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Original article

Water relations of adult Norway spruce (*Picea abies* (L) Karst) under soil drought in the Vosges mountains: water potential, stomatal conductance and transpiration

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Summary — The effects of soil water depletion on sap flow, twig water potential, stomatal and canopy conductance were analysed in 2 plots of a 30-year-old stand of Norway spruce. One was subjected to an imposed drought; the other was watered by irrigation. Predawn water potential in trees from the dry plot decreased to –1.2 MPa. In the watered plot, a low between-tree variability of sap flux density was observed, with maximum values of 1.2–1.9 $dm^3 \bullet dm^{-2} \bullet h^{-1}$, corresponding to about 0.5 $mm \bullet h^{-1}$. In the dry plot, sap flux density showed a higher variability, and decreased during the summer to a minimum midday value of 0.05 $dm^3 \bullet dm^{-2} \bullet h^{-1}$. Tree transpiration and stomatal conductance showed a strong reduction in association with drought development, during which the predawn water potential decreased from –0.4 to –0.6 MPa. Canopy conductance was calculated from the reverse of the Penman–Monteith equation assuming that vapour flux over the stand was equal to the estimated stand sap flow. Effects of climatic factors and drought on canopy conductance variations were taken into account in a multi-variable transpiration model.

transpiration / stomatal conductance / canopy conductance / water potential / drought / sap flow / *Picea abies*

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Abbreviations: Ψ_f: twig water potential (MPa); Ψ_{pd}, Ψ_m: predawn and diurnal minimal twig water potential (MPa), respectively; F_d: xylem sap flux density ($dm^3 \bullet dm^{-2} \bullet h^{-1}$); F: total xylem sap flow ($dm^3 \bullet h^{-1}$); SA: sapwood area (dm^2); T_w, T_d: transpiration of watered and dry plot ($mm \bullet h^{-1}$, $mm \bullet d^{-1}$), respectively; TM: maximal plot transpiration ($mm \bullet h^{-1}$, $mm \bullet d^{-1}$); g_s: stomatal conductance ($cm \bullet s^{-1}$); g_c: canopy conductance to water vapour ($cm \bullet s^{-1}$); VPD: vapour pressure deficit (Pa, hPa); R_g: global radiation ($W \bullet m^{-2}$).

Résumé — Relations hydriques chez l'épicéa commun (*Picea abies* (L) Karst) soumis à une sécheresse édaphique dans les Vosges : potentiel hydrique, conductance stomatique et transpiration. *Les effets du dessèchement du sol sur le flux de sève, le potentiel hydrique des rameaux, la conductance stomatique et du couvert ont été analysés dans 2 placeaux d'un peuplement d'épicéas âgés de 30 ans. L'un des placeaux a été soumis à une sécheresse par couverture du sol, le second ayant été irrigué. Le potentiel hydrique de base des arbres du placeau sec est descendu jusqu'à –1,2 MPa. Dans le placeau irrigué, une faible variabilité de la densité de flux de sève a été observée entre les arbres mesurés, les maxima étant de l'ordre de 1,2 à 1,9 dm^3•dm^{-2}•h^{-1}, ce qui correspondait à environ 0,5 mm•h^{-1}. Dans le placeau desséché, la densité de flux de sève a diminué tout au long de l'été jusqu'à atteindre au minimum 0,05 dm^3•dm^{-2}•h^{-1} pour certains arbres, la variabilité entre arbres étant beaucoup plus importante que chez les arbres arrosés. La transpiration ainsi que la conductance stomatique ont fortement diminué avec la sécheresse, la plus grande part de cette réduction ayant été observée lorsque le potentiel hydrique de base est passé de –0,4 à –0,6 MPa. La conductance du couvert, calculée en inversant la formule de Penman-Monteith, a été modélisée au moyen d'un modèle multi-variable prenant en compte les facteurs climatiques et la sécheresse édaphique.*

***transpiration / conductance stomatique / conductance de couvert / potentiel hydrique / sécheresse / flux de sève /* Picea abies**

INTRODUCTION

Norway spruce is one of the most important coniferous forest species used for timber production in Europe. Extensive ecophysiological studies have been done on seedlings and saplings of this species. In contrast, only limited ecophysiological investigations have been reported on adult spruce under field conditions (Schulze *et al,* 1985; Werk *et al,* 1988; Granier and Claustres, 1989; Schulze *et al,* 1989; Cienciala *et al,* 1992), and these studies did not report the long-term effects of limiting soil water conditions.

During the 1980s, a new phenomenon of spruce forest decline occurred in Europe, especially in its western part. Dendochronological and biogeochemical investigations in the Vosges massif (eastern France) suggested that the decline of spruce in eastern France and western Germany might be mainly related to repeated severe drought events that had occurred since the mid-1970s in these regions (Lévy and Becker, 1987; Probst *et al,* 1990). Further research on spruce decline therefore requires more knowledge of the ecophysiological behaviour of mountain spruce under long-term soil drought.

In a forest ecosystem, transpiration is one of the major water fluxes; its measurement or estimation is of great importance for forest ecologists and hydrologists. In a conifer forest, as demonstrated by Tan *et al* (1978) and Jarvis and McNaughton (1986), transpiration is mainly controlled by vapour pressure deficit (VPD) and stomatal conductance. At the stand level, canopy conductance is considered to be the integration of all the stomatal (including the boundary layer) conductances in the canopy. If transpiration and climatic variables are known over the same time-scale, canopy conductance can be derived from the Penman–Monteith equation (Monteith, 1973). However, with this approach, the key problem is to determine stand transpiration. In this study, we estimate canopy transpiration from the measurement of xylem sap flow with a method suitable for adult forest trees.

