

Transpiration of a hybrid poplar plantation in Saxony (Germany) in response to climate and soil conditions

Rainer Petzold · Kai Schwärzel · Karl-Heinz Feger

Received: 22 April 2010/Revised: 9 September 2010/Accepted: 23 November 2010/Published online: 21 December 2010
© Springer-Verlag 2010

Abstract The aim of this study was to investigate transpiration and its main driving factors on the example of a hybrid poplar plantation with the clone *Populus maximowiczii* × *P. nigra*, cv. Max 1 on a site in the hilly loess region of Saxony (Germany). Transpiration was measured using sap flow techniques during the 2007 and 2008 growing season. At the same time, throughfall, soil moisture dynamics and soil physical properties were also measured. Total transpiration rates amounted to 486 mm and 463 mm, respectively, during the 2 years. Maximum daily transpiration rates reached 6.7 mm/day, while an average of 2.2 mm/day for the entire growing season was recorded. The main controlling factors for stand transpiration included the evaporative demand, water availability and soil temperature. The information was implemented into a simple empirical model for the prediction of transpiration. It can be concluded that large-scale establishment of poplar plantations will result in a distinct reduction in groundwater recharge. On the other hand, surface run-off and soil erosion may decrease. Due to limited water availability in the late growing season, the growth potential of the tested clone cannot fully be exploited at many sites in Germany.

Keywords Evapotranspiration · Soil water · Poplar · Plantation · Sap flow

Abbreviations

ETP	Potential evapotranspiration over grass
LAI	Leaf area index
REW	Root extractable water [fraction]
T	Stand transpiration
Tn	Stand transpiration normalised by LAI
Ts	Soil temperature

Introduction

Interest in the utilisation of fast growing tree species as a renewable energy source and raw material is increasing worldwide. In Germany, short rotation plantations are being established on agricultural land. Hybrid poplars (*Populus spec.*) and willows (*Salix spec.*) are favoured in northern temperate climates due to their rapid growth rates, ease of propagation, broad genetic base, short breeding cycles and ability to resprout after multiple harvests (Volk et al. 2004). The demand of short rotation forests with an optimal supply of nutrients, water and light is high. Nutrient supply on former arable land is sufficient, at least during the initial rotations or if not, can easily be adjusted by means of fertilisation. The light situation can be controlled by optimising stand structure and density. However, at many sites, water can present a problem. It is generally accepted that poplar stands use significantly more water than field crops or other deciduous trees (Stephens et al. 2001). On sites where either precipitation rates are too low or irrigation is not feasible, soil water availability becomes the main growth limiting factor (e.g. Jug et al. 1999, Linderson et al. 2007). Due to the high levels of water uptake by poplar, the conversion of arable land to short rotation plantations, of this species, may result in a reduced groundwater recharge and surface water yield (Hall et al.

Communicated by R. Matyssek.

R. Petzold (✉) · K. Schwärzel · K.-H. Feger
Institute of Soil Science and Site Ecology, Technische
Universität Dresden, Piennner Str. 19, 01737 Tharandt, Germany
e-mail: Petzold@forst.tu-dresden.de

1996; 1998, Allen et al. 1999). In order to exploit the high yield potential of short rotation forests, but simultaneously minimise negative effects of the high water demand, it is necessary to carefully select adequate sites for plantations. Moreover, poplar species and their hybrids show a wide range of physiological mechanisms to control transpiration and canopy conductance in response to changing environmental variables (Blake et al. 1996; Monclus et al. 2006; Souch and Stephens 1998). Therefore, the specific water relationship of the various clones has to be taken into account when assessing hydrological effects of poplar plantations.

Only sparse information exists about the water demand and transpiration of poplar species and their hybrids, for site conditions in Germany. Bungart and Hüttl (2004) studied the relationship between water of poplar plantation with *P. trichocarpa* × *P. deltoides*, cv. Beaupré and *P. trichocarpa* × *P. maximowiczii*, cv. Androscoggin on rehabilitated sites in the mining region in South Brandenburg, Germany. They found significant differences in transpiration between the two clones. However, more than 50 different poplar clones exist in Germany, which have shown superior growth characteristics and have legal authorisation for use in plantation practise. To date, there is no information available about the relationship between soil water dynamics, root water uptake, transpiration and yield under field conditions with the often planted clone of *Populus maximowiczii* × *P. nigra*. Nevertheless, the knowledge of site- and plant-specific interactions supports planning of short rotation forests and is therefore necessary for the economic success and ecological sustainability of plantations.

Objectives

The main objectives of this study were (i) to determine stand transpiration of the clone *Populus maximowiczii* × *P. nigra*, cv. Max 1 by sap flow measurements, (ii) to identify the main environmental variables controlling stand transpiration and (iii) to derive an empirical model for predicting actual canopy transpiration in response to evaporative demand, soil moisture and soil temperature.

Materials and methods

Study site

The study site is located near Methau, a village in the hilly loess region of Saxony, Germany (51°05'N, 12°49'E) at 210 m asl. The region is characterised by a subcontinental climate. According to the records of the Methau agrometeorological station (1994–2008), the mean annual air temperature is 8.7°C and the mean annual precipitation is 770 mm. Table 1 presents monthly values of precipitation and the precipitation deficit for the study duration of 2007 and 2008 in comparison with the average of 1994 through 2008. The 2 years are characterised by similar mean air temperatures but significantly higher monthly precipitation rates than the long-term averages.

The poplar plantation was established in 1999 on former arable land. The goal of this plantation was to demonstrate the production potential of raw material for the paper industry within an exploitation cycle of 10 years. Different clones and management schemes were tested. It covers an area of 13.4 ha on a gentle NW facing slope. The soil cover consists of a mosaic of Haplic Luvisols which transitions to Stagnic Luvisols, derived from loess, above a deeply weathered argillite. Twelve different poplar clones (cuttings) had been planted in several blocks. The plot of our study consisted of a poplar block (*Populus maximowiczii* × *P. nigra*, cv. Max 1) in growth years nine and ten, respectively, covering an area of 828 m². The original spacing in the block was 2 × 3 m (1,667 cuttings/ha). Due to plant mortality after planting, the actual tree density is 1,570 trees/ha. To the west of the trees, in the centre of the plantation, was a block of the *Populus trichocarpa* × *P. deltoides*, cv. Beaupré clone and to the east a block of the *Populus maximowiczii* × *P. nigra*, cv. Max 3 clone. In December 2006, the average tree height was 11.0 m and the mean diameter at breast height was 13.2 cm.

