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Disturbances in European beech water relation during an extreme drought

Marianne Peiffer · Nathalie Bréda · Vincent Badeau · André Granier

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Abstract

• **Context** In the context of a probable increase in intensity and frequency of extreme summer drought events, a better understanding of the key processes involved in water relations is needed to improve the theoretical foundations of predictive process-based models.

• **Aims** This paper aims to analyse how temperate deciduous trees cope with water shortage.

• **Methods** The exceptional summer drought of 2003 in Europe provided an opportunity to monitor stomatal conductance and twig water potential in European beech (*Fagus sylvatica* L.) at predawn and midday and to analyse variations with respect to leaf height within the canopy. By comparing our field measurements of twig water potential to values found in the literature, we confirmed the strong impact of soil water shortage on crown water relations.

• **Results** This paper shows that (1) the vertical gradient of stomatal conductance within the crown disappeared under extreme soil water depletion; (2) at maximum drought intensity, predawn twig water potential (ψ_{pd}) reached -2.3 MPa at a

height of 14 m in the crown and -2.0 MPa at a height of 10 m. The significant differences in ψ_{pd} between the two measurement heights in the canopy may be due to night transpiration; (3) there was a close relationship between predawn twig water potential and relative extractable soil water; (4) as drought conditions intensified, there was a close relationship between canopy radiation interception and predawn water potential, as estimated daily from relative extractable soil water.

Keywords *Fagus sylvatica* · Stomatal conductance · Leaf water potential · Soil water deficit · Crown position · Seasonal pattern

1 Introduction

The water potential gradient between the soil, the tree and the atmosphere allows water to be transported through the xylem elements in trees. This thermodynamic process is beneficial for trees, although when xylem water potential exceeds the maximum capillary pressure sustainable without air entry (Cochard 2006), xylem embolism results (Sperry and Tyree 1988). Evidence that stomatal closure avoids xylem embolism has been reported for contrasting tree species (Jones and Sutherland 1991; Bréda et al. 1993a; Lu et al. 1996). On the other hand, experimental data demonstrating that stomatal aperture is driven by solar radiation, air vapour pressure deficit, temperature and extractable soil water is also well established (Bréda et al. 1993b; Kutsch et al. 2001; Herbst 1995). Many studies have also reported that, as a rule, leaf position within the crown determines physiological and anatomical leaf traits (Aussenac and Ducrey 1977). In European beech trees, stomatal conductance increases from the base to the top of the crown (Aranda et al. 2000, Cochard et al. 1999, Herbinger et al. 2005; Lemoine et al. 2002a; Wieser et al. 2003), whilst diurnal leaf water potential decreases (Aranda

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Contribution of the co-authors Marianne Peiffer: Writing the paper (75 %), field work (100 %), designing part of the project (50 %), running part of the data analysis (50 %).

Nathalie Bréda: Designing part of the project (50 %) and supervising the project (100 %).

Vincent Badeau: Running part of the data analysis (25 %).

André Granier: Running part of the data analysis (25 %), writing the paper (25 %) and coordinating the research project (100 %).

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et al. 2000; Lemoine et al. 2002a, b). Leaf morphology and leaf orientation also show adaptations: leaf mass area increases from the base to the top of the crown (Peiffer 2005; Montpied et al. 2009), whilst leaf angle becomes more vertical (Planchais and Sinoquet 1998). However, much less is known about how transpiration regulation relates to soil and plant hydraulic properties, in particular with respect to leaf position in the crown. Above all, little is known about the spatial variation of stomatal conductance in crown leaves under extreme soil water depletion.

This work aims to investigate the effects of an exceptionally severe summer drought event on gas exchange and water relations at the tree level in mature *Fagus sylvatica*. We focused on water stress levels (predawn and midday water potentials) experienced by the trees and compared these levels with those published in the literature. Ecophysiological tree responses were analysed during the soil water deficit increase and synchronisms between them were analysed, with special attention being paid to the variability of water relations within crowns. We tested the strength of the thermodynamic equilibriums under extreme soil water shortage: (1) whether microclimatic determinism changes stomatal conductance depending on different heights in the crowns and (2) whether predawn twig water potential is constant within tree crowns. In addition, a relationship between predawn water potential and relative extractable soil water (REW) was established. Finally, the synchronism between water stress intensity (i.e. predawn twig water potential) and radiation interception during drought is analysed and discussed.

2 Materials and methods

2.1 Experimental site

The study was carried out on a CarboEurope experimental plot located in the state forest of Hesse, in Lorraine, in north-eastern France (48° 40' N, 7° 05' E, 300-m elevation). The stand is mainly (90 %) composed of naturally established European beech (*F. sylvatica* L). When the study was carried out in 2003, the trees were on average 37 years old, stand density was 3,186 stems/ha, stand basal area was 25.4 m²/ha and leaf area index was 7.6, as measured by litter collection. The soil type is a luvic cambisol with local stagnic tendencies (WRB 2006). Clay content ranged from 25 to 35 % within the 0–100-cm depth layer and was about 40 % below 100 cm (see Granier et al. 2000 for a detailed site description).

2.2 Site equipment

For ecophysiological measurements, a scaffolding tower (15-m high) with platforms at 10, 12 and 14 m above the ground allowed access to the canopy of five beech trees.

Meteorological data were collected above the canopy (at a height of 22 m) with a weather station composed of a pyranometer (CMP6, Kipp & Zonen, Netherlands), a net radiometer (CNR1, Kipp & Zonen, Netherlands), a ventilated psychrometer with pt-100 platinum sensors (model INRA, France), a rain gauge (model ARG 100, Campbell Scientific, Logan, USA), an anemometer (Vector Instruments, UK) and a sunshine pyranometer measuring total and diffuse photosynthetic photon flux density (PPFD) (model BF3, Delta-T Devices, UK). Meteorological data were logged every 10 s with a datalogger (Model CR7, Campbell Scientific, France) and 30-min averages were stored. Near the investigated trees, the vertical gradient of water vapour in the air was measured half-hourly with an IRGA (Li- 6262, Li-Cor) at heights of 0.2, 0.7, 2.0, 5.2, 10.4 and 22.0 m.