In 1990, in the framework of the French Forest Decline Research Program (DEFORPA), extensive ecophysiological investigations were undertaken in a *Picea abies* stand at the Aubure catchment area in the Vosges with the following objectives: 1) to examine forest canopy transpiration and stomatal behaviour under long-term soil water deficit, as well as the sensitivity of spruce to soil drought (for this point, a comparison of mountain- and plain-growing Norway spruces was carried out); 2) to analyse and model the seasonal variation of canopy conductance under water constraint; and 3) to characterise the alteration of hydraulic conductance on the soil–leaf pathway and monitor the occurrence of xylem cavitation under intensive drought. This paper reports results from the investigation into the first two points; the hydraulic functioning of spruce will be reported in a forthcoming paper.

METHODS

Study site

The study site was located on the southern slope of the Aubure catchment area at a mean elevation of 1 050 m. This catchment is situated on the eastern side of the Vosges mountains, France (7°15'E, 48°12'N) and lies on a base-poor granite bedrock. Annual rainfall is about 1 500 mm and the annual average air temperature is 6°C (Viville *et al,* 1987). A detailed description of the catchment can be found in Probst *et al* (1990). The spruce stand is a dense, 30-year-old plantation, whose main characteristics are presented in table I. Projected leaf area index (LAI) was estimated through 2 independent methods: 1) the relationship between sapwood area and leaf area (Oren *et al,* 1986) gave a value of 5.6; and 2) direct sampling and measurement of needle dry weight (Le Goaster, 1989) gave 6.1.

Two adjacent plots (water stressed (dry) and control (watered)) were selected in autumn 1989. A 12-m-high scaffolding tower was set up in each plot. In the dry plot (30 trees) water was withheld by a surrounding trench (1 m deep) and a plastic roof extending 2 m above soil surface, from July 10 to September 7 1990. Because a natural drought occurred in this region during the experiment, the watered plot was irrigated 6 times (total 58 mm) in July and August 1990.

Sap flow and stand transpiration

Xylem sap flux density (F_d, $dm^3 \cdot dm^{-2} \cdot h^{-1}$) was measured using 2-cm-long continuously heated

Table I. Characteristics of the studied stand and trees.

Treatment	*Number of trees*	*Height (m)*	*Circumference at 1.3 m (cm)*	*Sapwood area (dm^2)*	*Crown status*
Dry	49	11.4	42.5	0.996	Codominant
	63	13.3	58.0	1.944	Dominant
	64	13.2	46.5	1.240	Dominant
	66	11.8	44.0	1.087	Codominant
Watered					
	58	13.5	48.0	1.332	Dominant
	59	14.9	71.2	2.752	Dominant
	60	12.0	50.6	1.491	Codominant
	71	12.8	45.5	1.179	Codominant

Age (years): 30; mean height (m): 12.6; mean circumference (cm): 49.1 ± 10.1; stem basal area ($m^2 \cdot ha^{-1}$): 45.9; sapwood area ($m^2 \cdot ha^{-1}$): 31.9; density ($stems \cdot ha^{-1}$): 2 343; projected leaf area index ($m^2 \cdot m^{-2}$): 5.6 (6.1) (2 independent estimates (see text)); altitude (m): 1 050; slope: 15°; slope orientation: SE; mean annual precipitation (mm): 1 500; mean annual air temperature (°C): 6.

sap flowmeters (Granier, 1985, 1987) on 4 trees from each plot, from June to mid-October 1990. The sensors were connected to a datalogger (Campbell Ltd, 21X); measurements were taken every 10 s and hourly means were stored for further processing.

Total sap flow ($dm^3 \cdot h^{-1}$) was calculated for each tree by multiplying F_d by the sapwood cross-sectional area (SA, dm^2) of the trees at the sensor level. SA was estimated using a relationship between tree circumference (C) and SA, established from a sampling of cores on the surrounding trees (Granier, 1985; Lu, 1992):

$$SA\ (dm^2) = 0.00047C\ (cm)^{2.052}$$

$r^2 = 0.973$ [1]

Hourly stand transpiration (T, $mm \cdot h^{-1}$) was computed as:

$$T = SA_T \Sigma\ (F_{di} \cdot p_i) \qquad [2]$$

where SA_T was the plot sapwood area per unit of ground area ($31.9\ m^2 \cdot ha^{-1}$), F_{di} the mean sap flux density of trees in the class of circumference i, $p_i = SA_i/SA_T$, and SA_i the sapwood area of the trees in the class of circumference i; 3 classes were used: dominant trees ($C \geq 55$ cm); codominant ($40 \leq C < 55$ cm); and intermediate plus suppressed trees ($C < 40$ cm).

The characteristics of the studied trees are shown in table I. Daily plot sap flow ($mm \cdot d^{-1}$) was calculated as the total of the hourly values.

Twig water potential

Twig water potential was measured twice a month on 3 one-year-old twigs from each of the studied trees (8 sap flow measured trees plus 2 additional trees from the dry plot), using a pressure chamber. Twigs were sampled in the upper third part of the crown just before dawn (predawn water potential, Ψ_{pd}) and at 12:00 solar time during sunny days (midday water potential, Ψ_m).

Throughout the study period, 2 trees in each plot (No 66 and 49 from the dry plot; No 59 and 71 from the watered plot) were selected for extensive measurements of diurnal courses of twig water potential. These trees were chosen for the easy access to their crown from the towers.

Stomatal conductance

Midday stomatal conductance (g_s) was measured between 12:00 and 13:00 solar time on 7 sunny days (days 206, 213, 214, 220, 235, 255 and 284) throughout the growing season using a Li-Cor 1600 porometer (Lincoln, USA). Four exposed sun twigs and 4 exposed shade twigs were selected in the upper half of the crown of the 4 extensively measured trees.