Sap flow measurements

The transpiration T of the poplar stand was estimated based on sap flow measurements using the trunk heat balance method (THB) (Čermák et al. 1973; Kučera et al. 1977;

Table 1 Monthly sum of corrected precipitation and monthly precipitation deficit (P – ETP) during the growing season, average values for the period during 1994–2008

Period	Precipitation [mm/month]							Precipitation deficit [mm/month]						
	Apr	May	Jun	Jul	Aug	Sep	Apr–Sep	Apr	May	Jun	Jul	Aug	Sep	Apr–Sep
1994–2008	44	73	67	91	87	65	428	–17	–19	–35	–18	–9	14	–84
2007	2	123	84	119	119	109	556	–83	16	–30	2	29	58	–9
2008	119	23	85	78	106	68	479	69	–76	–32	–34	0	15	–57

Table 2 Biometric data of sample trees for sap flow measurements, each individual tree was only measured during one growing season, height estimation by optical measurement (Vertex III, Haglöf, Sweden)

Sample tree	2007		2008	
	DBH [cm]	Height [m]	DBH [cm]	Height [m]
1	12.3	9.7	13.1	14.2
2	12.9	8.1	14.0	14.6
3	13.6	11.4	15.2	14.9
4	14.2	11.2	15.8	13.2
5	15.5	11.2	18.1	15.0
6	16.6	11.3	18.4	13.5

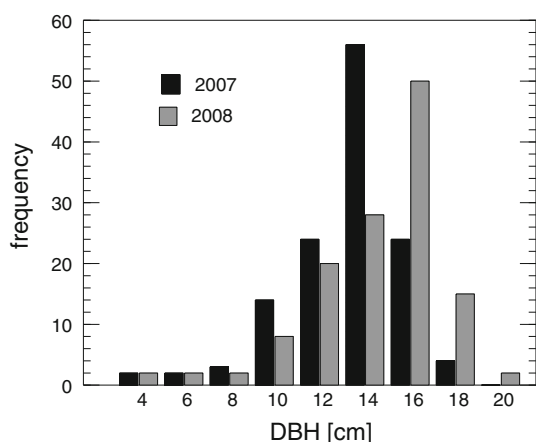


Fig. 1 Distribution of tree diameters at breast height (DBH) for the measured poplar stand (area = 828 m²) used for calculation of stand transpiration

Čermák et al. 2004). Sap flow sensors from EMS (Environmental Measurement Systems Inc., Brno, Czech Republic) were installed on six trees (Table 2) according to the tree diameter distribution (Fig. 1).

Between three heated sensors, which cover an effective tangential width of 5.5 cm and a reference sensor, the system kept a constant temperature difference of 1 K. Stainless heating plates and electrodes covering a xylem depth of 35 mm were used. The assumption that electrodes cover the main part of the conducting xylem depth was confirmed by visual differentiation between the wet, dark heartwood and the dryer, lighter sapwood (c.f. Čermák and Nadezhdina 1998). Samples of cores of different trees at different expositions taken with an increment borer were therefore evaluated. The output voltage for heating the stainless plates of the three upper sensors was logged every 10 min (EMS minicube). The values represent the integral over the heated volume of the trunk segment. They were directly converted to the sap flow rate by a physical-based heat balance equation (Čermák et al. 1973, 2004; Kučera et al. 1977; Tatarinov

et al. 2005). Mini32 software (EMS) automatically calculated the sap flow rate (kg/h) for each measured tree according to biometric parameters. Baseline correction was manually performed using Mini32 (EMS), assuming zero flow at 3:00 pm. For more information, see the manual of the used sap flow system of EMS (2006). Daily mean values of sap flow rate were calculated according to recommendations by Phillips and Oren (1998) by averaging values from 6:00 pm to 5:00 am on the following day. Upscaling of single tree transpiration to stand transpiration is based on sap flow distribution in DBH classes (Čermák et al. 2004).

Simple linear regression curves were constructed between the diameter of the investigated trees and the averaged sap flow rate (in 2007, $R^2 = 0.84$ and in 2008, $R^2 = 0.58$). However, the R^2 values were not improved by using an upscaling procedure for each individual day, and obtained daily values for stand transpiration did not differ significantly from values calculated by a seasonal scaling approach. Some gaps exist in sap flow data due to sensor failures during a part of the 2008 growing season. Between tree three and four ($R^2 = 0.95$) and tree two and six ($R^2 = 0.97$), respectively, functions of linear regression were performed in undisturbed measuring periods and used for gap filling.

Leaf area index (LAI) was measured using the optical instrument LAI 2000-PCA (LI-COR Inc., Lincoln, USA) in an interval of one to 3 weeks during the whole growing season. Below the canopy, 24 permanent points were measured with the 90° cap, and a second sensor was used to measure in an open field near the plantation. Due to the size of the plot, only rings one to three were analysed. In accordance with recommendations by Eriksson et al. (2005), no further correction for clumping index and winter LAI were made. The optical measurement was reassessed by estimating the leaf area index based on the specific leaf area at different tree heights (July 2007) and leaf collection during leaf fall 2007.

Soil hydrological and soil physical measurements

Soil moisture was measured with TDR sensors (IMKO GmbH, Ettlingen, Germany). After determining the main rooting zone, based on soil profile assessment (Table 3), three sensors were horizontally installed at 5 cm, two at 20 cm and one at 45 cm depths. Soil temperature was measured by Pt100-sensors in 5, 20 and 45 cm depths. A Logger (DL2e-Logger, Delta-T) monitored in 1 h intervals. To evaluate the heterogeneity of the plot and observe soil moisture development deeper in the soil profile, we used a TRIME PR3 tube probe (IMKO) designed for water content profiling, with a mobile FM3 measuring device (IMKO). Nine IMKO-TECANAT plastic access tubes were randomly installed and weekly profiled during

Table 3 Soil physical and hydrological properties at the study site

Horizon	Thickness [cm]	Sand	Silt	Clay	C_{org}	dB	AC per dm	AWC per horizon	Hydraulic conductivity at pressure head [cm]			Fine roots per horizon ^a [roots/dm ²]
									–31	–63	–316	
			[M.–%]		[g/cm ³]	[Vol.–%]	[mm]		[mm/day]			
Ap	32	6	82	12	1.58	1.41	13	90	8.9	1.6	0.3	73
E	18	3	85	12	0.41	1.54	6	47	6.0	3.6	0.8	7
Btg 1	17	9	73	18	0.20	1.57	7	36	0.9	0.7	0.3	8
Btg 2	25	29	55	17	0.12	1.77	5	53	n.m.	n.m.	n.m.	2
Bt	–	28	51	21	0.11	1.72	4	n.m.	0.8	0.6	0.2	–

The soil is a Stagnic Luvisol with C_{org} organic carbon, dB Bulk density, AC air capacity = volume between pF 0 and pF 1.8, AWC plant available water = water stored between pF 1.8 and pF 4.2, pF logpressure head, *n.m.* not measured; (^a determined in a soil trench; coarse roots deeper than 1.2 m below the trunk assessed by complete stump excavation of two sample trees)

the 2007 growing season down to 100 cm soil depth. In 2007, soil suctions were measured weekly using 26 permanently installed pressure head tensiometers in 5, 30, 45, 60 and 100 cm depths.

The measured soil water contents, at 5 and 20 cm, were assumed to apply to soil depth intervals at 0–10 cm and 10–30 cm, respectively. Based on the results from the tensiometers, TDR and PR3 probes, the soil water dynamics below 30 cm only showed small variations. This allowed scaling of the water content measurements, of the TDR probe at 45 cm, to a range of 30–100 cm. The root extractable water (REW) was calculated from TDR measurements as proposed by Granier et al. 2000

$$\text{REW} = \frac{\Theta_{\text{FC}} - \Theta}{\Theta_{\text{FC}} - \Theta_{\text{min}}} \quad (1)$$

with Θ , Θ_{min} and Θ_{FC} (Vol.%) as actual, minimum and volumetric water content at field capacity estimated from field measurements. Field capacity was defined as the soil water content, after three dry days, following a period of saturated soil, in early spring 2008. REW was calculated to a depth of 100 cm using averaged daily TDR readings in the scaling intervals as mentioned.