The radiation intercepted by the trees was calculated from global radiation measurements (wavelength from 400 to 2,200 nm) taken above and below the canopy. Below-canopy global radiation was measured using three 1-m-long tubular solarimeters (Delta-T Device, UK) located 1 m above the ground.

Global radiation interception (I_n) was calculated as:

$$I_n = 1 - \left(\frac{I_z}{I_0} \right) \quad (1)$$

Where I_z =below-canopy irradiation at noon and I_0 =incoming irradiation at noon.

Litter fall was assessed from a periodic collection of leaves in 45 0.25-m² litter traps installed in the experimental plot.

2.3 Ecophysiological measurements

A portable gas exchange chamber LI-6200 (LI-COR Inc., Lincoln, NE, USA) was used to measure stomatal conductance (gs), photosynthetic photon flux density (PPFD), air temperature and vapour pressure deficit (vpd), under ambient conditions. Leaf gas exchange was measured on 7 days during the 2003 growing season: 26 May, 28 May, 12 June, 24 July, 8 August, 21 August and 5 September, i.e., respectively, DOY 146, 148, 163, 205, 220, 233 and 248. Measurements were taken on the five trees accessible from the scaffolding platforms and were carried out on the same leaves throughout the growing season. At 14 m in height, all the leaves sampled on the five investigated trees were fully exposed to the sun since the trees (16 m in height on average) belonged to the dominant or co-dominant crown class (Granier et al. 2000). One diurnal course usually consisted of 108 measurements (3 heights × 12 leaves with 3 replicates performed every 2 h from approximately 0800 to 1420 UT), except on DOY 146 (44 measurements) and on DOY 148 (96 measurements).

Twig water potential was measured with a Scholander-type pressure chamber on current-year twigs bearing a single undamaged leaf. We checked that these measurements carried out on twigs were similar to measurements obtained on petioles. Twigs were randomly collected from three of the five trees used for leaf gas exchange measurements and two to four replicates were performed in the upper, sun-exposed crown (14 m above the ground) and in the lower, shaded crown (10 m above the ground). The two other trees, of similar height, were too far from the scaffolding platform to permit satisfactory sampling for twig water potential measurements. Predawn twig water potential was measured before sunrise (between 0200 and 0400 UT) on 8 days starting with DOY 205, whilst midday twig water potential was measured on the last 4 days of the leaf gas exchange campaign. In order to establish a relationship between predawn water potential and soil water content over a large range of soil water availability conditions, additional measurements performed in 1996 (medium dry year) and in 2008 (wet year) on dominant and co-dominant trees on the same plot were also included in our study. In 1996 and 2008, water potential was measured on five and three trees, respectively, with 2 to 3 replicates per tree, at 10 m in height. To better compare soil water content and water potential measured at different crown heights, the gravitational component of water potential was subtracted (0.01 MPa m^{-1}) from the measurements.

2.4 Soil water content estimate

Soil water content was calculated daily using the BILJOU© water balance model (Granier et al. 1999), which was calibrated for a large range of tree species, soil types and climates. This generic model calculates elementary water fluxes: (i) transpiration, which is a function of potential evapotranspiration (as calculated with the Penman formula), leaf area index (LAI) and relative soil extractable water (REW); (ii) rainfall interception, which is a function of incident rainfall and LAI; and (iii) understory evapotranspiration, calculated from the radiation transmitted through the canopy and from available water in the upper soil layer. We had previously checked that this model accurately simulated soil water content variations in various European forests, especially during drought intensification (Granier et al. 2007). The model uses (i) four soil properties in each of six soil layers encompassing the whole rooting zone from 0 to 160 cm in depth: maximum extractable soil water, soil humidity at the permanent wilting point, bulk density and proportion of fine roots and (ii) three canopy parameters: maximum leaf area index, budburst and leaf fall dates.

Soil water content was expressed in terms of relative extractable water (REW) in the root zone, according to Granier et al. (1999), as:

$$REW_t = (W_t - W_{\min}) / (W_{\max} - W_{\min}) \quad (2)$$

where W_t is the actual soil water content (in mm, at time t); W_{\max} is the maximum content (at field capacity, i.e. at soil water matric potential = -0.03 MPa); and W_{\min} is the minimum content (at permanent wilting point, i.e. soil water matric potential = -1.6 MPa). Extractable soil water was estimated as 175 mm over a depth of 1.6 m (Granier et al. 2008).

2.5 Modelling twig water potential

Twig water potential was related to relative extractable soil water (REW) with a non-rectangular hyperbola, where a , b and c were the fitted coefficients:

$$\psi_{wp} = \frac{a + b \times REW - \sqrt{((a + b) \times REW^2 - 2.8 \times a \times b \times REW)}}{1.4} + c \quad (3)$$

We used the Statistical Analysis System (SAS) non linear regression procedure (PROC NLIN) with the Marquardt algorithm to check that this function gave the best fits compared to other functions.

2.6 Data analysis

An analysis of variance (SAS GLM Procedure) was performed according to the following model:

$$Y = \text{height} + \text{DOY} + \text{height} \times \text{DOY} + e \quad (4)$$

where Y is the dependent variable (photosynthetic photon flux density, air temperature, vapour pressure deficit, stomatal conductance or twig water potential); height is the effect of the crown heights (three levels 10, 12 and 14 m above ground, or two levels (10 and 14 m) when Y = twig water potential); DOY is the date effect (seven levels: DOY 146, 148, 163, 205, 220, 233, 248.) and; e is the residual; height \times DOY is the interaction between height and DOY. To determine the significant differences in Y amongst the three heights at different dates, a Tukey test with a confidence level of 95 % was applied. All statistical analyses were performed with SAS version 9.1 (SAS Institute, 2002–2003, Cary, North Carolina, USA).

