Water transfer in a mature oak stand (*Quercus petraea*): seasonal evolution and effects of a severe drought

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The reactions of sessile oak (*Quercus petraea* (Mattuschka) Liebl.) to drought were studied under natural conditions in a 32-year-old stand near Nancy (northeastern France) during the summers of 1989 (strongly rain deficient) and 1990. A plot of five trees was subjected to imposed water shortage, while a group of irrigated trees was used as a control. Measurements of xylem sap flows and water potential enabled the computation of plot transpiration, canopy conductance, and specific hydraulic conductance in the soil–tree continuum. Stomatal conductance was measured directly with a porometer. Specific hydraulic conductance of our oaks was of the same order of magnitude as that reported for other species. It decreased significantly during spring because of a time lag between cambial growth and leaf area expansion. Measured transpiration was close to potential evapotranspiration, except during days with high vapor pressure deficits, which promoted stomatal closure in the absence of soil water deficits. Imposed drought caused predawn leaf water potentials to reach values as low as −2.0 MPa and a progressive decline in hydraulic conductance, which was probably attributable to modifications in hydraulic properties at the soil–root interface. This gradual decline in conductance was attributed to their deep rooting (1.40 m). This study revealed that *Q. petraea* may be considered as drought tolerant because of adaptations like deep rooting, efficient and safe xylem sap transport, maintenance of significant stomatal conductance, and significant transpiration, even during strong drought stress.

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Les réactions du chêne sessile (*Quercus petraea* (Mattuschka) Liebl.) à la sécheresse ont été étudiées en conditions naturelles dans un perchis d'une trentaine d'années dans le nord-est de la France, au cours de l'été 1989, qui a été particulièrement déficitaire en pluviométrie, et de ceux de 1990 et 1991. Un placeau de cinq arbres a été soumis à une sécheresse artificielle, tandis qu'un groupe d'arbres irrigués servait de témoins. Les mesures de densité de flux de sève brute et de potentiel hydrique ont permis de calculer la transpiration de chaque placeau, la conductance de couvert ainsi que la conductance hydraulique spécifique des arbres. La conductance stomatique était mesurée par porométrie sur les feuilles de lumière. La conductance hydraulique spécifique mesurée sur les chênes était du même ordre de grandeur que celle reportée chez d'autres espèces. Une diminution brutale de cette conductance est apparue pendant la phase d'installation du feuillage, due à une latence entre la mise en place du bois de printemps et celle de la surface foliaire. Par ailleurs, la transpiration s'est révélée inférieure à l'évapotranspiration potentielle, lors de journées à fort déficit de saturation de l'air, du fait d'une fermeture des stomates. La sécheresse imposée aux arbres a été particulièrement marquée (potentiel hydrique de base inférieur à −2,0 MPa en fin de traitement). La baisse progressive de conductance hydraulique qui en a résulté a été attribuée à des modifications de propriétés hydrauliques de l'interface sol–racines. Le déclin très progressif de cette conductance a été relié à la grande profondeur d'enracinement des arbres (décrite au moins jusqu'à 1,40 m). Le chêne sessile est apparu au travers de cette étude comme une espèce assez tolérante à la sécheresse du fait à la fois de son enracinement, de l'efficience de son système de transport de sève, et de la capacité à maintenir une certaine ouverture stomatique, et donc une transpiration non négligeable jusqu'à des niveaux de dessèchement poussés.

Introduction

Many oak stands in Europe have been reported to be declining following years with marked climatic stress (Delatour 1983). Drought is generally considered as one of the major predisposing factors for these declines. A clear correlation between the drought of 1976 and the occurrence of strong dieback of *Quercus robur* L., and of moderate decline of sessile oak *Quercus petraea* (Mattuschka) Liebl.), has been established (Becker and Lévy 1983). Dendrochronological studies confirmed the strong correlation between water availability and growth (M. Becker, personal communication). Many reports analyzing the occurrence of oak decline during the 1980s in central Europe linked it to particularly rain deficient years, although some pathogens are thought to amplify the persisting effects of such climatic constraints (Delatour 1990). Moreover, much stronger ecological differences than previously accepted are now reported to separate the species *Q. petraea* and *Q. robur*, the latter being more sensitive to decline, less productive under limited water supply, and having probably been artificially spread beyond its natural range by silviculturists during past centuries (Lévy et al. 1992).

Extensive studies conducted on North American mesic to xeric oak species revealed that they have a relatively good tolerance to soil water depletion (Abrams 1990). Deep rooting is supposed to be one of the important traits enabling this tolerance through maintenance of sufficient water supply (Hinckley et al. 1979; Teskey and Hinckley 1981). Many tested species have also been shown to maintain lowered but still significant stomatal conductance even during very stressful periods (Dougherty and Hinckley 1981; Bahari et al. 1985). In contrast, water relations of mesic European oaks species like *Q. petraea*, and their degree of tolerance to drought, are still poorly documented.