Climatic measurements

Climatic factors above the stand (global radiation, relative humidity, air temperature and wind speed) were measured hourly in a weather station 500 m from the stand. Incident rainfall and throughfall were measured weekly in a cutting and in the watered plot, respectively.

Maximum transpiration (TM, $mm \cdot h^{-1}$) was calculated hourly from the climatic data using the Penman–Monteith equation:

$$TM = \frac{s\ (R_n - G) + \rho\ C_p\ VPD\ g_a}{\lambda\ [s + \gamma (1 + g_a/g_{cm})]} \qquad [3]$$

where:

s: rate of change of saturation vapour pressure ($Pa \cdot C^{-1}$)

R_n: net radiation above stand ($W \cdot m^{-2}$)

G: rate of change of heat in the biomass, plus heat in the soil ($W \cdot m^{-2}$)

ρ: density of dry air ($kg \cdot m^{-3}$)

C_p: specific heat of dry air at constant pressure ($J \cdot kg^{-1} \cdot C^{-1}$)

VPD: vapour pressure deficit (Pa)

g_a: aerodynamic conductance ($cm \cdot s^{-1}$)

g_{cm}: maximum (non-limiting soil water) canopy conductance ($cm \cdot s^{-1}$)

λ: latent heat of vaporisation of water ($J \cdot kg^{-1}$)

γ: psychrometric constant ($Pa \cdot C^{-1}$)

In this study, heat flow in the soil was not measured but was assumed to be negligible. R_n was calculated as 75% of global radiation (unpublished data, from a previous experiment in a spruce stand near Nancy, France). Rate of storage of heat in biomass was calculated from the above-ground estimated biomass and from hourly changes in air temperature (Stewart, 1988). Aerodynamic conductance (g_a) was calculated using the logarithmic equation of Monteith (1973) from wind speed and mean height of the stand (12.6 m). Daily TM (mm•d^{-1}) was then calculated as the cumulated values of hourly TM.

The maximum canopy conductance (g_{cm}) was modelled. It was first calculated hourly from sap flow (in both plots) and climatic data during the beginning of the measurement period (days 164 to 190) under non-limiting soil water conditions, using equation [3]. It was assumed that vapour flux was equal to the stand sap flow scaled up from the trees sap flow, as in Cienciala *et al* (1992). The first tests have shown a 1 h time lag between sap flow and simulated TM. Thus, maximum canopy conductance was recomputed from sap flow measured over hour (h) and climatic factors measured over hour (h – 1). A multiple regression was made on hourly daylight data over the period of days 165 to 190, using a non-linear model close to the equation proposed by Lohammar *et al* (1980):

$$g_{cm} = (R_g/(R_g + 310))(5.34 - 1.33 \ln (\text{VPD})) \quad [4]$$

$r^2 = 0.70$

with g_{cm} in cm•s^{-1}, R_g in W•m^{-2}, and VPD in hPa.

In a forest stand, g_{cm} can be considered in the first approximation as the average of leaf stomatal conductances over the entire canopy:

$$g_{cm} = g_s\text{LAI}•2.6 \quad [5]$$

where LAI•2.6 is the developed leaf area index of the stand (Oren *et al,* 1986).

Additional experiment

Another experiment has been undertaken previously near Nancy, France (6°14'E, 48°44'N, elevation 250 m) on a 21-year-old Norway spruce plantation. The stand density was 4 200 stems•ha^{-1}, average tree circumference 31.3 cm, and average tree height 11.3 m. The soil was a Gleyic luvisol developed on loam. This experiment was described by Granier and Claustres (1989). Sap flow and xylem water potential measurements were performed on 5 trees from different crown classes, by means of the same technique.

RESULTS

Twig water potential variations

The year 1990 was characterised by a relatively dry spring followed by an exceptionally dry summer and autumn (Dambrine *et al,* 1992).

Figure 1 shows the seasonal course of average predawn (Ψ_{pd}) and midday water potential (Ψ_m) of trees in the dry and watered plots. Before the roof was put in place, when the soil was well-watered, the Ψ_{pd} values in watered and dry plots were –0.55 and –0.45 MPa, respectively, on day 176. Later, a slight difference (about 0.15 to 0.20 MPa) was noticed between both plots, probably due to the trench which immediately provoked a decrease in soil water potential in the dry plot, as was also reported by Biron (1994) from tensiometer measurements. During the following drier and warmer period (days 190 to 238), Ψ_{pd} and Ψ_m in both plots first decreased gradually and concurrently until the beginning of the August. Afterwards, due to irrigation in the watered plot (especially on days 220, 225 and 233), the Ψ_{pd} of the watered plot increased and remained relatively stable around –0.4 MPa. In contrast, Ψ_{pd} of the dry plot continued to decrease gradually to about –1.0 MPa, and then slightly increased due to several rainfall events from mid-August to mid-September.

After the removal of the roof (September 15), Ψ_{pd} continued to decrease in both plots in the absence of rainfall and irrigation. At this time, trees in the dry plot were exposed to the most severe drought observed in this experiment (Ψ_{pd} and Ψ_m were –1.2 and –2.0 MPa, respectively).

Variations of Ψ_m progressed in parallel with Ψ_{pd}, with a difference of about 1.0 MPa. Except for 1 day (day 235), the trees in the dry plot revealed a more negative Ψ_m than those in the watered plot.