Soils were described according to WRB soil classification. The coarse and fine root distribution was mapped according to the method used by Böhm (1979). Excavation of two stumps, in 2008, gave additional information about rooting behaviour below the trunk. Disturbed and undisturbed soil samples (250 cm³) were taken from every horizon (five replicates) to measure water retention, unsaturated hydraulic conductivity, bulk density, soil texture and carbon content. The complete description of the investigated soil profile is given in Table 3. The upper soil horizon is characterised by a higher available water capacity than the lower horizons. Higher bulk densities and low hydraulic conductivities determine stagnic conditions in the lower horizons.

Climatological measurements

An automatic weather station was placed under the canopy to record relative humidity, temperature (SKH 2011, Skye Instruments, Powys, UK) and small throughfall events (Hellmann with tipping bucket, Thies, Göttingen, Germany). Throughfall was collected using plastic gutters (collecting area 2.24 m²) and transferred into a barrel. The water level was recorded by a pressure sensor (PR -36 W, Keller, Winterthur, Switzerland), and all sensor data were logged at hourly intervals (DL2e-Logger, Delta-T-Devices, Burwell, UK).

Stemflow could be observed during heavier rainfall, but no measurements were conducted. In order to obtain an estimate of total interception, stemflow was assumed to be 5% of net rainfall (Levia and Frost 2003).

Data for the open land climatological conditions were taken from the nearby agrometeorological station Methau operated within the network of the Saxon State Agriculture Office. The station (Lambrecht Meteorological Instruments, Göttingen, Germany) recorded air temperature and relative humidity (No. 8093), global radiation (pyranometer No. 16103), precipitation (Hellmann with tipping bucket No. 15188), wind speed and wind direction. Original precipitation values were corrected in order to account for systematic underestimation following official standards (Richter 1995).

Data analysis and modelling approach

The evaporative demand of the atmosphere was expressed as potential evapotranspiration over grass ETP according to Allen et al. (1998).

Stand transpiration T was normalised by LAI (T_n) due to known influence of LAI dynamics on T . ETP was then contrasted with daily transpiration T_n , and a general

relationship in an adapted form of Ewers et al. (2008) was established.

$$T_n = a * [1 - e^{-b * ETP}] \tag{2}$$

The stand transpiration can then be calculated as follows:

$$T = T_n * LAI \tag{3}$$

We identified environmental variables controlling T_n (i.e. explaining its daily and seasonal variation). The variables were then used to parameterise response functions in the general empirical model (Eq. 3). The upper envelope of data points in the relationship between T_n and ETP was constructed. This upper boundary represents transpiration under optimal conditions of the investigated poplar stand. The boundary line was calculated by the quantile regression approach. Quantile regression models can describe a response variable, in our case, stand transpiration T , which is often modified by several independent and/or interacting multiple factors (cf. Cade and Noon 2003; Koenker 2005; Poyatos et al. 2005). We analysed the transpiration of the poplar stand during periods with LAI >3. Under such conditions, soil evaporation can be assumed to be negligible in the energy balance (Kelliher et al. 1995). We fitted parameters a and b to the upper 95% quantile for calculation of optimum transpiration $T_{n0.95}$. Upon further analysis, we introduced modifier functions to decrease soil moisture $f(\text{REW})$ and soil temperature $f(T_s)$. Depending on environmental conditions, these functions yielded values between 1 (no limitation of transpiration) and 0 (totally inhibited transpiration). The soil moisture response function was used in the following form (i.e. Poyatos et al. 2005):

$$f(\text{REW}) = 1 - s_1 * e^{-s_2 * \text{REW}} \tag{4}$$

where s_1 and s_2 are fitting parameters. The soil temperature response function for water uptake by roots was adapted from Mellander et al. (2006)

$$f(T_s) = \begin{cases} 1 - e^{-t_1 * (T_s - t_{lim})^2} & T_s > t_{lim}^\circ\text{C} \\ 0 & T_s \leq t_{lim}^\circ\text{C} \end{cases} \tag{5}$$

where t_1 and t_2 are fitting parameters and T_s is the soil temperature at 20 cm depth (°C). The parameter t_{lim} represents the threshold temperature below where no root water uptake (and thus, transpiration) occurs. We assumed a tight coupling of root activity and gas exchange at leaf level in the early growing season, when soil water is not limiting but soil temperature significantly controls processes in fine roots (Pregitzer et al. 2000); therefore, we fixed t_{lim} at 10°C. This is according to Lyr (1996) who observed in pot experiments of *Populus nigra* that there was no root activity at soil temperatures <10°C. The complete transpiration model was then obtained:

$$T = T_{n0.95} * f(\text{REW}) * f(T_s) * LAI \tag{6}$$

All statistical analysis, nonlinear and quantile regressions were done in R, version 2.7.1. (R Development Core Team 2008). The appropriate response functions were selected by maximising the fit of the regression line between measured and modelled stand transpiration and visual evaluation of residuals. Akaike’s Information Criterion (AIC), which represents a value of log likelihood penalised by the number of used fitting parameters, was minimised. If no other information was given, statistical tests and fitted parameters were significant with a t -test significance level of $P < 0.001$.

Results

Environmental conditions

The temporal dynamics of environmental variables during the 2007 and 2008 growing seasons are presented in Fig. 2.

The 2007 growing season was characterised by a dry and warm start, followed by a period with continuously distributed precipitation. Due to the dry winter, there was no full soil water storage at the beginning of April 2007. There was only 85% of root extractable water available. In contrast to 2007, the beginning of the growing season in 2008 was colder and wetter. Due to relatively dry conditions in the following months, the decrease in root extractable water was steeper than in 2007. In both years, the transpiration T of the fully developed poplar stand was similar to the course of the potential crop evapotranspiration ETP. However, at the beginning of the growing season in both years, with increasing soil temperatures and canopy development, the first reduced transpiration reaches the level of ETP in the first half of May. During July and August, T clearly fell behind ETP, which corresponds with the lowest levels of REW.

Canopy development in both years started at the beginning of April and autumn leaf fall was finished in the middle of October. The LAI calculation from specific leaf area and leaf collection in 2007 yielded an average of five and was in good agreement with the LAI obtained by the PCA-2000 measurement during the same period. Measured LAI values, particularly from July 2007, are one unit higher than in the same period in 2008. However, in 2007 after three storms, LAI decreased by approximately one unit due to loss of branches and leaves. Also, the decrease observed at the end of June 2008 was induced by a storm.