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Many techniques involving either micrometeorological methods (Shuttleworth 1989) or direct monitoring of stemflow (Granier 1987) have been developed in recent years to investigate drought tolerance of mature trees growing in natural stands. Moreover, the measurement of both water flow and gradients of water potential in trees allows the calculation of a total liquid conductance on mature trees (Cohen et al. 1983; Granier et al. 1989; Reich and Hinckley 1989). The evolution of this conductance during increasing water shortage is a useful indicator of the efficiency and safety of water transport.

Stomatal conductance plays a major role in controlling the intensity of transpiration, and therefore the gradient of water potential between soil and leaves. The combined analysis of stomatal closure and potential dysfunctions in the water transfer to crowns provides a powerful tool to assess the sensitivity to drought. We used it with mature trees of *Q. petraea*, growing in a natural stand near Nancy, that were submitted to an imposed water shortage by means of covering soil to exclude precipitation.

Material and methods

The study site was located in the Forêt domaniale de Champenoux, 15 km east of Nancy, France (48°44′N, 6°14′E, elevation 237 m), in a 32-year-old stand of *Q. petraea* regenerated from seed. The main parameters describing the growth status of this stand were as follows: mean leaf area index (LAI) of 6, as estimated from collected leaf litter during autumn 1989 to autumn 1991; density of 3644 stems/ha; basal area of 24.7 $m^2 \cdot ha^{-1}$; mean and maximal diameter at breast height (DBH) of 85.9 and 175 mm, respectively; mean and dominant height of 14.8 and 15.7 m, respectively.

The soil was a typical "sol brun lessivé "(French classification), or a Gleyic Luvisol (Food and Agriculture Organization), developed on a rather deep loam. The top horizons, consisting of a silty clay loam, presented a crumb structure. Hydromorphic lenses appeared below 30 cm. An argillic horizon, with a clay content of about 45%, bordered this upper layer between 60 and 80 cm depth. Below 1 m depth, the clay content decreased but bulk density increased continuously up to 1.55 at 1.15 m. Rooting profiles showed that 75% of total roots were contained in the upper layer (0–60 cm), only a few percent were present in the argillic layer (60–70 cm), and 25% were present in the deep layers (80–140 cm). This last soil fraction contained mainly thin and ramified rootlets.

During 1989, a group of five randomly selected trees was used as a representative sample and included all diameter classes present in the stand. Annual rainfall was very low that year (i.e., −70 mm, which was 10% below the normal mean over the 30 last years), and summer was particularly dry. These trees experienced a significant natural water stress.

During 1990, the group of five trees was watered at regular intervals and used as a well-watered control, while a second group of eight trees was encircled by a 1.20 m deep trench, forming a 14-m^2 simplified lysimeter. Vertical walls were covered with a black polyethylene sheet. A 2 m high roof intercepted all precipitation below the canopy, and the gley layer at 70 cm depth strongly limited vertical water transport. Water was withheld beginning at the end of June, and the whole lysimeter was rewatered manually on August 23 (day 235); 140 mm of water was applied upon reirrigation. Two scaffolds allowed access to the crowns at 12.5 and 15 m height.

During 1991, another group of 17 trees was submitted to water shortage using the same method. The roof was installed in mid-June, and rewatering was done on November 13 (day 317). Unfortunately, a partial rehydration occurred in this treatment during a thunderstorm (day 269). A small plot of four trees was left under natural conditions and irrigated once at the end of August (day 241).

A weather station including a pyranometer (Kipp & Zonen), a ventilated psychrometer with platinum sensors (model INRA), and an anemometer (Vector Instruments) monitored the microclimate 2 m

above the canopy. Data were logged every 30 min with a Campbell (CR7) data logger, and Penman (1948) potential evapotranspiration (PET) was computed. Rainfall was measured with a rain gauge installed in a nearby clearing.

Canopy interception of global radiation was measured with three linear thermopyranometers (INRA) placed just below the crowns at 13 m above ground level in 1990; they were located at 1.5 m above the soil surface in 1991. Seasonal variation of this parameter was used as an estimate of changes in LAI.

Soil moisture was estimated during the 3 years of the experiment with a Neutron probe (NEA), using three to twelve 1.60 m deep access tubes according to the area of each treatment. Measurements were performed every week during the growing season. Counts were logged every 10 cm for the upper 100 cm, and every 20 cm below 100 cm depth. A polyethylene reflector was used for measurements in the upper soil levels. Soil moisture profiles were used to compute relative extractable water (REW) using eq. 1:

$$[1] \quad REW = \frac{R - R_{min}}{EW}$$

where R was the actual soil water content, R_{min} is the minimal soil water content observed in the dry plot during the experiments, and EW is extractable water. EW was estimated to be equal to 180 mm from measured water content/water potential relationships.