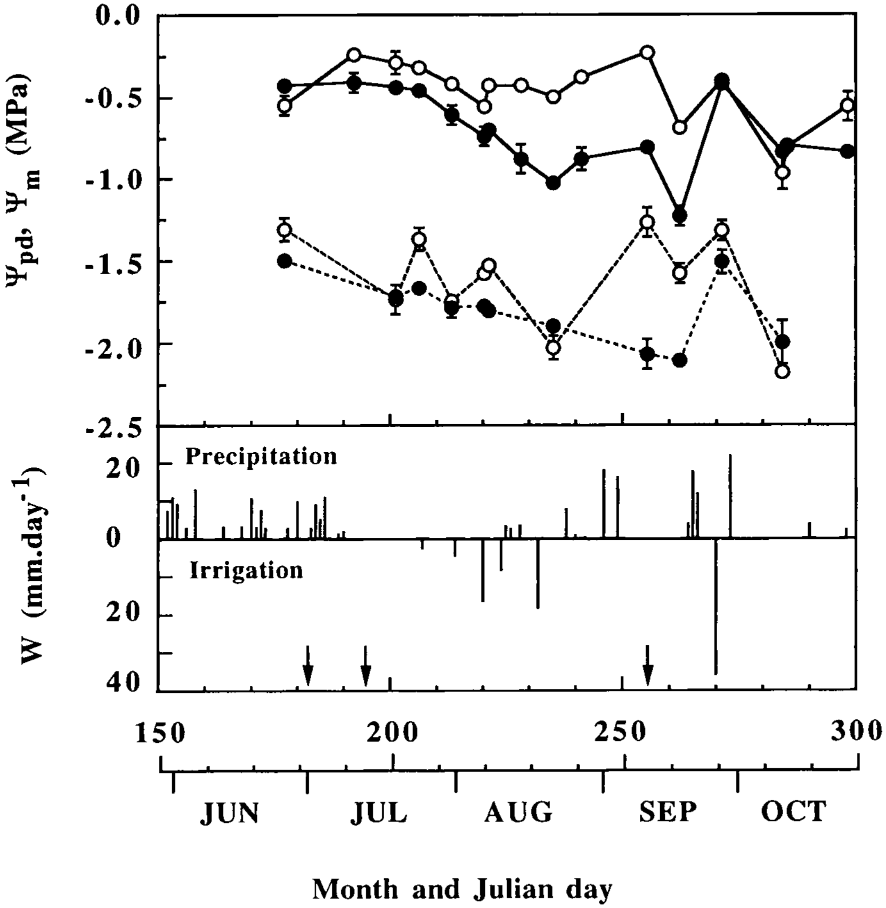

Fig 1. Seasonal variations in twig predawn (Ψ_{pd}, full lines) and minimum water potential (Ψ_m, dotted lines) in the dry plot (closed symbols) and in the watered plot (open symbols). Rainfall and irrigation in the watered plot (except the last irrigation = 40 mm applied to dry plot) are indicated on the bottom part of the figure. The arrows indicate successively the date of the opening of the trench, the installation of the roof and the removal of the roof. Error bars indicate standard deviation.

Daily variations of sap flux density (F_d)

Examples of diurnal course of F_d during 3 bright days over the season are shown in figure 2. On day 201, under high water availability conditions (Ψ_{pd} = –0.29 MPa in the watered plot, and Ψ_{pd} = –0.44 MPa in the dry plot), F_d courses were very similar, and between-tree variability was low. Nevertheless, some differences could be noticed. In the morning, the sharp increase in sap flux densities did not occur at the same time for all the trees, and some of them displayed their maxima earlier than others. Throughout the season, the maximum F_d varied between 1.2 and 1.9 $dm^3 \cdot dm^{-2} \cdot h^{-1}$, according to the trees.

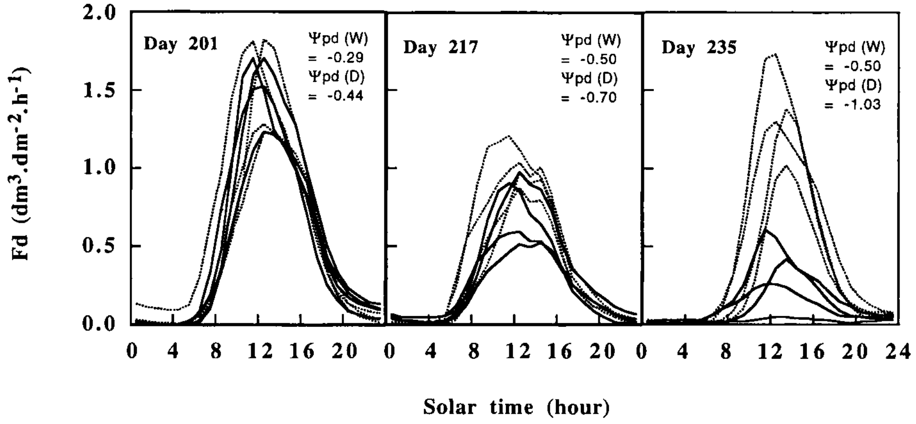

Fig 2. Diurnal patterns of sap flux densities (F_d) during 3 bright days on the 4 watered (dotted) and the 4 dry (full lines) measured spruce trees. Mean value of predawn water potential in each plot is also indicated (Ψ_{pd}(W): watered plot; Ψ_{pd}(D): dry plot).

Increasing the soil water deficit induced a gradual decrease in F_d and the increase in between-tree variability, as shown on days 217 and 235. Under the driest conditions (*eg*, on day 235), maximum F_d (mean Ψ_{pd} = −1.03 MPa) dropped to very low values (0.05–0.5 $dm^3 \cdot dm^{-2} \cdot h^{-1}$), while F_d in the watered trees remained higher, ranging between 1.0 and 1.75 $dm^3 \cdot dm^{-2} \cdot h^{-1}$. It was also observed that the 2 dominant trees in the dry plot exhibited a much lower F_d than codominant trees, while no relationship between crown status and F_d was apparent for the watered trees.