Maximum daily transpiration rates in 2007 reached 5.7 mm/day (6.7 mm/day in 2008), while average transpiration of all measured days reached 2.3 mm/day

Fig. 2 Time series of stand transpiration (T), crop reference evaporation (ETP), root extractable water (REW), precipitation (P), leaf area index (LAI), soil temperature at 20 cm depth (T_s), global radiation (RG) and vapour pressure deficit (VPD) in 2007 and 2008. Dashed lines refer to the left y-axis, running mean (5 days) for T , ETP , T_s and VPD ; single values of leaf area index with error bars (1 standard deviation, $n = 24$)

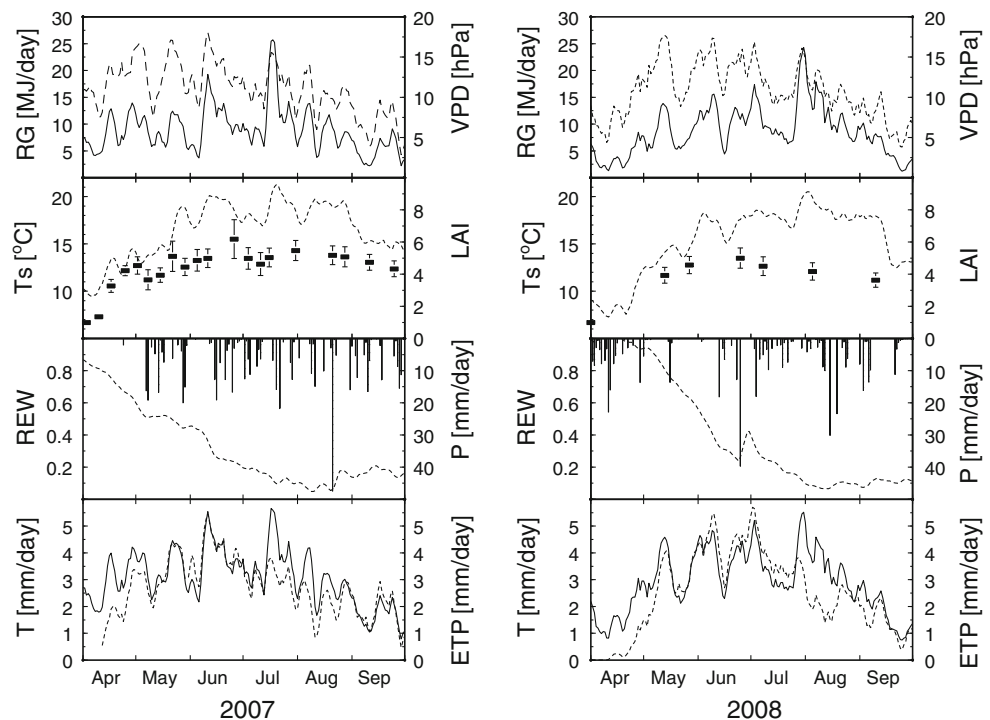
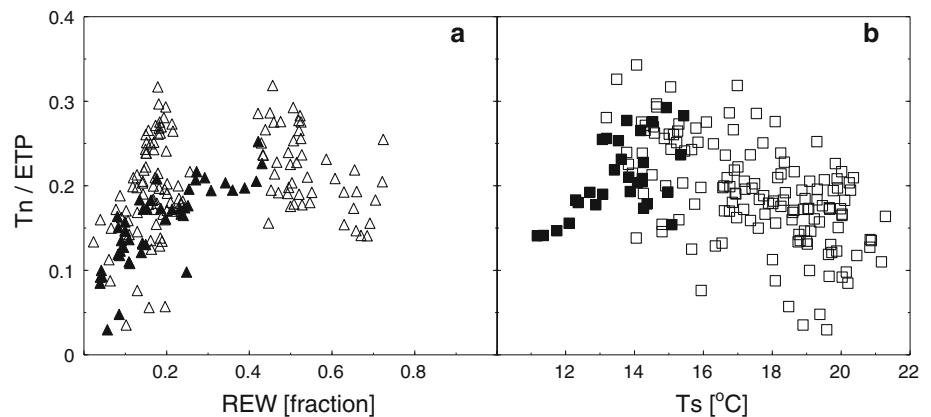


Fig. 3 Ratio of normalised Transpiration T_n to crop reference Evapotranspiration ETP in relation **a**) to root extractable water REW ; filled triangles represent the data pool at $T_s > 19^\circ\text{C}$, open triangles at $T_s \leq 19^\circ\text{C}$, **b**) to soil temperature, T_s ; filled boxes represent the data pool at $REW > 0.5$, open boxes at $REW \leq 0.5$; data of 2007



(2.2 mm/day) and in total 486 mm (463 mm). The transpiration of 2007 and 2008 calculated by the soil water balance method yielded 495 mm and 467 mm, respectively. Values of total interception during growing seasons reached 163 mm (2007) and 113 mm (2008) which corresponds to 28 and 24% of open field precipitation, respectively.

Transpiration response to soil moisture and soil temperature

Different soil moisture conditions modified the magnitude of transpiration response to evaporative demand. Decreasing root extractable water, REW , led to a reduced ratio of T_n/ETP (Fig. 3a). Although this relationship only became noticeable when the data were pooled into a set at higher or lower soil temperatures, respectively. The threshold in the example was

19°C . In contrast, at high levels of $REW > 0.5$, we observed a reduced ratio of T_n/ETP (Fig. 3a). This was due to relatively low soil temperatures, T_s , in April and the beginning of May. In Fig. 3b, the ratio of T_n/ETP is contrasted to the soil temperature, T_s . A significant correlation was only observed at low soil temperatures and high soil moisture conditions (threshold for data pooling $REW > 0.5$).

Modelling transpiration

The fitted general model (Eqs. 2, 3) was able to predict actual transpiration, depending on evaporation demand. Larger differences between predicted and measured transpiration were observed at low and high evaporation demand. Based on modelled optimum transpiration, $T_{n,0.95}$, we implemented the response functions for REW (Eq. 4)

Table 4 Regression statistics for the transpiration model

Model for T prediction	a	b	s ₁	s ₂	t ₁	t ₂	Intercept	Slope	Adj. R ²	AIC
T _n *LAI	1.440 (0.215)	0.173 (0.037)	–	–	–	–	0.68 (0.10)	0.75 (0.03)	0.74	369
T _{n0.95} *f(REW)*LAI	1.449 (0.211)	0.274 (0.058)	0.605 (0.040)	4.239 (0.437)	–	–	0.62 (0.07)	0.80 (0.02)	0.86	274
T _{n0.95} *f(REW)*f(Ts)*LAI	1.449 (0.211)	0.274 (0.058)	0.668 (0.043)	5.151 (0.489)	0.459** (0.138)	1.292 (0.283)	0.48** (0.07)	0.84 (0.02)	0.89	235

T_n represents the modelled ETP response according to Eq. (3), standard error in brackets, most parameters are significant at *t*-test level $P < 0.001$ (** $P < 0.01$)

and T_s (Eq. 5). The regression statistics for all modelling steps is given in Table 4.

The introduced response functions for soil moisture and soil temperature improved both model fit and model quality (Table 4). The consideration of only REW response increased the adjusted R² from 0.74 to 0.86 with only slight improvement of the intercept and slope of the regression between modelled and measured daily values. The complete model (Eq. 6) reduced the intercept, which means a decreased overestimation in the lower ETP range. The model was able to explain 89% of variation in 2007, simultaneously yielding the lowest value of Akaike’s Information Criterion (AIC). Nevertheless, daily transpiration estimates were slightly overestimated in the lower range of ETP (Fig. 4).