Leaf water potential was measured once weekly on two leaves from all tested trees, with a pressure chamber. Leaves were sampled in the upper third of the crown, either just prior to dawn (predawn leaf water potential, Ψ_{wp}) or at 1:00 p.m. universal time (UT) during sunny days (minimal leaf water potential, Ψ_{wm}). For the latter case they were kept in polyethylene bags from cutting until measurement (maximum 5 min).

Mean xylem sap-flux density (F_d, $dm^3 \cdot dm^{-2} \cdot h^{-1}$) was monitored on five trees during summer 1989 and on five drought-stressed and four control trees during 1990; in 1991, sap-flux densities were measured on six drought-stressed and four "natural" trees. Thermal devices as described by Granier (1985, 1987) were inserted in the stems for the whole growing season. Total sap flows (F, $dm^3 \cdot h^{-1}$) were estimated from F_d multiplied by actual sapwood area (SA, dm^3), which was computed from DBH (dm) using following equation:

$$[2] \quad SA = 2.449\pi \ DBH - 34.098, \qquad r^2 = 0.951, n = 10 \ cores$$

Specific hydraulic conductance from soil to leaves (g_L, $\mu mol \cdot m^{-2} \cdot s^{-1} \cdot Pa^{-1}$) was computed as in Cohen et al. (1983) from

$$[3] \quad g_L = \frac{F_d}{\Psi_{wp} - \Psi_{wm}}$$

g_L was only estimated from data obtained on bright, sunny days.

Stand transpiration (T_h, $mm \cdot h^{-1}$) was computed as

$$[4] \quad T_h = SA_T \ \Sigma \ F_{di} \ p_i$$

where SA_T is the stand sapwood area per unit of ground area ($dm^2 \cdot m^{-2}$), F_{di} is the sap-flux density of tree i, and p_i is the proportion of trees with sapwood area SA_i in the stand; five classes of SA were used in 1989, three in 1990, and three in 1991.

To validate this evaluation of T, we computed stand evapotranspiration obtained with the water balance method. Weekly measurements of soil water content and of throughfall during the three consecutive growing seasons were used.

Canopy conductance was evaluated hourly from sap flow and climatic data using the Monteith (1973) transformation of the Penman equation and assuming that vapor flux was equal to instantaneous stand transpiration (T_i) calculated from xylem sap-flux densities:

$$[5] \quad g_c = \frac{1}{r_c} = \frac{\lambda\gamma \ T_i/r_a}{\Delta(R_n - G) + \rho C_p \ VPD/r_a - \lambda T_i(\Delta + \gamma)}$$
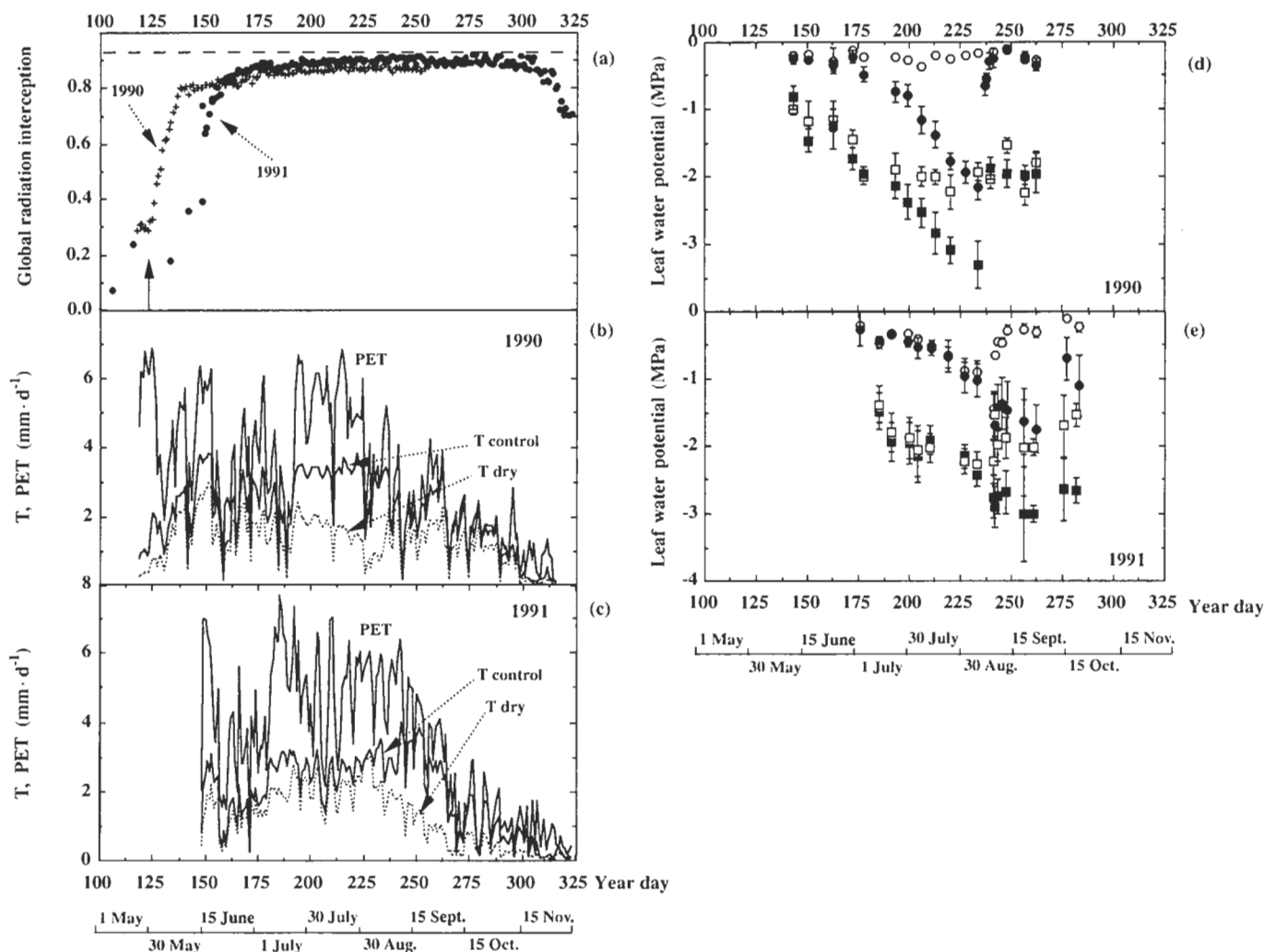
FIG. 1. Seasonal evolution of (a) interception of global radiation by the canopy during 1990 (crosses) and 1991 (circles) (the vertical arrow shows the date of frost in 1991), (b–c) daily transpiration (T) of control (line) and stressed (broken line) trees and of Penman potential evapotranspiration (PET) during summers 1990 and 1991, and (d–e) predawn (circles) and minimal (squares) leaf water potentials (means of five replicates ± SD) of control (open symbols) and drought-stressed (solid symbols) *Quercus petraea* trees during summers 1990 and 1991. The dry plot was rewatered at day 233 in 1990.

where

g_c is canopy conductance to water vapor (cm·s^{-1})

r_a is aerodynamic conductance, calculated from wind speed and mean height of the stand using the Monteith (1973) equation

T_i is stand transpiration (kg·m^{-2}·s^{-1})

λ is latent heat of water evaporation (J·kg^{-1})

Δ is slope of the saturation vapor pressure function (Pa·°C^{-1})

R_n is net radiation (W·m^{-2})

G is heat flux in soil and canopy (W·m^{-2})

VPD is vapor pressure deficit (Pa)

γ is psychrometric constant (Pa·°C^{-1})

ρ is air density (kg·m^{-3})

C_p is heat capacity of the air (J·kg·°C^{-1})

Morning values (before 8:00 a.m. UT), and measurements made during rain events and 1 h after, were discarded from the calculation, as in this case available energy is consumed for free-water evaporation and not for transpiration. Heat fluxes into soils have been computed

during another experiment at this site (L. Gay, personal communication). As they never exceeded 30 W·m^{-2}, and usually were between 10 and 20 W·m^{-2}, we neglected them for final computation. Heat fluxes in the biomass were computed from a simple model based on (i) hourly temperature variations, (ii) an estimate of stand biomass, and (iii) a mean heat capacity of trees.

Stomatal conductance to water vapor (g_s) was averaged from five individual measurements on sun-exposed leaves from the upper crown between 11:00 and 12:00 a.m. UT, once weekly on bright, sunny days. A steady-state porometer (LI-1600, LI-COR, U.S.A.) was used, and the leaf area enclosed in the porometer was measured with a video camera coupled to an image analyzer (Delta-T Devices, U.K.).