Diurnal and seasonal courses of plot transpiration

Over the study period, 5 diurnal courses of plot transpiration (T_w, T_d), maximum transpiration (TM) and average twig water potential (Ψ_f) are shown in figure 3, to illustrate the effects of increasing soil drought on plot transpiration. At the beginning of the season, transpiration values in the 2 plots were similar, with maximal transpiration rates at midday of 0.43 $mm \cdot h^{-1}$. Significant differences between the 2 plots were observed under the higher soil water deficit (days 213 and 235). For example, on day 235, transpiration of the dry plot decreased to less than 25% of that of the watered plot. After irrigation (day 284), transpiration in the dry plot almost recovered to a similar level of the watered plot.

As shown in figure 1, day 235 had one of the lowest Ψ_{pd}. At this time, comparable values of Ψ_m (about −2.0 MPa) were observed in the dry and watered plots, suggesting that stomatal closure prevented trees in the irrigated plot from developing more severe water stress. It was also observed that the recovery of twig water potential after sunset was slow under severe water deficits (fig 3, day 235).

Seasonal courses of daily TM, T_w and T_d are shown in figure 4. TM was higher during July and August (from days 190 to 235), with maximum values of 5.5 $mm \cdot d^{-1}$,

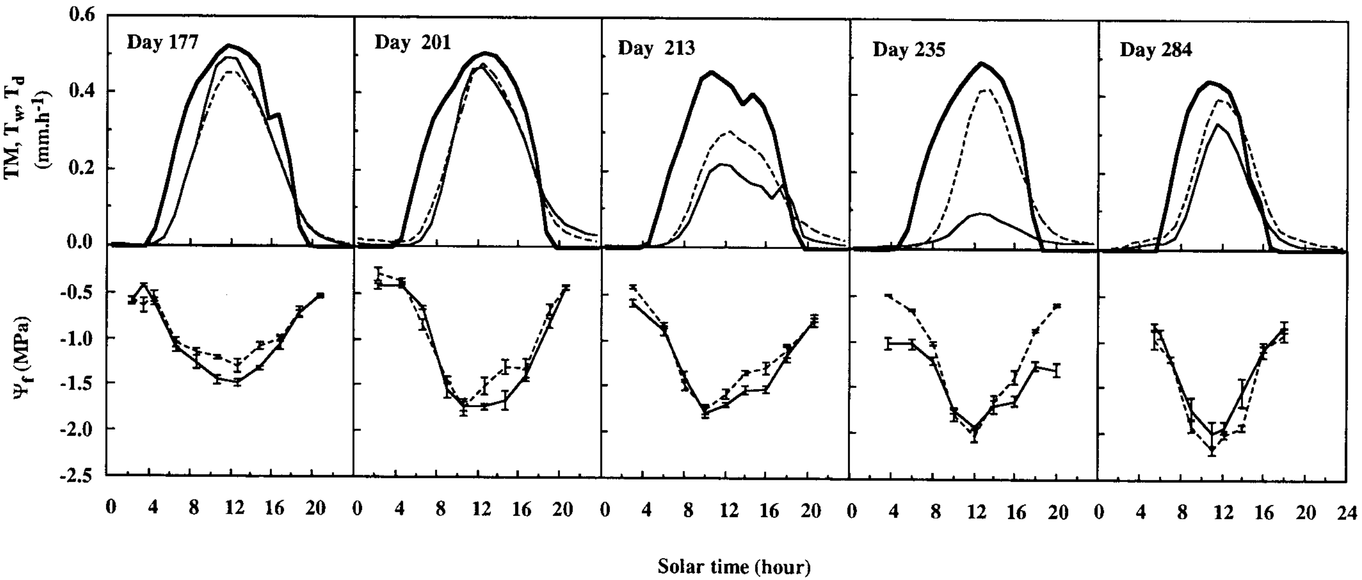

Fig 3. Top: diurnal patterns of transpiration in watered (T_w, dotted) and dry (T_d, full lines) plots and maximum stand transpiration (TM, thick lines). Bottom: diurnal variations of average twig water potential (Ψ_f) in the watered (dotted) and dry plot (full lines). Error bars indicate standard deviation.

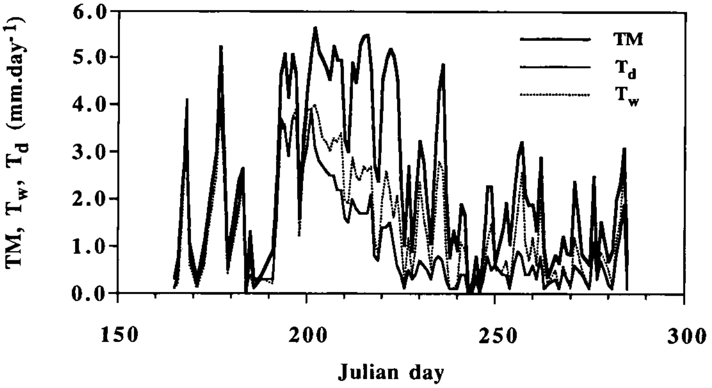

Fig 4. Seasonal variations of dry (T_d, full line) and watered (T_w, dotted) plot transpiration as compared to maximum transpiration (TM, thick line).

and during the remainder of the measurement period, it ranged between 1.0 and 4.0 mm•d^{-1}. Plot transpiration rates were first at maximum and close to TM from days 160 to 195. After the beginning of July (day 200), plot transpiration decreased in both plots, revealing stomatal closure. Lower transpiration rates were observed in the dry plot where T_d fell to 0.08 mm•d^{-1}. In the watered plot, after an initial decrease, a tendency to stabilise from days 210 to 225 was observed, the maximum transpiration rate being around 2.5 mm•d^{-1}.

The ratios T_d/TM and T_w/TM were close to 1 until day 190; afterwards, T_d/TM gradually decreased to 0.2 at the end of August, and T_w/TM to 0.5, just before irrigation occurred. Over the period from days 165 to 285, the total sums of TM, T_w and T_d were 252, 190 and 150 mm, respectively.