3 Results

3.1 Seasonal progression of edaphic drought and impact on tree water potential

The summer of 2003 was characterised by exceptionally high air temperatures and vapour pressure deficits, with daily mean values of 30 °C and 29.5 hPa, respectively, in mid-August. The average June to August air temperature was 20.3 °C, i.e. 4 °C more than the previous 30-year average. Average vapour pressure deficit for this 3-month period was 16.3 hPa, i.e. 11 hPa more than the long-term average. The seasonal progression of soil water depletion corresponded to a continuous decrease in REW, which was calculated with the BILJOU water balance model (Figs. 1 and 2). REW was lower than 0.4, i.e. the minimum threshold for stomatal closure in tree species (Granier et al. 1999), from DOY 178 until the beginning of leaf fall, which occurred on DOY 300 (Fig. 2). Hence, the soil water deficit in 2003 lasted 122 days. As a result of this progressive soil water depletion, the predawn water potential of the beech trees (ψ_{pd}) decreased during the same period from ca. -1.00 MPa (DOY 205, Fig. 1) to -2.04 MPa at 10 m in height (DOY 239) and to -2.28 MPa at 14 m in height (DOY 225). From DOYs 205 to 248, ψ_{pd} at 14 m in height was always significantly lower than at 10 m in height; furthermore, the water potential gradient was large, varying from 0.19 to 0.54 MPa (Fig. 1). Twig water potential measured at midday (ψ_{md}) dropped to extremely negative values: down to -2.88 MPa at 14 m in height on DOY 233 (Fig. 2). A few days later (DOY 239), the soil was partially re-watered following several light rains. This resulted in temporary increases in ψ_{pd} , though REW did not significantly increase (Figs. 1 and 2, open circles, DOYs 215, 233 and 248). Finally, after DOY 274, REW progressively increased until the end of the growing season.

In order to analyse how tree water potential responds to soil water content, we fitted a non-rectangular hyperbola (Eq. 3) between ψ_{pd} (1996, 2003 and 2008 data) and REW, excluding data measured soon after rainfall events. For the year 2003, we used measurements performed at 10 m in height. A strong relationship was found (Fig. 2), the fitted coefficients being $a=2.769$, $b=15.997$, $c=-2.604$ with $r^2=0.98$ ($P<0.0001$)

Modelled predawn water potential variations ($\psi_{pd, \text{modelled}}$) are shown in Fig. 2 together with REW measured during the growing season. Between DOYs 205 and 248, both REW and $\psi_{pd, \text{modelled}}$ showed a general decreasing trend, with some short-lasting increases just after light rain events.

3.2 Seasonal variations in stomatal conductance and twig water potential

At the beginning of spring (DOY 146 and 148), the rather low values of stomatal conductance (g_s) were probably due to

incomplete leaf development (Fig. 2). On DOY 163, as REW was above the regulation threshold of 0.4, stomatal conductance reached the highest values observed during the whole sampling period, i.e., $146.4 \text{ mmol m}^{-2} \text{ s}^{-1}$. Then, from DOY 205 to the end of the measurement campaign (DOY 248), when REW was below 0.4 and water potentials decreased sharply (ψ_{pd} to -2.04 MPa at 10-m height and ψ_{md} to -2.88 MPa at 14-m height), stomatal conductance was strongly and linearly reduced (Fig. 2), finally reaching $12.7 \text{ mmol m}^{-2} \text{ s}^{-1}$ ($r^2=0.99$; $P=0.0066$).

Vertical microclimatic gradients were observed on most sampling dates (Fig. 3). Generally, photosynthetic photon flux density (PPFD), air temperature (T_a) and vapour pressure deficit (VPD) increased with increasing height in the canopy. Stomatal conductance also showed vertical gradient at all sampling dates. On DOY 163, a large range of g_s values was observed according to the position of the leaves in the crown: 71.0, 128.3 and $240.0 \text{ mmol m}^{-2} \text{ s}^{-1}$ at respective heights of 10, 12 and 14 m (g_s at 12 m was about 53 % of the one at 14 m, whilst g_s at 10 m was about 30 % of the one at 14 m). Thereafter, from DOY 220 to 248, g_s values decreased strongly and were not statistically different amongst heights on any one sampling date, reaching on average 9.2, 17.3 and $26.5 \text{ mmol m}^{-2} \text{ s}^{-1}$ at heights of 10, 12 and 14 m, respectively.

3.3 Variations in canopy radiation interception

The seasonal course of radiation interception (In) exhibited three superimposed patterns, corresponding to different time scales (Fig. 4): (i) a clear low-frequency variation linked to the seasonal phenological cycle, with In increasing from budburst (DOY 113) to complete leaf development (DOY 148), then stabilising thereafter; (ii) medium-frequency variations lasting from 29 to 38 days (Fig. 4); (iii) high-frequency (day to day) variations, probably resulting from rapid changes in light intensity and quality (diffuse vs. direct or occurrence of sun flecks).