Results

Evolution of radiation interception, daily transpiration, and leaf water potentials

Seasonal evolution of radiation interception in 1990 showed a steep increase until day 140 (Fig. 1a), caused by leaf expansion during the first growth flush, and a slow increase until day 180, accompanying the second leaf flush. A third leaf flush was observed on a few trees, but it had no effect on total
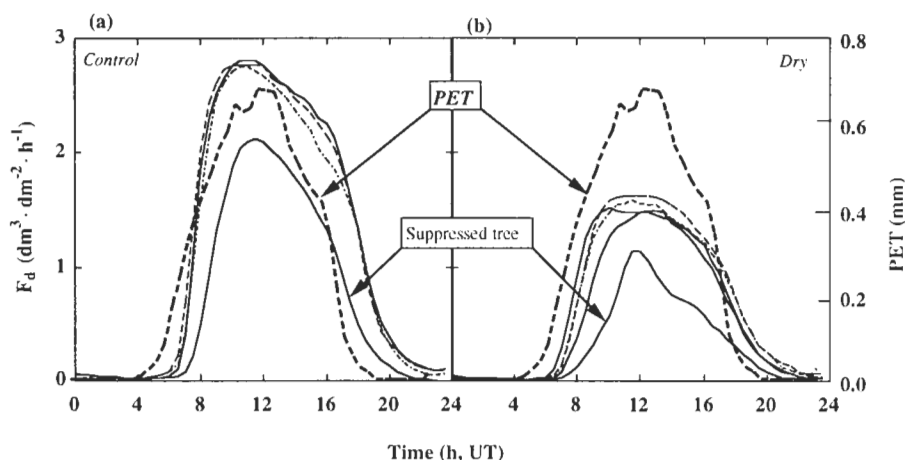
FIG. 2. Diurnal variation of xylem sap-flux density (F_d) measured on (a) four control and (b) five drought-stressed *Quercus petraea* on July 19, 1990, as compared with Penman potential evapotranspiration (PET) measured above the canopy. Measurements were made on four dominant and one suppressed tree. Predawn leaf water potential = −0.8 MPa for the stressed trees and −0.3 MPa for the control trees.

TABLE 1. Comparison of values of annual stand transpiration as estimated from the water balance technique (ET) and from sap-flow measurements (SF), during three successive growing seasons

	Period (days)*	Treatment	ET (mm)	SF (mm)	Difference (%)
1989	200–306	Control	157	138	−12
1990	201–312	Control	235	222	−6
	138–235	Drought	154	141	−8
1991	163–289	Control	308	294	−5
	163–239	Drought	151	150	−1

*Days of the year.

LAI nor on radiation interception. In 1991, a frost occurred during bud break and delayed leaf expansion by about 3 weeks in comparison with 1990. As a consequence, a rather slow but continuous increase was observed all summer 1991 until autumn, probably due to lamma shoots expansion or disorders in growing flushes. Maximal values of radiation interception during summer 1991 (around 80%) were higher than during 1990, as below-canopy radiation was measured closer to the soil surface.

Two methods of measuring stand transpiration were compared: evapotranspiration, which was calculated by means of the water balance method, and sap flow. Table 1 shows good agreement between both methods over the 3 years of the experiment. Evapotranspiration displayed slightly higher values than sap flow, probably because of soil evaporation; the maximal difference (12.1%) was observed during 1989.

Figures 1b and 1c display the seasonal fluctuations of the daily Penman PET and of transpiration (T) of control and drought-stressed trees during 1990 and 1991. In the control plot T was slightly, but not significantly (Student's t-test, $p = 0.05$), higher than in the drought-stressed plot, even at high soil water content. Increasing drought (between days 195 and 235 during 1990; between 225 and 260 during 1991, Fig. 1c) significantly reduced transpiration of stressed trees.

Figure 1d shows the evolution of Ψ_{wp} and Ψ_{wm} during 1990. Ψ_{wp} of control trees remained almost constant during the whole period, with a slight reduction from −0.3 to −0.4 MPa during the driest periods; in fact, and despite frequent rewa-

tering, control trees were probably subjected to a slight water stress during approximately 10 days from day 200 on. The difference between Ψ_{wp} and Ψ_{wm} ($\Delta\Psi_w$) increased during the first weeks, in parallel with leaf expansion (second growth flush), and remained relatively constant thereafter at the high value of about 2 MPa. Drought induced a progressive and parallel decline of Ψ_{wp} and Ψ_{wm} to values of −2.2 and −3.6 MPa, respectively, prior to reirrigation. $\Delta\Psi_w$ remained almost constant during drought at about 1.3 MPa. During 1991 (Fig. 1e), mean Ψ_{wp} and Ψ_{wm} were −1.7 and −2.9 MPa, respectively, on September 19 (day 262), indicating that the 1991 drought had been less severe and had occurred later in the season. Control trees showed lower predawn water potential than in 1990 because of inadequate irrigation.

Water fluxes and transpiration

The daily evolution of xylem sap-flux densities (F_d) of well-watered trees, as monitored during a bright day in 1990 on all trees, revealed a good correlation with Penman PET (Fig. 2). All well-watered trees displayed the same F_d (but not the same total sap flow), with the exception of a suppressed individual with much lower values. This observation confirms the uniform participation of dominant and codominant trees to the canopy transpiration on a sapwood area basis, as assessed in eq. 4. Drought-stressed trees were at a moderate stress intensity ($\Psi_{wp} = -0.8$ MPa) and already displayed a strongly reduced F_d. The suppressed individual in the stressed plot again displayed a lower F_d.