Visual inspection of residuals (measured-modelled) confirmed that the variation of daily transpiration can be explained by our empirical modelling approach (Fig. 5a-e). The error of modelled daily transpiration ranged between +1 mm/day and –1 mm/day (Fig. 5a). Residuals against explaining variables ETP, REW and T_s showed a somewhat balanced scatter (Fig. 5b-d). The implementation of modifier function for root extractable water and soil temperature resulted in an unbiased representation of residuals over the whole growing season (Fig. 5e).

A generalised representation of the empirical model is illustrated in Fig. 6. While the reduction in transpiration begins at REW <0.4 (Fig. 6a), at a reduced transpiration due to low temperatures, it is noticeable only in the range of 10–15°C (Fig. 6b).

The application of the calibrated model with the environmental data of 2008 led to an exceptional prediction of transpiration (adj. R² = 0.83). However, the total transpiration for days with LAI >3 was systematically underestimated and amounted to 387 mm, which is 13% less than the measured total transpiration of 443 mm (Table 5). Although 2008 was characterised by lower precipitation, there were less days with precipitation and lower interception than in 2007.

Discussion

Transpiration rates estimated from measured sap flow

The physical background of the applied THB method for sap flow measurements is robust against radial variation of sap flow density and does not require any calibration (Čermák et al. 2004). However, our applied upscaling procedure from measured tree trunk segment to tree level, by multiplying the circumference, assumed a uniform azimuthal flow pattern. Nevertheless, azimuthal flow variation is a crucial point in sap flow measurements and discussed elsewhere (e.g. Cohen et al. 2008). Differences of

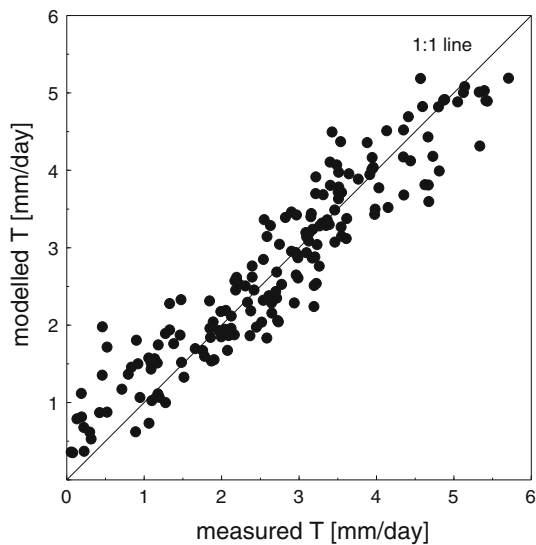


Fig. 4 Modelled versus measured transpiration in 2007, complete transpiration model with response functions for soil moisture and soil temperature

sun exposure, heterogeneity in soil structure or position of sensors in relation to large branches may lead to different azimuthal flow patterns. Cohen et al. (2008) concluded that the variation of the azimuthal sap flow pattern within a single tree may have the same magnitude to that between trees. Čermák et al. (2004) showed that the upscaling error in homogenous stands sharply decreases with increasing number of sample trees and reaches approximately 15% for

$n = 4$ and 10% for $n = 12$, respectively. Meiresonne et al. (1999), who measured sap flow with multi-point sensors in a 13-year-old poplar plantation (*P. trichocarpa* × *P. deltoides*, cv. Beaupré), concluded that a relatively low number of trees could be sufficient for upscaling from tree to stand level ($R^2 = 0.98$ for regression between sap flow rate and basal area of eight sample trees). However, in our linear upscaling approach, 82% of single tree sap flow could be explained by stem diameter. The lower R^2 of this linear upscaling equation in 2008 (0.55) may be the result of sensor failure and the chosen gap filling method or a higher variation of sap flow patterns within the selected samples as discussed above. Therefore, six sample trees in that particular poplar stand were the minimum in order to match a measurement error <20%.

The maximum daily transpiration rates at 5.7 mm/day (2007) and 6.7 mm/day (2008) and the average transpiration rates of 2.3 mm/day resp. 2.3 mm/day are in the range of reported values for stand transpiration of the genus *Populus* (Meiresonne et al. 1999). The accumulated transpiration values at our site in Saxony, at 486 mm (2007) and 463 mm (2008), for the entire growing season are rather high in comparison with the range of 153–310 mm at a mining reclamation site in South Brandenburg (Germany; Bungart and Hüttl 2004). These authors investigated the water balance of the poplar clones *P. trichocarpa* × *P. deltoides*, cv. Beaupré and *P. maximowiczii* × *P. trichocarpa*, cv. Androscoggin during a period of 7 years. Meiresonne et al. (1999) extrapolated daily values

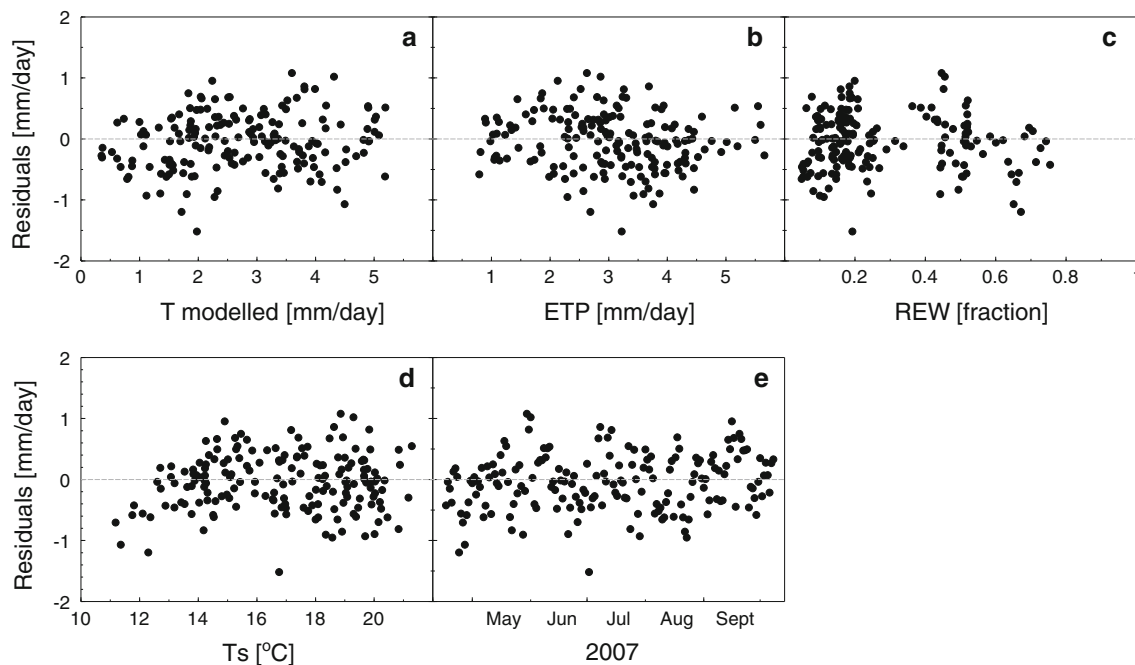


Fig. 5 Residuals (measured—modelled canopy transpiration) as a function of **a**) modelled T; **b**) ETP; **c**) root extractable water REW; **d**) soil temperature T_s ; **e**) time

Fig. 6 Empirical transpiration model **a**) Transpiration as a function of ETP and REW at $T_s = 20^\circ\text{C}$ **b**) as a function of ETP and T_s at $\text{REW} = 0.5$; $\text{LAI} = 4$