At the beginning of the measurement period, In rapidly increased (DOYs 122 to 148) and then stabilised until DOY 181. This period corresponded to leaf area development followed by a period of maximum LAI without soil water depletion. From DOYs 184 to 212, we observed (Fig. 4) surprising synchronism between In and $\Psi_{pd, \text{modelled}}$ variations. Peaks in $\Psi_{pd, \text{modelled}}$ occurring on DOYs 184, 197, 208 and 211 coincided to In peaks on the same days or with a 1-day time lag: DOYs 184, 198, 208 and 212. From DOYs 212 to 249, a third phase with two sharp drops in In occurred. First, a regular decrease was noticed from DOYs 212 to 240, whilst during the same period, $\Psi_{pd, \text{modelled}}$ also fell regularly to reach the minimum value of -2.2 MPa on DOY 239. This parallelism between radiation interception and $\psi_{pd, \text{modelled}}$ is clearly shown in Fig. 4, the fitted relationship being curvilinear ($r^2=0.81$). Then, a second decline occurred and $\Psi_{pd, \text{modelled}}$ dropped to

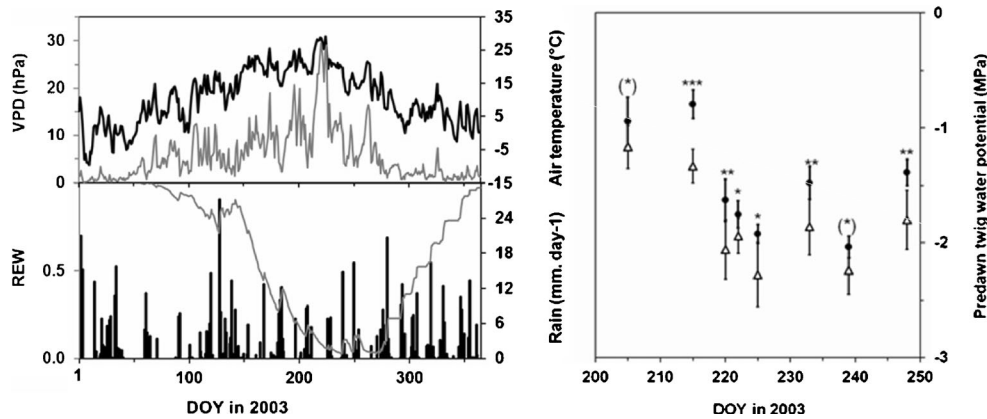


Fig. 1 Upper left variation in above-canopy daily vapour pressure deficit (VPD, grey line) and air temperature (black line) during the 2003 growing season. Lower left daily rainfall (black bars) and time course of the relative extractable soil water (REW, solid grey line) during 2003. Right seasonal variations in predawn twig water potential at 10 m in height

(filled black circles) and 14 m in height (open triangles) from DOYs 200 to 250. Each data point is the mean of 7 to 10 measurements. Vertical bars represent 95 % confidence intervals and asterisks indicate statistically different means between heights for a same sampling date: (*) $P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

-2.1 MPa on DOY 249. This 38-day period was particularly warm, with an average air temperature of 24 °C (± 6 °C). PPFD was also high over this period, the average being $1,272 \pm 254 \text{ mmol m}^{-2} \text{ s}^{-1}$ (between 0800 to 1430 UT, see Fig. 3). During this period, an abnormal fall of green leaves occurred, reaching $1.74 \text{ m}^2 \text{ m}^{-2}$.

4 Discussion

4.1 Beech trees experienced extreme water stress in summer 2003

The predawn water potential we recorded at the height of the drought in 2003 was comparable to values measured the same

year by Bréda et al. (2004) in adult beech trees growing in another forest in Lorraine (N–E France). In Lorraine, predawn water potentials for beech were lower than in other studies (Supplemental Table S1).

Midday water potential (ψ_{md}) dropped to extremely negative values (-2.88 at 14 m in height, Fig. 2). In our study, the beech trees experienced the lowest ψ_{md} levels ever published, except for one study carried out by Raftoyannis and Radoglou (2002) in Greece, i.e., the southern limit of European beech, during the 1998 drought (see Supplemental Table S1).

4.2 Stomata opening during night?

Contrary to what could have been expected, we observed significant differences in predawn twig water potential values