Stand transpiration

Daily stand transpiration (T) of control trees, calculated from eq. 4 during the period of optimal water supply (i.e., before day 200), reached maximal values of about 3.8 mm·d⁻¹, while PET attained 6 mm·d⁻¹. The relationship between T and PET diverged from linearity with increasing PET (Fig. 3), probably because of decreased canopy conductance induced by stomatal closure during days of high PET. In fact, canopy conductance, computed as in eq. 5 on an hourly basis, could be fitted to a model derived from Lohammar (as cited in Halldin et al. 1980). This model uses hourly means of global radiation above the canopy (R_g) and of vapor pressure deficit (VPD) as variables, and a nonlinear regression (Gauss–Marquardt algorithm):
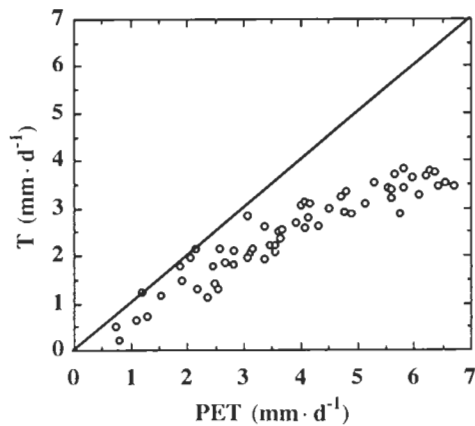
FIG. 3. Relationship between Penman potential evapotranspiration (PET) and daily transpiration (T) of control trees in the *Quercus petraea* stand (in 1990) as calculated from measured xylem sap-flux densities. Values from days 140 to 200, that is, after completion of the second growth flush and during the period of optimal water supply to control trees, were plotted. The diagonal represents the optimal 1:1 relationship.
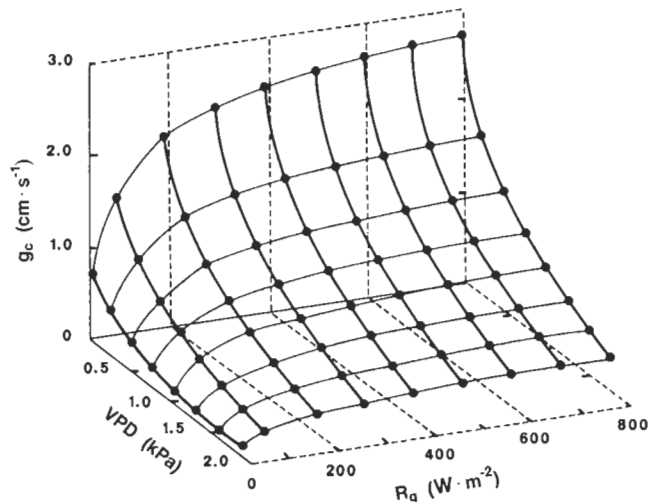

FIG. 4. Response surface relationship between canopy conductance (g_c), as calculated on an hourly basis from Penman–Monteith equation; global radiation (R_g); and vapor pressure deficit (VPD) for control trees of the *Quercus petraea* stand. Data were gathered during summer 1990.

$$[6] \quad g_c = \frac{R_g}{R_g + 65} (3.26 - 0.98 \ln(VPD))$$

$$r^2 = 0.89, \, n = 500$$

The resulting model is presented in Fig. 4. It clearly shows very strong negative effects of VPD on canopy conductance, at all levels of irradiance.

Effects of restricted water supply

The evolution of the weekly averaged ratio of transpiration of drought-stressed versus control trees as a function of decreasing relative extractable soil water (REW) displayed two successive phases during 1990: relative stability around 0.8 until a REW threshold of about 0.4 and a strong decrease thereafter (Fig. 5). But transpiration of drought-stressed trees
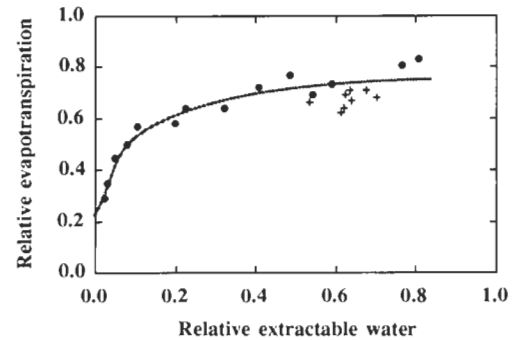