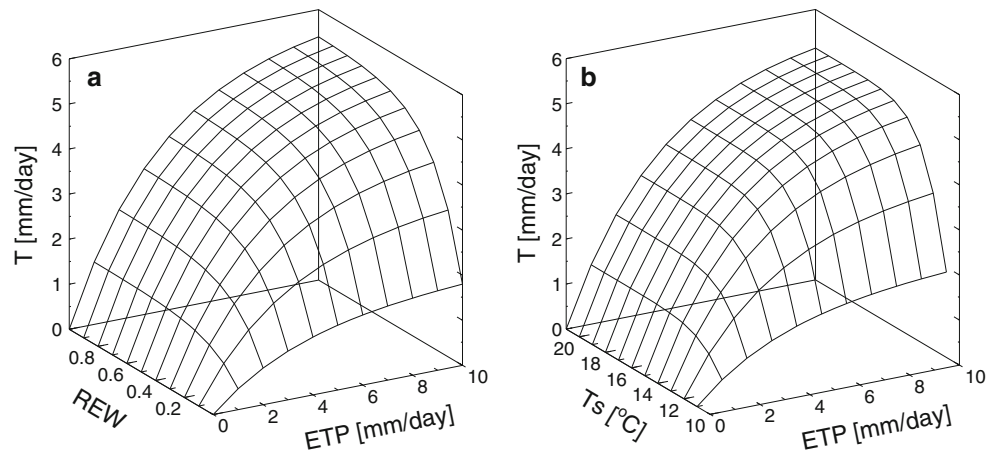


Table 5 Measured T ($\text{SF} =$ upscaled from sap flow), modelled T and measured weather conditions ($P =$ precipitation; $I =$ interception) of the poplar stand in Methau

Year	Meas.T (SF)	Mod.T	Days with $\text{LAI} > 3$	P total	P mean	Days with precipitation		I total	I mean
	[mm]					[mm]	[no]		
2007	473	481	175	557	3.2	58	33	155	8.9
2008	443	387	153	353	2.3	36	24	92	6.0

of a poplar stand in Belgium with an annual transpiration of 329 mm. In contrast, Hall et al. (1996) measured transpiration rates of a poplar stand (*Populus trichocarpa* \times *P. deltoides*) in the United Kingdom by means of hydrological modelling with an annual transpiration of 527 mm (precipitation 676 mm/year), which is slightly higher than our observations.

The shape and the magnitude of the leaf area development at Methau (Fig. 2, $\text{LAI}_{\text{max}} = 6$ in 2007 and 5 in 2008) are similar to the LAI dynamics reported in other studies on poplar plantations (Hall 1998; Bungart and Hüttl 2004). There is no information available about variation in LAI because of branch and crown breakage. However, the vulnerability to wind damage, especially for Tacamahaca poplars (Balsam Poplars), is known in management practice. Furthermore, branch abscission as well as branch and crown breakage after high wind are propagation strategies in particular for Tacamahaca poplars (Braatne et al. 1996). However, the observed reduction in LAI by approximately 20% due to such phenomena and the seasonal dynamic course of LAI influences transpiration rates and have to be considered when analysing transpiration and responses to environmental variables.

Comparison of transpiration rates on poplar with other tree species and field crops in Saxony

Afforestation of former arable land may affect the hydrological cycle at the site and landscape level. In order

to assess the potential environmental impacts, a comparison of stand evapotranspiration of poplar to other species is necessary. Therefore, summed transpiration and interception of the studied poplar plantation at Methau were compared to stands of other tree species and agricultural crops in Saxony. As shown in Table 6, evapotranspiration during the growing season of the poplar plantation exceeds that of water demanding agricultural crops, such as winter wheat and sugar beets, by 25–40%. This can be explained by a longer growing season with higher daily evapotranspiration rates. In particular, higher interception rates from leaves and shoots of the dense canopy of poplar plantation in comparison with annual crops may contribute to the higher evapotranspiration rates of poplar plantations. In contrast to adult forest stands, evapotranspiration of the young poplar stand is up to 90% higher. Although the age of the forest stands and unfavourable site conditions in the low mountain range may be responsible for these large differences in evapotranspiration rates. Furthermore, relatively high interception rates of evergreen conifers (e.g. Norway spruce) outside the growing season have to be taken into account for a complete assessment of evapotranspiration rates. Hall et al. (1996) confirmed that the annual water use of short rotation plantations of poplar coppice (3-year-old shoots on 7-year-old stools) in the United Kingdom is higher than any agricultural crops and deciduous forest stands. According to these authors, only pine stands use more water.

Table 6 Comparison of measured evapotranspiration of stands of poplar, Norway spruce, European beech and various agricultural crops on sites in Saxony (Germany)

Species	Age [years]	Site, altitude (m asl)	Soil	Length of GS, year	P [mm/GS]	ET _{total} [mm/GS]	Av. ET rate [mm/day]
<i>Populus maximowiczii</i> × <i>P. nigra</i> ^a	8	Methau, 210 m	Stagnic Luvisol	188 days 2007	558	622	3.3
<i>Picea abies</i> (Norway spruce) ^b	115	Tharandt, 380 m	Skeletal Cambisol	206 days 2007	558	328	1.6
<i>Fagus sylvatica</i> (European beech) ^b	97	Tharandt, 380 m	Dystric Cambisol	190 days 2007	619	386	2.0
<i>Triticum aestivum</i> (Winter wheat) ^c	1	Brandis, 136 m	Haplic Luvisol	136 days 2007	349	466	3.4
<i>Triticum aestivum</i> (Winter wheat) ^d	1	Brandis, 136 m	Haplic Luvisol	158 days 1991	280	460	2.9
<i>Solanum tuberosum</i> (Potato) ^d	1	Brandis, 136 m	Haplic Luvisol	128 days 1985	255	339	2.6
<i>Beta vulgaris</i> (Sugar beet) ^d	1	Brandis, 136 m	Haplic Luvisol	164 days 1990	356	493	3.0

GS growing season, P precipitation, ET_{total} Evapotranspiration, av. ET rate = average ET rate during GS

^a present study with cv. Max 1; ET_{total} = Transpiration + Interception

^b Department of Meteorology, TU Dresden (personal communication); ET_{total} from Eddy-flux measurements

^c Haferkorn (personal communication); ET_{total} from lysimeter measurements

^d Haferkorn (2000); lysimeter measurements

Transpiration response to environmental conditions and modelling

Instead of the known atmospheric drivers for transpiration, like radiation, vapour pressure deficit and temperature, we chose ETP to express the evaporative demand of the atmosphere. It allowed us to successfully model daily transpiration dynamics of the stand level with a nonlinear relationship between transpiration and ETP. This correlation reflects the often described stomata behaviour characterised by an increasing closure in a logarithmic form with increasing vapour pressure deficits (Hinckley et al. 1994; Oren et al. 1999; Zhang et al. 1999; Kim et al. 2008). In the generalised approach presented here, 74% of variation could be explained by ETP which corresponds to the range of reported values for other tree species (e.g. Poyatos et al. 2005; Ewers et al. (2008)). The observed strong reduction in transpiration ratios when REW drops below 0.4 (Fig. 3a) was reported for many tree species in Europe (Bernier et al. 2002; Granier et al. 2000; Schwärzel et al. 2009). Braatne et al. (1992), who investigated the behaviour of the cv. Beaupré in pot experiments, reported a threshold value of 0.6 for the response to REW. In contrast, Allen et al. (1999) did not find a clear change of transpiration ratios in response to decreasing REW for the black poplar clone *P. deltoides* × *P. nigra*, cv. Dorschkamp. Although in the same study, a threshold value 0.32 was found for the Beaupré clone. A general extraction of exact thresholds is dependant on the definition of REW. The minimum water content Θ_{\min} in Eq. (1) was defined according to the observed minimum during the studied years which were both characterised by extraordinary precipitation without long dry periods. Furthermore, we referred REW to a constant soil depth of 100 cm assuming that no proliferation of fine roots occur from sinker roots

deeper in the soil. However, root water uptake from horizons below 100 cm may occur when water occurs in cracks or fractures of the argillite rock soil complex.