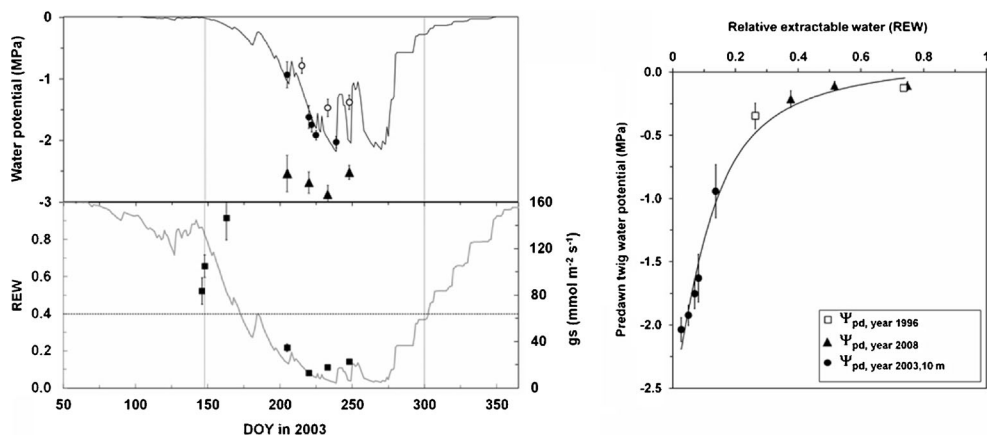
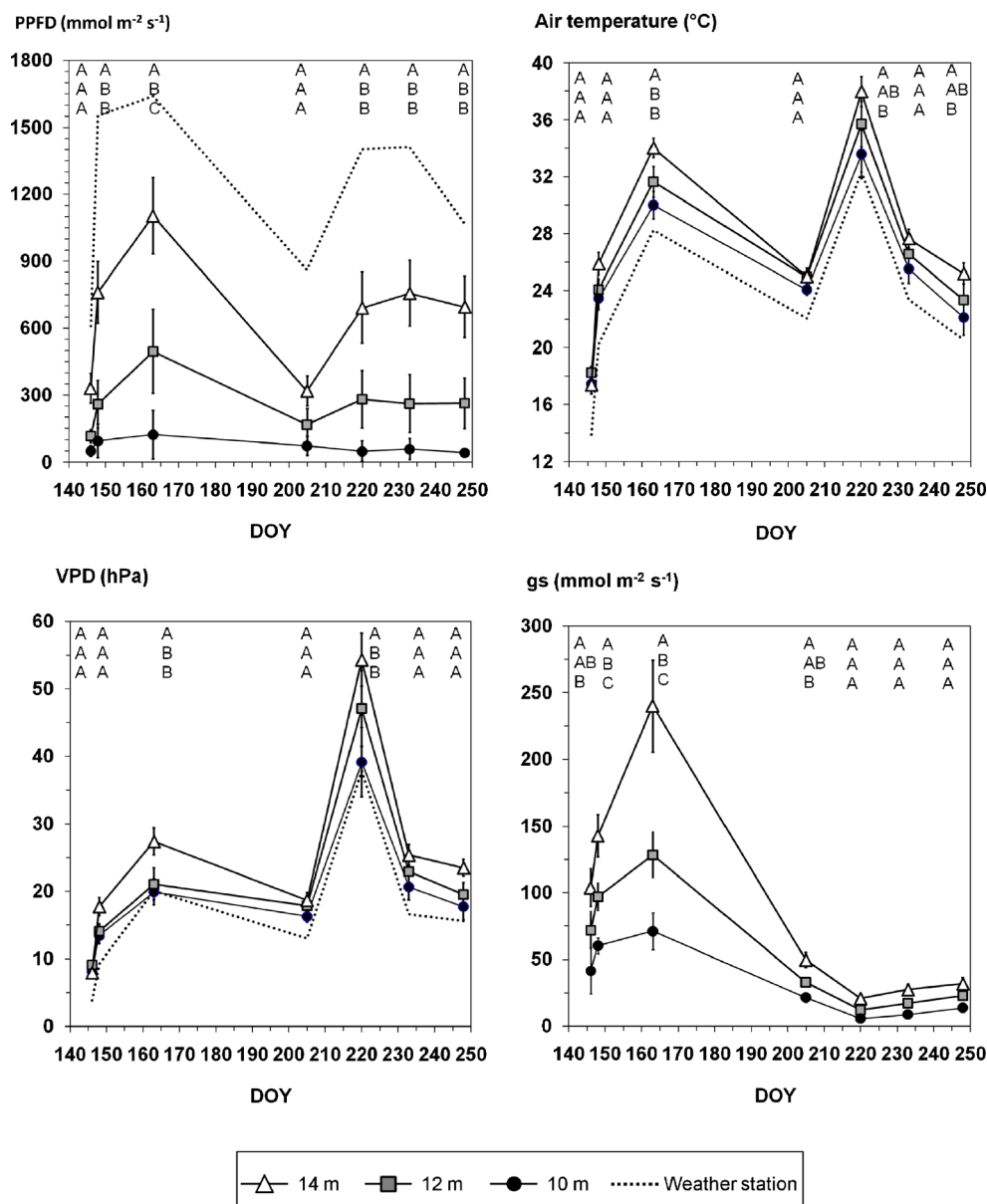


Fig. 2 Upper left predawn twig water potential at 10 m in height, without rainfall 2 days before measurements (filled circles) and with rainfall 2 days before measurements (open circles); midday twig water potential measured at 14 m in height (black triangles); and modelled predawn water potential from modelled REW (solid black line) during the 2003 growing season. Lower left daily mean stomatal conductance (gs, black squares) and time course of the modelled relative extractable soil water (REW, solid grey line) during the 2003 growing season. The vertical bars

represent 95 % confidence intervals. The two dashed vertical lines delimit the period between full leaf expansion and the beginning of leaf fall (DOYs 148 to 300). The dashed horizontal line indicates the REW value of 0.4. Right, predawn twig water potential as a function of relative extractable water (REW) in European beech trees. Ψ_{pd} in 2003 at 10 m in height ($\Psi_{\text{pd}, 10\text{m}}$, black circles), Ψ_{pd} in 1996 ($\Psi_{\text{pd}, \text{year } 1996}$, open squares) and Ψ_{pd} in 2008 ($\Psi_{\text{pd}, \text{year } 2008}$, black triangles). Values are fitted against REW. The vertical bars show the 95 % confidence intervals

Fig. 3 Seasonal variations in photosynthetic photon flux density (PPFD), air temperature, air vapour pressure deficit (VPD) and stomatal conductance (g_s) measured with the gas exchange chamber at the three measurement heights in the beech crowns: 10 m (filled circles), 12 m (grey squares) and 14 m (open triangles). Each data point is the mean of 8 to 36 measurements between 0800 and 1420 UT; vertical bars show the 95 % confidence intervals. The same letters indicate that means are not statistically different between heights for a same sampling date at $P < 0.05$. Concurrent variations in PPFD, air temperature and VPD measured at the weather station above the canopy are also shown (dashed line)



for 2003 according to sampling height in the tree crown. Such phenomenon can be explained by night transpiration, especially in the upper part of the crowns, since the stomata are partly open under non-saturated air conditions. This phenomenon has been reported in several studies (Dawson et al. 2007), including on 3-year-old *Fagus grandifolia* (Marks and Lechowicz 2007) and on adult *F. sylvatica* (Seibt et al. 2007; Samson et al. 2003). During the period of strongest water stress (DOYs 200 to 235), when predawn water potential measurements were performed, the air was not saturated and air vapour pressure deficit was 5.6 hPa on average above the canopy. Water vapour concentrations in the air were on average $0.5 \text{ mmol mol}^{-1}$ lower at a height of 22 m than at 10 m during the same period.

Very dry air conditions induce significant night transpiration, especially in the upper part of the crown, thus resulting in a vertical water potential gradient.