FIG. 5. Relationship between the ratio of transpiration rates of drought-stressed and control *Quercus petraea* trees (weekly mean values) and relative extractable soil water during an increasing drought in 1990. Circles represent the drought, and crosses represent values after complete rehydration of the dry plot. Line was fitted by eye.
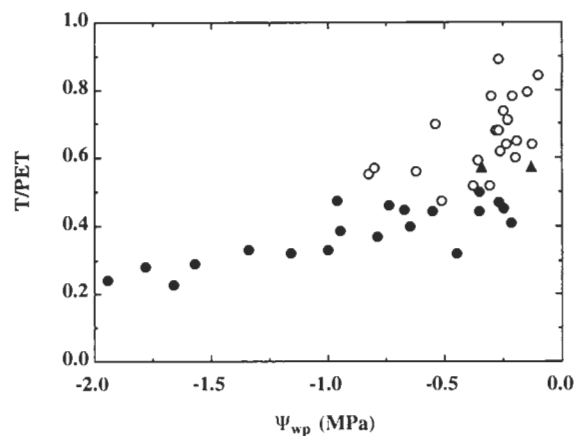

FIG. 6. Relationship between mean relative daily canopy transpiration (ratio T/PET) of control (open circles) and drought-stressed (solid circles) trees and predawn leaf water potential (Ψ_{wp}). Black triangles represent values measured on previously stressed trees after rewatering. Only values measured after completion of the second growth flush were plotted. Means were calculated over a 10-day period, during 1990 and 1991 summers.

remained significantly high for very low values of REW (60% of controls at 0.2, and 30% with maximal drought). Rehydration allowed an almost immediate (i.e., in 2–3 days) recovery to values very close to the initial ones. The stress effects on transpiration were therefore almost completely reversible. Maximal values of relative transpiration were significantly lower than 1.0; this was probably due to wounding of the root system of the dry plot during the trench excavation.

Another interesting feature of these stress effects involved the relationship between Ψ_{wp} and the ratio of transpiration and PET (Fig. 6). This ratio declined slowly from 0.8 to about 0.2 at maximal stress ($\Psi_{wp} = -2.0$ MPa), indicating maintenance of significant transpiration during water shortage. As already stated, rehydration was followed by an almost complete and rapid recovery of relative transpiration.

The seasonal variation (1990 experiment) of the specific hydraulic conductance (g_L) of *Q. petraea* (Fig. 7) showed a decline during early summer in both treatments, despite an important interindividual variability. Later, g_L remained constant over the summer for control trees, but declined again with drought on stressed trees. Reirrigation of the latter allowed
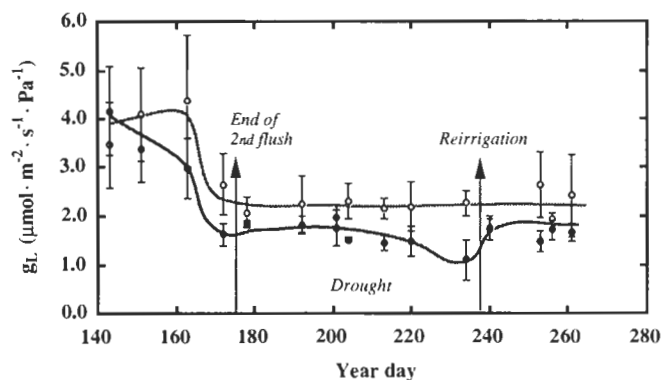
FIG. 7. Seasonal variation of mean specific hydraulic conductance (g_L) of control and drought-stressed trees of *Quercus petraea* during 1990. Arrows show end of second leaf flush, and end of drought, respectively. Solid circles represent the drought-stressed trees, and the open circles represent the control trees. Data presented are means of three dominant trees ± SD of the mean for each treatment. Lines are fitted by eye.
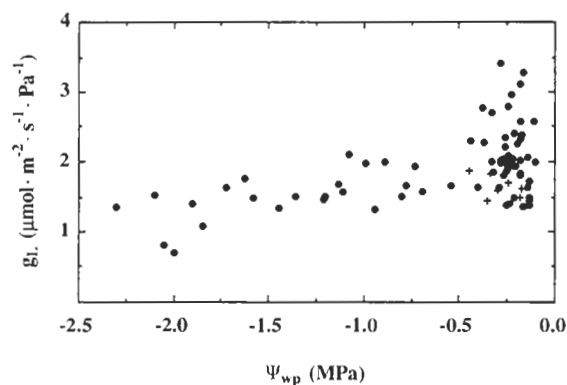

FIG. 8. Relationship between specific hydraulic conductance (g_L) and predawn leaf water potential (Ψ_{wp}) of individual *Quercus petraea* during 1990. Values presented are from day 180 to the end of measurement period. Crosses represent previously stressed trees after rewatering.