Low soil temperature was found to explain reduced transpiration (Fig. 3b) in early spring when soil water is not a limiting factor and anaerobic conditions can be excluded. Only a few studies consider low soil temperature as a controlling variable for transpiration. For *Pinus sylvestris*, a reduced transpiration at soil temperatures <8°C was demonstrated by Mellander et al. (2004). This was explained by reduced stomata conductance due to abscisic acid signals and reduced root permeability at lower soil temperatures. However, evapotranspiration and net photosynthesis are correlated, and therefore, increased root growth productivity may also be an indicator for transpiration (Coté et al. 1998; Pregitzer et al. 2000). Lyr (1996) investigated root productivity of eight European tree species, under fertilised and optimal water conditions and constant air temperature in relation to different soil temperature regimes. For *Quercus robur* and *Larix decidua*, he found increased activity at soil temperatures > 5°C. Root growth of *Populus nigra* developed at soil temperatures > 10°C. This threshold value was also found by Zalesny et al. (2005) for cuttings of 21 poplar clones. Nevertheless, soil temperature effects on transpiration are not constant due to plant interaction with aboveground climatic conditions and soil moisture dynamics.

Quantile regression allowed us to define a boundary relationship between Tn and ETP in the data set in an objective way. Therefore, we could avoid uncertainties in the definition of nonlimiting conditions for transpiration which are necessary to fit multiplicative models in a step-wise process with pooled data (cf. Ewers et al. 2008; Granier et al. 2000). According to the generalised model (Fig. 6a), transpiration occurs even when REW = 0, which

should be impossible from a theoretical point of view. The reason for this phenomenon is associated with the uncertain definition of REW as discussed above.

The test of the model to the independent data set of 2008 resulted in a slight but systematic underestimation of transpiration (Table 5). This may be acceptable because data uncertainty of the upscaled stand transpiration in 2008 are higher. Nevertheless, neglecting interception in our modelling approach may also bias the results. A part of evaporative demand (ETP) on wet days is requested by evaporation of intercepted water from wet leaves more than by transpiration. The calibration of Eq. (2), by quantile regression under wet conditions, will then lead to parameters which systematically underestimate optimal transpiration under dry conditions. The informative value of modelling results will decrease as site conditions show greater differences than those incorporated in the parameterisation procedure. Nevertheless, the empirical model is suited to generalise a relationship between transpiration and controlling environmental factors that have to be accounted for when implementing a more process-oriented modelling approach.

Conclusions

Our results demonstrate that water consumption of the studied poplar plantation during growing season exceed that of any other agricultural crop and mature broad leaved forest stands and even old conifer stands reported for comparable site conditions in Saxony (Germany). These findings have to be carefully considered, when short rotation plantations are established on a large scale on arable land. In particular, this will be essential for site conditions and management schemes which allow the development of canopies with high LAI values. The higher evapotranspiration will lead to a reduced infiltration and hence decrease in groundwater recharge. However, as a positive effect, surface run-off may be clearly reduced, thus leading to reduced soil erosion. The high retention potential of drier plantation soils also contributes to improved water retention and, thus, flood prevention. Such conflicting hydrological effects have to be taken into account when short rotation plantations are assessed on a landscape scale. Quantitative data are indispensable to negotiate trade-offs between conflicting sectors providing ecosystem services.

Evaporative demand, water availability and soil temperature were found to be the main controlling factors for stand transpiration. We conclude that at our site in Methau, the plant-specific maximum transpiration was not reached because of the low soil temperature when soil water is not limiting, especially in spring. In contrast, transpiration is reduced in periods with favourable soil temperature but

sustained soil drought. These interactions inhibit higher gas exchange rates, hence photosynthesis and assimilation, especially in the early and late stages of growing seasons. This appears to be a major reason why the growth potential of this highly productive poplar clone cannot fully be exploited under the given site conditions. However, it is quite clear that the multiple interactions are highly dependant on site and clone characteristics. This has to be adequately considered, when transferring the findings to other sites in Saxony, in particular to wetter, colder regions in mountainous areas or to warmer, drier regions in the lowlands. Our empirical modelling approach is only a step in the way of differentiated assessment of potentials and risks of poplar cultivation, based on process-oriented modelling.

Acknowledgments We like to express our thanks to J. Kučera (Brno) for his introduction to sap flow techniques and fruitful discussions, U. Haferkorn (Lysimeter station Brandis) and the Department of Meteorology, TU Dresden for providing additional lysimeter and eddy-flux data. The study was financially supported by the Federal Ministry of Education and Research (BMBF, project AGROWOOD - 0330710 A).

References

- Allen RG, Pereira LS, Raes D, Smith M (1998) Crop evapotranspiration: guidelines for computing crop water requirements. FAO Irrigation and Drainage Paper no. 56, Rome, Italy
- Allen SJ, Hall LR, Rosier PTW (1999) Transpiration by two poplar varieties grown as coppice for biomass production. *Tree Physiol* 19:493–501
- Bernier PY, Bredá 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 Manage* 163:185–196
- Blake TJ, Sperry JS, Tschaplinski TJ, Wang SS (1996) Water relations. In: Stettler RF, Bradshaw HD, Heilman PE, Hinckley TM (eds) *Biology of populus and its implications for management and conservation*. NRC Research Press, Ottawa, Ontario, pp 401–422
- Böhm W (1979) *Methods for studying root systems*. Ecological studies Vol. 33. Springer-Verlag, Berlin
- Braatne JH, Hinckley TM, Stettler RF (1992) Influence of soil water on the physiological and morphological components of plant water balance in *Populus trichocarpa*, *Populus deltoides* and their F1 hybrids. *Tree Physiol* 11:325–339
- Braatne JH, Rood SB, Heilman PE (1996) Life history, ecology, and conservation of riparian cottonwoods in North America. In: Stettler R, Bradshaw H Jr, Heilman P, Hinckley T (eds) *Biology of populus and its implications for management and conservation*. NRC Research Press, Ottawa, pp 57–85
- Bungart R, Hüttl R (2004) Growth dynamics and biomass accumulation of 8-year-old hybrid poplar clones in a short-rotation plantation on a clayey-sandy mining substrate with respect to plant nutrition and water budget. *Eur J Forest Res* 123(2):105–115
- Cade BS, Noon BR (2003) A gentle introduction to quantile regression for ecologists. *Front Ecol Environ* 1:412–420