Stomatal control of trees and stand transpiration

The seasonal course of stomatal conductance (g_s) measured at midday is shown in figure 5. Before day 220, stomatal conductances of the watered trees were slightly lower than those in the dry plot, probably resulting from the sampling done at different crown exposures from the towers. A strong decrease of g_s was observed during July and August in both plots, but it was more pronounced in the dry plot. Mean g_s in the dry plot decreased by about 75% from the beginning (0.08 cm•s^{-1}) until mid-August (0.02 cm•s^{-1}), while in the watered plot, g_s remained quite stable, around 0.05 cm•s^{-1}. After the rain at the end of August and the beginning of September, and rehydration of the dry plot, the g_s in both plots recovered to the pre-stress value.

The decreases in the ratios T/TM and g_s were well correlated with the decrease of predawn water potential in both plots (fig 6). However, most of the decrease in g_s occurred within a very limited change in predawn water potential (between –0.4 and –0.6 MPa).

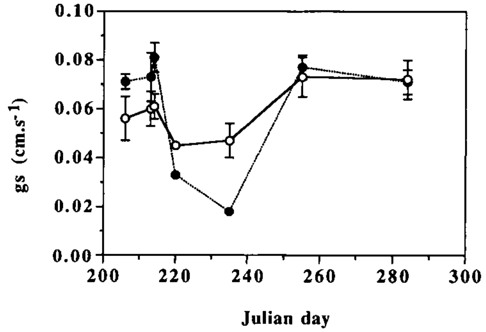

Fig 5. Seasonal variations of midday stomatal conductance in dry (closed circles) and watered (open circles) trees. Error bars indicate standard deviation.

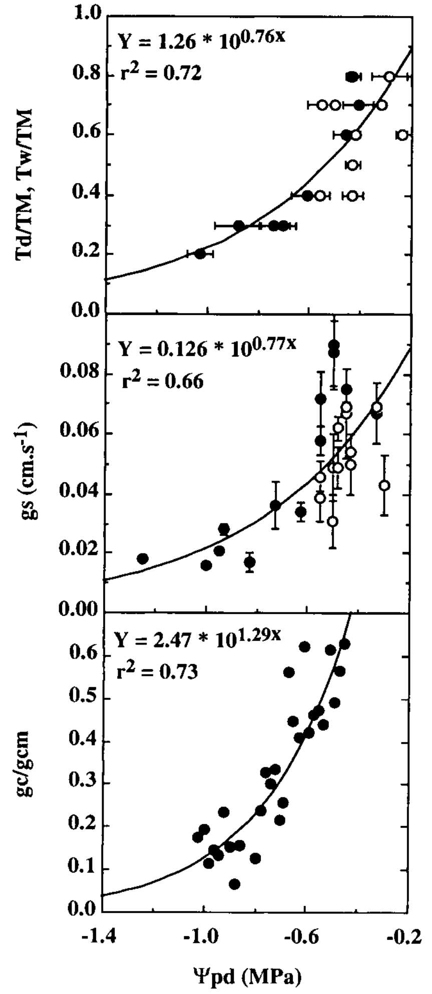

Fig 6. Top: ratios of dry (T_d, closed circles) and watered (T_w, open circles) plot transpiration to maximum transpiration (TM) as a function of predawn water potential (Ψ_{pd}). Middle: average midday stomatal conductances in dry (closed circles) and watered (open circles) trees as a function of predawn water potential (Ψ_{pd}). The regression curves are fitted with all data from dry and watered trees. Bottom: variation of the ratio of calculated (g_c) on modelled maximum (g_{cm}) canopy conductance in the dry plot as a function of predawn water potential (period from day 206 to 235, midday values).

At the stand level, drought effects were taken into account in a more general transpiration model than equation [3]. Following Stewart (1988), it was assumed that variations in g_c could be modelled as the product of a maximum canopy conductance function (under non-limiting soil water conditions, modelled as in equation [4]) and of a function varying between 0 and 1, depending on soil drought. In this study, predawn water potential (Ψ_{pd}) was taken as the driving variable. Only midday data were used in order to be compared with stomatal conductance measurements. As previously observed for g_s variations, figure 6 shows the strong dependence of g_c/g_{cm} on predawn water potential. A non-linear regression was made between g_c/g_{cm} and Ψ_{pd} over the period of dehydration (from day 206 to 235):

$$g_c/g_{cm} = 2.47 \times 10^{1.294\Psi pd}$$

$r^2 = 0.73$

Simultaneous variations of g_c and g_s (midday values) in the dry plot are shown on figure 7. A good agreement between both courses is observed; the ratio between g_c and g_s corresponded approximately to the developed leaf area of the stand, as stated in equation [5].

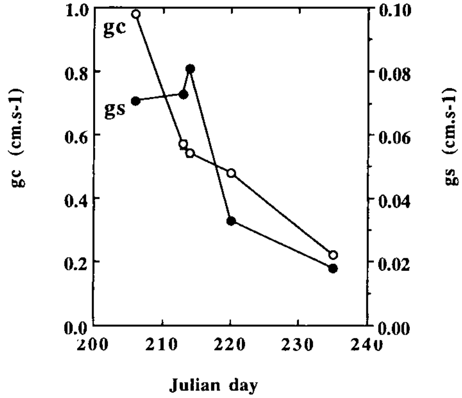

Fig 7. Simultaneous variations in midday canopy conductance (g_c, open circles) and stomatal conductance (g_s, closed circles) in the dry plot over the period of increasing soil water deficit.