This finding underlines the need to measure predawn leaf water potential when no transpiration conditions are present.

4.3 Stomatal conductance response to microclimate and soil water shortage

In this study, we followed the course of stomatal conductance at different crown heights under both well-watered and low soil water conditions (Fig. 3). At leaf scale, we showed that stomata of European beech were more responsive to the microclimatic environment (radiation and vapour pressure

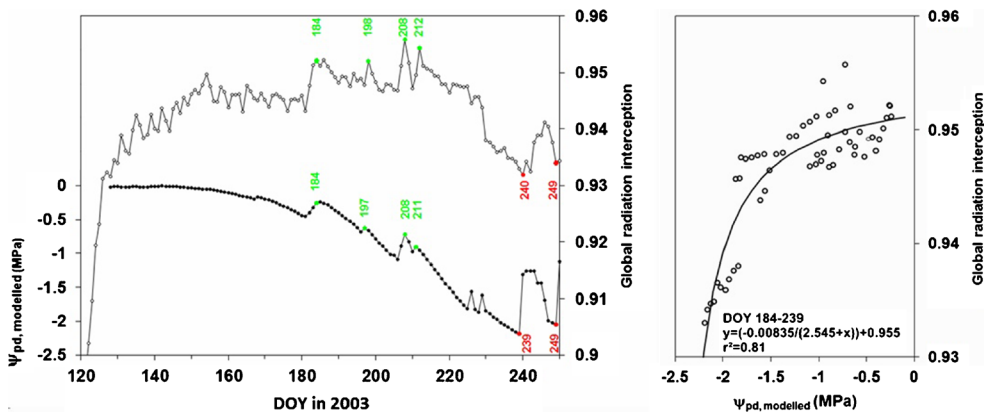


Fig. 4 *Left*, seasonal course of daily global radiation interception and modelled predawn water potential ($\Psi_{pd, modelled}$) from DOYs 120 to 250. DOY associated with notable peaks are shown in *green* and those associated with slumps are in *red*. *Right*, relationship between global radiation

interception by the beech canopy and modelled predawn water potential ($\Psi_{pd, modelled}$) from DOYs 184 to 239, i.e. the period of increasing soil water shortage

deficit) under high water availability ($REW > 0.4$) than under water stress ($REW < 0.4$, since DOY 178) conditions. Similar behaviour had previously been reported at the canopy level for canopy conductance related to water vapour variation (Granier et al. 2000, 2002, 2007; and Bréda et al. 2006). In our study, under high soil water availability, stomatal conductance values were significantly different for sun-exposed leaves located at 14-m height and shaded leaves at 10 m = 240 vs. 71 $\text{mmol m}^{-2} \text{s}^{-1}$, respectively. This range of stomatal conductance is in agreement with that reported in other studies = 218.2 and 33.6 $\text{mmol m}^{-2} \text{s}^{-1}$ in Cochard et al. (1999), 115.5 and 36 $\text{mmol m}^{-2} \text{s}^{-1}$ in Wieser et al. (2003) and 100 and 25 $\text{mmol m}^{-2} \text{s}^{-1}$ in Herbinger et al. (2005). On the other hand, when soil water was greatly depleted, i.e. $REW < 0.1$ (DOY 220), we found no significant difference in stomatal conductance according to height and no more day-to-day variation thereafter. However, even under the most severe water stress conditions, stomatal conductance was not null; the studied beech trees progressively approached the threshold of water stress-induced cavitation, which is around -2 MPa in the shade and -3 MPa in sun-exposed branches (Lemoine et al. 2002b). Bréda et al. (2006) also pointed out a similarly limited canopy response when $REW < 0.1$. At such strong water stress level, besides maintaining safety leaf water status and protecting against cavitation, extreme stomatal closure likely leads to high leaf temperature.

4.4 Leaf adaptation to severe drought: current assumptions

At the canopy level, the most visible response to drought was a *In* reduction between DOYs 212 and 240. Simultaneously, an important LAI loss of 1.74 $\text{m}^2 \text{m}^{-2}$ occurred, explaining partially this *In* decrease. After this period of strong water stress during August 2003, a partial recovery of radiation interception took place on DOY 240 (Fig. 4), whilst no leaf regrowth was observed during this period in the plot. This

recovery coincided exactly to the rapid predawn water potential increase after a short rain episode. We propose two hypotheses to explain the link between radiation interception and predawn water potential:

- (i) A decrease in leaf water potential with increasing drought severity generally induces water content variations in living plant tissues, especially in leaves. Therefore, variations in radiation interception may reflect leaf water content changes. This mechanism is reversible, as long as the water content does not fall below a critical level of relative water content, which would lead to irreversible wilting and leaf abscission. It is known that leaf optical properties vary with changes in water content (Baldini et al. 1997). Using PAR and near infrared measurements, the authors found that transmittance decreased in strongly dehydrated olive and peach tree leaves. The increased transmittance that we observed in our study can therefore not be attributed to changes in leaf water content.
- (ii) According to the literature, leaf angle may vary markedly in plants, allowing the plant to adjust to a given environment. A first mechanism, called heliotropism, consists in a rapid and reversible leaf movement linked to daily water potential variations. This often occurs in plants of the Fabaceae family, in annual plants (e.g. *Lupinus arizonicus*—Ehleringer and Werk 1986), woody vines (e.g. *Pueraria lobata*—Forseth and Teramura 1986) and trees (e.g. *Robinia pseudoacacia*—Arena and Ghia 2008; and *Millettia ferruginea*—Gindaba et al. 2004). In other families, *Arbutus unedo* (Ericaceae) leaves also move diurnally (Gratani and Ghia 2002). Some authors (Comstock and Mahall 1985) have related temporal changes in leaf angle to predawn water potential variation, showing a steeper angle for lower predawn water potential. This was demonstrated for two evergreen shrubs in the Californian chaparral, *Ceanothus*