- Čermák J, Nadezhkina N (1998) Sapwood as the scaling parameter—defining according to xylem water content or radial pattern of sap flow? *Ann Sci For* 55:509–521
- Čermák J, Deml M, Penka M (1973) A new method of sap flow rate determination in trees. *Biol Plant* 15:171–178
- Čermák J, Kučera J, Nadezhkina N (2004) Sap flow measurement with some thermodynamic methods, flow integration within trees and scaling up from sample trees to entire forest stands. *Trees* 18:529–546
- Cohen Y, Cohen S, Cantuarias-Aviles T, Schiller G (2008) Variations in the radial gradient of sap velocity in trunks of forest and fruit trees. *Plant Soil* 305:49–59
- Coté B, Hendershot WH, Fyles JW, Roy AG, Bradley R, Biron PM, Courchesne F (1998) The phenology of fine root growth in a maple-dominated ecosystem: relationships with some soil properties. *Plant Soil* 201:59–69
- EMS (2006) Sap flow system using LT 51.1 modules—instruction manual. Brno
- Eriksson H, Eklundh L, Hall K, Lindroth A (2005) Estimating LAI in deciduous forest stands. *Agric For Meteorol* 129:27–37
- Ewers BE, Mackay DS, Tang J, Bolstad PV, Samanta SS (2008) Intercomparison of sugar maple (*Acer saccharum* Marsh.) stand transpiration responses to environmental conditions from the Western Great Lakes region of the United States. *Agric For Meteorol* 148:231–246
- Granier A, Loustau D, Bredá N (2000) A generic model of forest canopy conductance dependent on climate, soil water availability and leaf area index. *Ann For Sci* 57:755–765
- Haferkorn U (2000) Größen des Wasserhaushaltes verschiedener Böden unter landwirtschaftlicher Nutzung im klimatischen Grenzraum des Mitteldeutschen Trockengebietes, Ergebnisse der Lysimeterstation Brandis. Dissertation, University of Göttingen
- Hall RL, Allen SJ, Rosier PTW, Smith DM, Hodnett G, Roberts JM, Hopkins R, Davies HN (1996) Hydrological effects of short rotation energy coppice. Final report to ETSU. Institute of Hydrology, Wallingford
- Hall RL, Allen SJ, Rosier PTW, Hopkins R (1998) Transpiration from coppiced poplar and willow measured using sap-flow methods. *Agric For Meteorol* 90:275–290
- Hinckley TM, Brooks JR, Čermák J, Ceulemans R, Kučera J, Meinzer FC, Roberts DA (1994) Water flux in a hybrid poplar stand. *Tree Physiol* 14:1005–1018
- Jug A, Hoffmann-Schielle C, Makeschin F, Rehfuess KE (1999) Short rotation plantations of balsam poplars, aspen and willows on former arable land in the Federal Republic of Germany. II. Nutritional status and bioelement export by harvest of shoot axes. *For Ecol Manage* 121:67–83
- Kelliher FM, Leuning R, Raupach MR, Schulze ED (1995) Maximum conductances for evaporation from global vegetation types. *Agric For Meteorol* 73:1–16
- Kim HS, Oren R, Hinckley TM (2008) Actual and potential transpiration and carbon assimilation in an irrigated poplar plantation. *Tree Physiol* 28:559–577
- Koenker R (2005) Quantile regressions. *Econometric Society Monographs* 38. Cambridge University Press
- Kučera J, Čermák J, Penka M (1977) Improved thermal method of continual recording the transpiration flow rate dynamics. *Biol Plant* 19:413–420
- Levia DF, Frost EE (2003) A review and evaluation of stem flow literature in the hydrologic and biogeochemical cycles of forested and agricultural ecosystems. *J Hydrol* 274:1–29
- 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. *Biomass Bioenergy* 31:460–468
- Lyr H (1996) Effect of the root temperature on growth parameters of various European tree species. *Ann Sci For* 53:317–323
- Meiresonne L, Nadezhkina N, Čermák J, Van Slycken J, Ceulemans R (1999) Measured sap flow and simulated transpiration from a poplar stand in Flanders (Belgium). *Agric For Meteorol* 96:165–179
- Mellander PE, Bishop K, Lundmark T (2004) The influence of soil temperature on transpiration: a plot scale manipulation in a young Scots pine stand. *For Ecol Manage* 195:15–28
- Mellander PE, Stähli M, Gustafsson D, Bishop K (2006) Modelling the effect of low soil temperatures on transpiration by Scots pine. *Hydrol Processes* 20:1929–1944
- Monclus R, Dreyer E, Villar M, Delmotte FM, Delay D, Petit JM, Barbaroux C, le Thiec BC, Brignolas F (2006) Impact of drought on productivity and water use efficiency in 29 genotypes of *Populus deltoides* × *nigra*. *N Phytologist* 169:765–777
- Oren R, Sperry JS, Katul GG, Pataki DE, Ewers BE, Phillips N, Schäfer KVR (1999) Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant Cell Environ* 22:1515–1526
- Phillips N, Oren R (1998) A comparison of daily representations of canopy conductance based on two conditional time averaging methods and the dependence of daily conductance on environmental factors. *Ann Sci For* 55:217–235
- Poyatos R, Llorens P, Gallart F (2005) Transpiration of montane *Pinus sylvestris* L. and *Quercus pubescens* Willd. forest stands measured with sap flow sensors in NE Spain. *Hydrol Earth Syst Sci* 9:493–505
- Pregitzer KS, King JS, Burton AJ, Brown S (2000) Responses of tree fine roots to temperature. *N Phytologist* 147:105–115
- Richter D (1995) Ergebnisse methodischer Untersuchungen zur Korrektur des systematischen Meßfehlers des Hellmann-Niederschlagsmessers. *Berichte des Deutschen Wetterdienstes* 194, Offenbach
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Schwärzel K, Menzer A, Clausnitzer F, Spank U, Häntzschel J (2009) Soil water content measurements deliver reliable estimates of water fluxes: a comparative study in a beech and a spruce stand in the Tharandt forest. *Agric For Meteorol* 149:1994–2006
- Souch CA, Stephens W (1998) Growth, productivity and water use in three hybrid poplar clones. *Tree Physiol* 18:829–835
- Stephens W, Hess T, Knox J (2001) Review of the effects of energy crops on hydrology. Report to MAFF. Institute of Water and the Environment, Cranfield University, Silsoe
- Tatarinov FA, Kučera J, Cienciala E (2005) The analysis of physical background of tree sap flow measurement based on thermal methods. *Measurement Sci Technol* 16:1157–1169
- Volk TA, Verwijst T, Tharakan PJ, Abrahamson LP, White EH (2004) Growing fuel: a sustainability assessment of willow biomass crops. *Front Ecol Environ* 2(8):411–418
- Zalesny RS, Hall RB, Bauer EO, Riemenscheider DE (2005) Soil temperature and precipitation affect the rooting ability of dormant hardwood cuttings of populus. *Silvae Genetica* 54(2): 47–58
- Zhang H, Morison JIL, Simmonds LP (1999) Transpiration and water relation of poplar trees growing close to the water table. *Tree Physiol* 19(9):563–573