grote bodembegroepen van Vlaanderen: Kenmerken van de ‘Reference Soil Groups’ volgens het internationaal classificatiesysteem World Reference Base. KL Leuven & Universiteit Gent in opdracht van Vlaamse overheid, Departement Leefmilieu, Natuur en Energie, Afdeling Land en Bodenscherming, Ondergrond, Natuur- lijke Rijksdiensten. doi: 10.13140/RG.2.1.12428.3104.

Ewers BE, Oren R, Johnsen KH, Landsberg JF (2001) Estimating maximum mean canopy stomatal conductance for use in models. Canadian Journal of Forest Research, 21, 198–207.

Fischer M, Tenka M, Kucera J et al. (2013) Evapotranspiration of a high-density poplar stand in comparison with a reference grass cover in the Czech-Moravian Highlands. Agricultural and Forest Meteorology, 181, 43–60.

Foken T, Wichura B (1996) Tools for quality assessment of surface-based flux measurements. Agricultural and Forest Meteorology, 78, 83–105.

Foster EA, Branch JD, Black TA, Jones H, Arevalo C, Bhatti JS, Sidders D (2013) Carbon sequestration in a hardrook poplar plantation. Biomass and Bioenergy, 57, 1–17.

Giovannelli A, Deslauriers A, Fragelli N, Scaletti L, Castro G, Rossa S, Crivellaro A (2007) Evaluation of drought response of two poplar clones (Populus × euramericana ‘M 101’ and P. deltoides Marsh. ‘Drina’) through high resolution analysis of stem growth. Journal of Experimental Botany, 58, 2673–2683.

Graham RL, Wright LL, Turhollow AF (1996) The potential for short-rotation woody crops to reduce United-States CO2 emissions. Climatic Change, 22, 223–238.

Griish, Halidam S, Lindroth A (1989) Water-use by intensively cultivated willow using estimated stomatal parameter values. Hydrological Processes, 3, 51–63.

Gustavsson L, Borjesson P, Johannson B, Svenningsson P (1995) Reducing CO2 emissions by substituting biomass for fossil-fuels. Energy, 20, 1897–1113.

Hall RL, Allen SJ (1997) Water use of poplar clones grown as short-rotation coppice at two sites in the United Kingdom. Aspects of Applied Biology, 49, 163–172.

Hall RL, Allen SJ, Rosier PTW, Hopkins R (1998) Transpiration from coppiced poplar and willow measured using sap-flow methods. Agricultural and Forest Meteorology, 90, 275–290.

Heilmann PE, Hinckley TM, Roberts DA, Ceulemans R (1996) Production physiology. In: Biology of Populus and its Implications for Management and Conservation (eds Stettle RF, Bradshaw HD Jr, Heilmann PE, Hinckley TM), Chapter 18, pp. 459–490.

HNC Research Press, Ottawa, Canada.

Herrick AM, Brown CL (1967) A new concept in cellulose production silage syca- more. Agricultural Science Review, 5, 8–13.

Hinckley TM, Brooks JR, Cermak P, Ceulemans R, Kucera J, Meinzer FC, Roberts DA (1994) Water fluxes in a hybrid poplar stand. Tree Physiology, 14, 1005–1018.

Hou LG, Xiao HL, Shi JH, Xiao SC, Zhou MX, Yang YG (2010) Evapotranspiration and crop coefficient of Populus euphratica Oliv. forest during the growing season in the extreme arid region northwest China. Agricultural Water Management, 97, 351–356.

Hsiao TC, Heng L, Steduto P, Rojas-Lara B, Raas D, Ferreres E (2009) Aquacrop— the FAO crop model to simulate yield response to water: III. Parameterization and testing for maize. Agronomy Journal, 101, 448–459.

IEA-Bioenergy (2011) Quantifying environmental effects of short rotation coppice on biodiversity, soil and water – Task 43. pp. 34.

Impens II, Schalck JM (1965) A very sensitive electric dendrogram for recording radial changes of a tree. Ecology, 46, 183–184.

Jassal RS, Black TA, Arevalo C, Jones H, Bhatti JS, Sidders D (2013) Carbon sequestra- tion and water use of a young hybrid poplar plantation in north-central Alberta. Biomass and Bioenergy, 56, 323–333.

Kauter D, Lewandowski I, Clausen C (1995) Quantity and quality of harvestable bio- mass from Populus short rotation coppice for solid fuel use – a review of the physi- ological basis and management influences. Biomass and Bioenergy, 24, 411–427.

Kim HS, Oren R, Hinckley TM (2008) Actual and potential transpiration and carbon assimilation in an irrigated poplar plantation. Tree Physiology, 28, 559–577.

Kim JS, Ceulemans R, Albahm JM et al. (2013) The challenge of lignocellulosic bioenergy in a water-limited world. BioScience, 63, 102–117.