megacarpus and *Ceanothus crassifolius*, where linear regression models relating leaf inclination to predawn xylem potential yielded high coefficients of determination ($r^2=0.61$ and $r^2=0.87$). Werner et al. (1999) also showed significant leaf angle changes with contrasting water availability periods, as assessed by predawn water potentials for semi-deciduous shrubs in the Mediterranean bush, *Cistus albidus* and *Cistus monspeliensis*. In the Fagaceae family, changes in leaf angle were shown in *Quercus ilex* (Gratani and Bombelli 1999) and *Quercus coccifera* (Werner et al. 1999). The main ecophysiological advantage of a shift to a steeper leaf inclination under dry conditions is a reduction in radiation absorption and therefore in leaf temperature and water loss. Changes in leaf angle may play a role in metabolic protection because they would occur when stomatal conductance could not (i.e. when $REW < 0.1$). The ability of European beech to cope with the severe drought in 2003 at our experimental site could partly result from strong stomatal regulation combined with a reversible change in leaf inclination. More research is needed under controlled conditions to test these new hypotheses.

5 Conclusion

The adult European beech trees in our study showed lower values of predawn water potential in Lorraine (N–E France) during summer 2003 than other previous studies. No significant within-crown differences in stomatal conductance were detected under very strong water depletion. Stomatal closure was almost complete within the crowns; therefore stomatal conductance could not adjust any further to the stressful microclimatic conditions and was no longer able to protect the leaves from high irradiance and air temperature, particularly in the upper crown layer.

We also unexpectedly found that radiation interception varied with predawn water potential under water stress conditions. We suppose that this mechanism was related to changes in leaf angle distribution, an adaptive adjustment to limit radiation absorption under very strong water depletion when stomatal conductance has failed.

Our finding that twig predawn water potentials differed according to the two crown layers reveals that night transpiration, at least at a height of 14 m, is a response to atmospheric drought. Concomitant edaphic and atmospheric drought conditions severely impacted the thermodynamic water potential equilibrium in our study trees.

Finally, the close relationship we found between twig predawn water potential and relative extractable water could be a basis for useful tools to estimate tree water potential from soil water content. This relationship should be tested at other sites.

References

- Aranda I, Gil L, Pardos JA (2000) Water relations and gas exchange in *Fagus sylvatica* L. and *Quercus petraea* (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. *Trees* 14:344–352
- Arena C, Ghia E (2008) Paraheliotropism in *Robinia pseudoacacia* L.: an efficient strategy to optimise photosynthetic performance under natural environmental conditions. *Plant Biol* 10:194–201
- Aussenac G, Ducrey M (1977) Étude bioclimatique d'une futaie feuillue (*Fagus sylvatica* L. et *Quercus sessiliflora* Salisb) de l'est de la France. I. Analyse des profils microclimatiques et des caractéristiques anatomiques et morphologiques de l'appareil foliaire. *Ann For Sci* 34: 265–284. <http://hal.archives-ouvertes.fr/hal-00882157>
- Baldini E, Facini O, Nerozzi F, Rossi F, Rotondi A (1997) Leaf characteristics and optical properties of different woody species. *Trees* 12: 73–81
- Bréda N, Cochard H, Dreyer E, Granier A (1993a) Field comparison of transpiration, stomatal conductance and vulnerability to cavitation of *Quercus petraea* and *Quercus robur* under water stress. *Ann For Sci* 50: 571–582. <http://hal.archives-ouvertes.fr/hal-00882868>
- Bréda N, Cochard H, Dreyer E, Granier A (1993b) Water transfer in a mature oak stand (*Quercus petraea*): seasonal evolution and effects of a severe drought. *Can J For Res* 23:1136–1143
- Bréda N, Granier A, Aussenac G (2004) La sécheresse de 2003 dans le contexte climatique des 54 dernières années: analyse écophysiological et influence sur les arbres forestiers. *Rev For Fr LVI* 2:109–131
- Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann For Sci* 63: 625–644. <http://hal.archives-ouvertes.fr/hal-00884012>
- Cochard H (2006) Cavitation in trees. *C R Phys* 7:1018–1026
- Cochard H, Lemoine D, Dreyer E (1999) The effects of acclimation to sunlight on the xylem vulnerability to embolism in *Fagus sylvatica* L. *Plant Cell Environ* 22:101–108
- Comstock J, Mahall BE (1985) Drought and changes in leaf orientation for two California chaparral shrubs: *Ceanothus megacarpus* and *Ceanothus crassifolius*. *Oecologia* 65:531–535
- Dawson TE, Burgess SSO, Tu KP, Oliveira RS, Santiago LS, Fisher JB, Simonin KA, Ambrose AR (2007) Nighttime transpiration in woody plants from contrasting ecosystems. *Tree Physiol* 27:561–575
- Ehleringer J, Werk KS (1986) Modifications of solar-radiation absorption patterns and implications for carbon gain at the leaf level. In: Givnish TJ (ed) *On the economy of plant form and function*. Cambridge University Press, Cambridge, UK, pp 57–82
- Forseth IN, Teramura AH (1986) Kudzu leaf energy budget and calculated transpiration: the influence of leaflet orientation. *Ecology* 67: 564–571
- Gindaba J, Rozanov A, Negash L (2004) Response of seedlings of two Eucalyptus and three deciduous tree species from Ethiopia to severe water stress. *For Ecol Manag* 201:119–129
- Granier A, Bréda N, Biron P, Villetle S (1999) A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. *Ecol Model* 116:269–283
- Granier A, Biron P, Lemoine D (2000) Water balance, transpiration and canopy conductance in two beech stands. *Agric For Meteorol* 100: 291–308
- Granier A, Aubinet M, Epron D, Falge E, Gudmundsson J, Jensen NO, Kostner B, Matteucci G, Pilegaard K, Schmidt M, Tenhunen JD (2002) Deciduous forests: carbon and water fluxes, balances and ecophysiological determinants. In "Fluxes of Carbon, Water and Energy of European Forests" (Ed. Valentini R.), *Ecological Studies* 163: 55–70