DISCUSSION

Under non-limiting water conditions, the maximum hourly sap flux density of the studied trees varied from 1.2 to 1.9 $dm^3 \bullet dm^{-2} \bullet h^{-1}$, which was similar to the values reported in another study on the same species, 1.4–2.2 $dm^3 \bullet dm^{-2} \bullet h^{-1}$ (Granier and Claustres, 1989). Cienciala *et al* (1992) have measured maximum daily sap flux densities of 16 $kg \bullet dm^{-2} \bullet d^{-1}$, which is in the same range than our values. Between-tree differences in F_d measured in our study could be attributed to the heterogeneity in crown exposure conditions. We have not found any relationship between F_d and crown status for the watered trees; dominant trees did not exhibit higher transpiration rates than codominant trees. But under decreasing soil water availability, the F_d values of the biggest trees were much lower than the F_d of the codominant trees, indicating a higher soil water depletion by the dominant trees. The minimum Ψ_{pd} observed in this study was about –1.4 MPa, and Ψ_m never decreased below –2.5 Mpa. This minimum value of Ψ_m coincided with the threshold of water potential inducing a significant xylem cavitation for this species (Cochard, 1992; Lu, 1992). The mechanism of stomatal closure prevented spruce from xylem dysfunction.

Assessment of the sensitivity of stomata to soil water deficit was one of the principal goals of this study. The relative reduction of g_s due to the decline of Ψ_{pd} reported here was comparable to what we observed on spruce growing under similar conditions, in a stand located in central Germany (Lu, unpublished results): g_s was reduced to about 50% of its initial value when Ψ_{pd} declined from –0.4 to –0.8 MPa.

Direct comparison of stomata sensitivity to drought between plain and mountain conditions is difficult, because little data are available for spruce growing on the plain. However, comparison between the ratio of stand transpiration to Penman potential evapotranspiration (T/PET) of the mountain *versus* the plain stands showed a much lower sensitivity to soil drought in the latter than in the former. When Ψ_{pd} decreased from –0.4 to –0.7 MPa, the reduction of T/PET ratio was only of 20% in the plain stand, compared to 50% in the mountain stand. Nevertheless, we cannot attribute this difference to an intrinsic difference in the stomatal behaviour, because soil and rooting characteristics differ dramatically between both sites. Our mountain stand was located on a shallow sandy soil, with the roots vertically limited by the bedrock. In such a site, soil water depletion develops very rapidly, and therefore a partially desiccated root system could quickly induce stomatal closure, controlled through a biophysical and/or biochemical communication between roots and leaves (Zhang and Davies, 1989; Malone, 1993). Moreover, care must be taken with the use of predawn water potential as a driving variable of stomatal closure. Under field conditions, Ψ_{pd} does not always seem to be the best indicator of the water stress actually experienced by plants (Reich and Hinckley, 1989; Améglio, 1991). A large decrease of g_s with only a limited variation in Ψ_{pd} was observed here, especially for trees in the watered plot (fig 6). This phenomenon has also been reported on the same species by Cienciala *et al* (1994) and in several broad-leaved species such as oak (Bréda *et al*, 1993). When the soil is drying, the upper layers may dehydrate without noticeable change in Ψ_{pd}. We have shown that during a rainless period, transpiration, g_s and g_c are well correlated with Ψ_{pd} (see fig 6 for the dry plot). However, under variable weather conditions, when some soil layers were dry and others humid (*eg*, after small rain events or irrigation), the implication of Ψ_{pd} is questionable. So far, there is no clear relationship between Ψ_{pd} and heterogeneity of water availability in the soil, and it is unclear how the stomatal aperture is controlled in this case. Therefore, more investigations are needed concerning the significance of Ψ_{pd} under field conditions.

As demonstrated by McNaughton and Black (1973), for a conifer stand under non-limiting soil water conditions, VPD is the major factor determining tree transpiration, because of a much smaller canopy conductance than aerodynamic conductance, and hence a high degree of coupling between canopies and the atmosphere (Tan *et al,* 1978; Jarvis and McNaughton, 1986; Granier and Claustres, 1989). Except in the morning (when light is limiting), during the course of a day, transpiration is strongly limited by stomatal conductance and its respponse to VPD variations. Zimmermann *et al* (1988) have indicated the same negative dependence of stomatal conductance to VPD regardless of needle age. Results from the calculation of the canopy conductance (equation [5]) showed that g_c decreased by about 50% as VPD increased from 0.5 to 1.5 kPa, with R_g ranging between 500 and 1 000 W•m^{-2}; in the spruce stand located in the plain, we have observed the same dependence of g_c to VPD (Granier, unpublished results). As previously emphasised, soil water deficit strongly reduced canopy conductance, decreasing to less than 15% of its initial value as Ψ_{pd} declined from –0.4 to –1.0 MPa (fig 6).

Maximum midday stomatal conductance values (about 0.1 cm•s^{-1}) were comparable to data reported in other studies for adult spruce under field conditions (Schulze *et al,* 1985; Claustres, 1987). Canopy conductance variations calculated from sap flow were in good agreement with variations of stomatal conductance (fig 7), even if they were only measured in the upper half of the tree crowns on young needles. Sap flow measured on a representative sample of trees within a stand thus appears to be a valuable method for estimating canopy conductance.

A slow recovery rate of twig water potential after sunset under high water deficit conditions (*eg,* day 235 in fig 3) was observed. This could be explained by modifications of hydraulic properties within the root zone, where drought induces a high water potential gradient during drought, while water movement is strongly limited by increasing soil hydraulic resistance. Further investigations were done on this question and have shown an important decline of hydraulic conductance, mainly located at the soil–root interface (Lu, 1992).