Kocher P, Horna V, Leuschner C (2012) Environmental control of daily stem growth patterns in five temperate broad-leaved tree species. Tree Physiology, 32, 1021–1032.

Kozlowski TT, Winget CH (1964) Diurnal and seasonal variation in radii of tree stems. Ecology, 45, 148–155.
Larcher W (2003) Physiological Plant Ecology. Springer-Verlag, New York, NY, USA.

Linderson ML, Iritz Z, Lindroth A (2007) The effect of water availability on stand-level productivity, transpiration, water use efficiency and radiation use efficiency of field-grown willow clones. *Biomas and Bioenergy*, 31, 460–468.

Meirensone L, Nadezhin N, Cermak J, Van Slycken J, Ceulemans R (1999) Measured sapflow and simulated transpiration from a poplar stand in Flanders (Belgium). *Agricultural and Forest Meteorology*, 96, 165–179.

Migliavacca M, Meroni M, Manca G et al. (2009) Seasonal and interannual patterns of carbon and water fluxes of a poplar plantation under peculiar eco-climatic conditions. *Agricultural and Forest Meteorology*, 149, 1460–1476.

Nagler P, Jetton A, Fleming J et al. (2007) Evapotranspiration in a cottonwood (*Populus fremontii*) restoration plantation estimated by sap flow and remote sensing methods. *Agricultural and Forest Meteorology*, 134, 95–110.

Navarro A, Facciotto G, Campi F, Mastrorilli M (2014) Physiological adaptations of five poplar genotypes grown under SRC in the semi-arid Mediterranean environment. *Trees*, 28, 983–994.

Oishi AC, Oren R, Stoy PC (2008) Estimating components of forest evapotranspiration: a footprint approach for scaling sap flux measurements. *Agricultural and Forest Meteorology*, 143, 1719–1732.

Oren R, Phillips N, Katul G, Ewers BE, Dosai AR, Davis KJ, Carey EV (2006) Sap flux: up-scaled canopy transpiration, stomatal conductance, and water use efficiency in an old growth forest in the Great Lakes region of the United States. *Journal of Geophysical Research-Biogeosciences*, 111, doi: 10.1029/2005gs003083.

Tricker PJ, Pecchiari M, Bunn SM, Vaccari FP, Peressotti A, Miglietta F, Taylor G (2009) Water use of a bioenergy plantation increases in a future high CO2 world. *Biomas and Bioenergy*, 33, 200–208.

Trnka M, Trnka M, Fialova J, Koutecky V, Fajman M, Zahud Z, Hejdus S (2008) Biomass production and survival rates of selected poplar clones grown under a short-rotation system on arable land. *Plant Soil and Environment*, 54, 78–88.

Unsworth MH, Phillips N, Link T et al. (2004) Components and controls of water flux in an old-growth Douglas-fir-western hemlock ecosystem. *Ecosystems*, 7, 468–481.

Vanuytrecht E, Raes D, Steduto P et al. (2014) AquaCrop: FAO’s crop water productivity and yield response model. *Environmental Modelling & Software*, 62, 351–360.

Verhulst MS, Fichot R, Broeckx LS, Vanholme B, Boerjan W, Ceulemans R (2015) Carbon isotope compositions (δ13C) of leaf, wood and holocellulose differ among genotypes of poplar and between previous land uses in a short-rotation biomass plantation. *Plant, Cell & Environment*, 38, 144–156.

Zalesny RS Jr, Wiese AH, Bauer ED, Riemenschneider DE (2016) Sapflow of hybrid poplar (*Populus nigra* L. x *P. maximowiczii* A. Henry NM 6) during phytoremidiation of landfill leachate. *Biomas and Bioenergy*, 30, 794–793.

Zenone T, Zona D, Gefand I, Gielen B, Camino-Serrano M, Ceulemans R (2015) CO2 uptake is offset by CH4 and N2O emissions in a poplar short-rotation coppice. *Global Change Biology Bioenergy*, doi: 10.1111/gcbb.12269.

Zona D, Janssens IA, Aubinet M, Gioli B, Vicca S, Fichot R, Ceulemans R (2013a) Fluxes of the greenhouse gases (CO2, CH4 and N2O) above a short-rotation poplar plantation after conversion from agricultural land. *Agricultural and Forest Meteorology*, 169, 100–110.

Zona D, Janssens IA, Gioli B, Jungkunst HF, Serrano MC, Ceulemans R (2013b) N2O fluxes of a bio-energy poplar plantation during a two years rotation period. *Global Change Biology Bioenergy*, 5, 536–547.

Zwietf R, Item H, Hasler R (2000) Stem radius changes and their relation to stored water in stems of young Norway spruce trees. *Tree-Structure and Function*, 15, 50–57.

Zwietf R, Item H, Hasler R (2001) Link between diurnal stem radius changes and tree water relations. *Tree Physiology*, 21, 869–877.