- Granier A, Reichstein M, Bréda N, Janssens IA, Falge E, Ciais P, Grünwald T, Aubinet M, Berbigier P, Bernhofer C, Buchmann N, Facini O, Grassi G, Heinesch B, Ilvesniemi H, Keronen P, Knohl A, Köstner B, Lagergren F, Lindroth A, Longdoz B, Loustau D, Mateus J, Montagnani L, Nys C, Moors E, Papale D, Peiffer M, Pilegaard K, Pita G, Pumpanen J, Rambal S, Rebmann C, Rodrigues A, Seufert G, Tenhunen J, Vesala T, Wang Q (2007) Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agric For Meteorol* 143:123–145
- Granier A, Bréda N, Longdoz B, Gross P, Ngao J (2008) Ten years of fluxes and stand growth in a young beech forest at Hesse, North-eastern France. *Ann For Sci* 65: 704–715. <http://hal.archives-ouvertes.fr/hal-00883444>
- Gratani L, Bombelli A (1999) Leaf anatomy, inclination, and gas exchange relationships in evergreen sclerophyllous and drought semideciduous shrub species. *Photosynthetica* 37:573–585
- Gratani L, Ghia E (2002) Adaptive strategy at the leaf level of *Arbutus unedo* L. to cope with Mediterranean climate. *Flora* 197:275–284
- Herbinger K, Then C, Löw M, Haberer K, Alexous M, Koch N, Remele K, Heerdt C, Grill D, Rennenberg H, Häberle KH, Matussek R, Tausz M, Wieser G (2005) Tree age dependence and within-canopy variation of leaf gas exchange and antioxidative defence in *Fagus sylvatica* under experimental free-air ozone exposure. *Environ Pollut* 137:476–482
- Herbst M (1995) Stomatal behaviour in a beech canopy: an analysis of Bowen ratio measurements compared with porometer data. *Plant Cell Environ* 18:1010–1018
- Jones HG, Sutherland RA (1991) Stomatal control of xylem embolism. *Plant Cell Environ* 14:607–612
- Kutsch WL, Herbst M, Vanselow R, Hummelshøj P, Jensen NO, Kappen L (2001) Stomatal acclimation influences water and carbon fluxes of a beech canopy in northern Germany. *Basic Appl Ecol* 2:265–281
- Lemoine D, Cochard H, Granier A (2002a) Within crown variation in hydraulic architecture in beech (*Fagus sylvatica* L.): evidence for a stomatal control of xylem embolism. *Ann For Sci* 59:19–27
- Lemoine D, Jacquemin S, Granier A (2002b) Beech (*Fagus sylvatica* L.) branches show acclimation of xylem anatomy and hydraulic properties to increased light after thinning. *Ann For Sci* 59: 761–766. <http://hal.archives-ouvertes.fr/hal-00883666>
- Lu P, Biron P, Granier A, Cochard H (1996) Water relations of adult Norway spruce (*Picea abies* (L.) Karst) under soil drought in the Vosges mountains: whole-tree hydraulic conductance, xylem embolism and water loss regulation. *Ann For Sci* 53: 113–121. <http://hal.archives-ouvertes.fr/hal-00883036>
- Marks OM, Lechowicz MJ (2007) The ecological and functional correlates of nocturnal transpiration. *Tree Physiol* 27:577–584
- Montpied P, Granier A, Dreyer E (2009) Seasonal time-course of gradients of photosynthetic capacity and mesophyll conductance to CO₂ across a beech (*Fagus sylvatica* L.) canopy. *J Exp Bot* 60:2407–2418
- Peiffer M (2005) Parameterisation of the water balance and establishment of water and nutrient fluxes in lowland beech forests. PhD Thesis, École Nationale du Génie Rural, des Eaux et Forêts, Nancy, France, 135 p. (in French)
- Planchais I, Sinoquet H (1998) Foliage determinants of light interception in sunny and shaded branches of *Fagus sylvatica* (L.). *Agric For Meteorol* 89:241–253
- Raftoyannis Y, Radoglou K (2002) Physiological responses of beech and sessile oak in a natural mixed stand during dry summer. *Ann Bot* 89: 723–730
- Samson R, Steppe K, Lemeur R (2003) Branch sap flow monitored at several heights in the crown of beech and ash. *Plant Water Relations and sap flux measurements* (eds. R. Tognetti & A. Raschi), ISBN 88-900981-0-4, 35–50.
- Seibt U, Wingate L, Berry JA (2007) Nocturnal stomatal conductance effects on the $\delta^{18}\text{O}$ signatures of foliage gas exchange observed in two forest ecosystems. *Tree Physiol* 27:585–595
- Sperry JS, Tyree MT (1988) Mechanism of water stress-induced xylem embolism. *Plant Physiol* 88:581–587
- Werner C, Correia O, Beyschlag W (1999) Two different strategies of Mediterranean macchia plants to avoid photoinhibitory damage by excessive radiation levels during summer drought. *Acta Oecol* 20: 15–23
- Wieser G, Hecke K, Tausz M, Häberle KH, Grams TEE, Matussek R (2003) The influence of microclimate and tree age on the defence capacity of European beech (*Fagus sylvatica* L.) against oxidative stress. *Ann For Sci* 60: 131–135. <http://hal.archives-ouvertes.fr/hal-00883686>
- WRB (2006) World reference base for soil resources 2006. 2nd edition. World Soil Resources Reports No. 103. FAO, Rome. <http://www.fao.org>