REFERENCES

Améglio T (1991) Relations hydriques chez le jeune Noyer, de l'échelle de la journée à celle de l'année, en liaison avec quelques aspects de la physiologie de l'arbre. Thèse de 3e cycle, Université Clermont II, France, 99 p

Biron P (1994) Le cycle de l'eau en forêt de moyenne montagne : flux de sève et bilans hydriques stationnels (bassins versant du Strengbach à Aubure, Hautes-Vosges). Thèse, université de Strasbourg, France, 114 p

Bréda N, Cochard H, Dreyer E, Granier A (1993) Water transfer in a mature oak stand *(Quercus petraea)*: seasonal evolution and effects of a servere drought. *Can J For Res* 23, 1136-1143

Cienciala E, Lindroth A, Cermark J, Hällgren JE, Kucera J (1992) Assessment of transpiration estimates for *Picea abies* trees during a growing season. *Trees* 6, 121-127

Cienciala E, Lindroth A, Cermark J, Hällgren JE, Kucera J (1994) The effects of water availability on transpiration, water potential and growth of *Picea abies* during a growing season. *J Hydrol* 155, 57-71

Claustres JP (1987) Caractérisation du fonctionnement hydrique d'épicéas en peuplement fermé : conséquences d'une éclaircie. DEA Dissertation, université de Nancy I, France, 46 p

Cochard H (1992) Vulnerability of several conifers to air embolism. *Tree Physiol* 11, 73-83

Dambrine E, Carisey N, Pollier B *et al* (1992) Dynamique des éléments minéraux dans la sève xylémique d'un peuplement d'épicéas dépérissants. *Ann Sci For* 49, 489-510

Granier A, Claustres JP (1989) Relations hydriques dans un épicéa (*Picea abies* L) en conditions naturelles : variations spatiales. *Acta Oecol, Oecol Plant* 10, 295-310

Granier A (1985) Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Ann Sci For* 42, 193-200

Granier A (1987) Evaluation of transpiration in a Douglas fir stand by means of sap flow measurements. *Tree Physiol* 3, 309-320

Jarvis PG, McNaughton KG (1986) Stomatal control of transpiration: scaling up from leaf to region. *Adv Ecol Res* 15, 1-48

Le Goaster S (1989) Influence de la croissance d'un peuplement sur le prélèvement en éléments minéraux ; relations avec le dépérissement. Mémoire ENITEF, France, 50 pp

Lévy G, Becker M (1987) Le dépérissement du sapin dans les Vosges : rôle primordial de déficits d'alimentation en eau. *Ann Sci For* 44, 403-416

Lohammar T, Larsson S, Linder S, Falk SO (1980) FAST — simulation models of gaseous exchange in Scots pine. *Ecol Bull (Stockholm)* 32, 505-523

Lu P (1992) Ecophysiology and reaction to drought of three conifer species (*Abies alba* Miller, *Picea abies* (L) Karsten and *Pinus sylvestris* L); effect of age. PhD Thesis, University of Nancy I, France, 204 pp

Malone M (1993) Hydraulic signals. *Phil Trans R Soc B (Lond)* 341, 33-39

McNaughton KG, Black TA (1973) Evapotranspiration from a forest: a micrometeorological study. *Water Resour Res* 9, 1579-1590

Monteith JL (1973) *Principles of Environmental Physics.* Edward Arnold, London, UK, 241 pp

Oren R, Schulze ED, Matyssek R, Zimmermann R (1986) Estimating photosynthetic rate and annual carbon gain in conifers from specific leaf weight and leaf biomass. *Oecologia* 70, 187-193

Oren R, Werk KS, Schulze ED (1986) Relationships between foliage and conducting xylem in *Picea abies* (L) Karst. *Trees* 1, 61-69

Probst A, Dambrine E, Viville D, Fritz B (1990) Influence of acid atmospheric inputs on surface water chemistry and mineral fluxes in a declining spruce stand within a small granitic catchment (Vosges massif, France). *J Hydrol* 116, 100-124

Reich PB, Hinckley TM (1989) Influence of pre-dawn water potential and soil-to-leaf hydraulic conductance on maximum daily leaf diffusive conductance in two oak species. *Funct Ecol* 3, 719-726

Schulze ED, Cermak J, Matyssek R *et al* (1985) Canopy transpiration and water fluxes in the xylem of the trunk of *Larix* and *Picea* trees: a comparison of xylem flow, porometer and cuvette measurements. *Oecologia* 66, 475-483

Schulze ED, Lange OL, Oren R (1989) Forest decline and air pollution: a study of spruce *(Picea abies)* on acid soils. *Ecological studies,* vol 77, Springer-Verlag, Berlin, Germany

Stewart JB (1988) Modelling surface conductance of pine forest. *Agric For Meteorol* 43, 19-35

Tan CST, Black TA, Nnyamah JU (1978) A simple diffusion model of transpiration applied to a thinned Douglas fir stand. *Ecology* 59, 1221-1229

Viville D, Ambroise B, Probst *et al* (1987) Le bassin versant du Strengbach à Aubure (Haut-Rhin, France) pour l'étude du dépérissement forestier dans les Vosges (Programme DEFORPA). I. Équipement climatique, hydrologique, hydrochimique. *In: Proc Int Symposium Air Pollution and Ecosystems,* Grenoble, Reidel publishing company, France, 823-828

Werk KS, Oren R, Schulze ED, Zimmermann R, Meyer J (1988) Performance of two *Picea abies* (L) Karst stands at different stages of decline. III. Canopy transpiration of green trees. *Oecologia* 76, 519-524

Zhang J, Davies WJ (1989) Abscissic acid produced in dehydrating roots may enable the plant to measure the water status of the soil. *Plant Cell Environ* 12, 73-81

Zimmermann R, Oren R, Schulze ED, Werk KS (1988) Performance of two *Picea abies* (L) Karst stands at different stages of decline. II. Photosynthesis and leaf conductance. *Oecologia* 76, 513-518