FIG. 9. (*a*) Seasonal variation of mean midday stomatal conductance (g_s, ± SD) measured on 10 sun-exposed leaves of the upper canopy of two control (open circles) and three drought-stressed (solid circles) *Quercus petraea* of each treatment. (*b*) Relationship between g_s and predawn leaf water potential (Ψ_{wp}) of individual trees (mean values of five replicates) of *Quercus petraea*.

return to prestress values of g_L. Between Ψ_{wp} of −0.5 and −2.5 MPa, drought induced a slight decline in g_L when plotted as a function of Ψ_{wp} (Fig. 8). Nevertheless, g_L remained relatively high even at the strongest stress intensities (around 50% of prestress values).

Seasonal variation of 1991 midday stomatal conductance (g_s) of sun-exposed leaves from the upper canopy displayed significant variations (Fig. 9*a*). On control trees, an initial increase, probably due to leaf maturation, was followed by a decline, which was reversed after manual rewatering (day 241) and was relatively constant during late summer. Stomatal conductance of dry trees was not significantly different from that observed on control trees up to day 240, as the control plot was not irrigated during this period. Later, dry trees showed much lower g_s. The relationship between Ψ_{wp} and g_s revealed a rather gradual decline with increasing stress intensity (Fig. 9*b*).

Discussion and conclusion

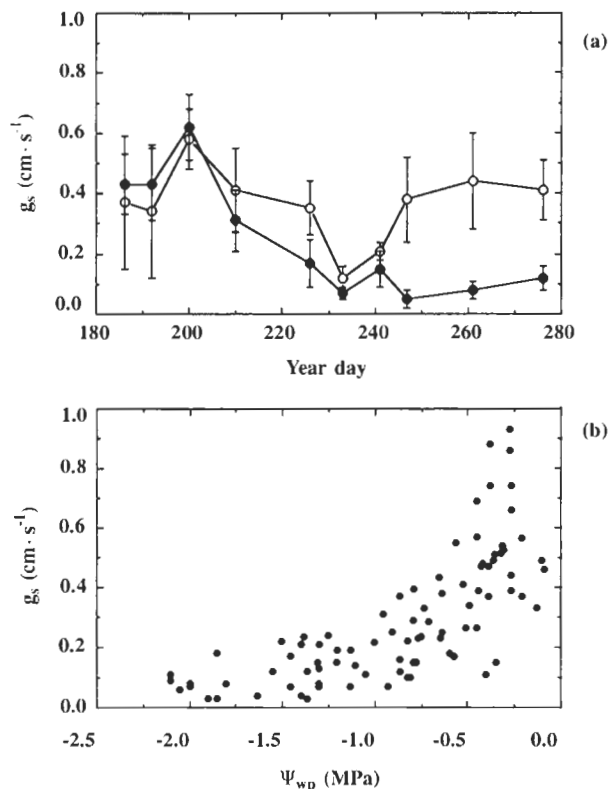The estimation of stand transpiration based on sap-flow monitoring yielded results very close to those obtained from the water balance method. This again demonstrated the reliability of this technique (Granier 1987; Granier et al. 1990). Daily transpiration of our oak stand reached 3.8 mm·d⁻¹ during the first weeks of summer. These values are of the same order of magnitude as those reported by Penka (1985) (3.2 to 3.4 mm·d⁻¹, measured with heat balance xylem flowmeters) and by Nizinski and Saugier (1989) (3.3 mm·d⁻¹, water balance method), both of which were obtained on older *Q. petraea* stands. Measurements made on conifer stands yielded similar values: around 3.6 mm·d⁻¹ on *Pseudotsuga menziesii* (Mirb.) Franco (Granier 1987) and 3 to 3.5 mm·d⁻¹ on *Pinus pinaster* Ait. (Loustau et al. 1990).

Transpiration of this stand under well-watered conditions was very close to the Penman PET at low values but diverged strongly when PET exceeded 4 mm·day⁻¹. This effect may be related to limitations of canopy conductance (g_c) by stomatal closure induced by high VPD. Calculations of g_c on an hourly basis confirmed this hypothesis. It was also reported by Shuttleworth (1989) on different temperate and tropical species, including conifers and broad-leaved species. Measurements of stomatal conductance and net CO_2 assimilation rates on the same trees revealed a strong midday stomatal closure during hot days with high VPD (Epron et al. 1992). In fact, midday stomatal closure induced by high VPD is a very common feature of most tree species (Tenhunen et al. 1987) and may explain limitations of maximal transpiration in the absence of soil water deficits.

Total specific hydraulic conductance (g_L) estimated from sap-flux densities and Ψ_{wp} (Cohen et al. 1983) revealed changes in the liquid-water path from soil to leaves. Values of g_L obtained from oaks during summer ($2.5\ \mu mol \cdot m^{-2} \cdot s^{-1} \cdot MPa^{-1}$) appeared significantly lower than those from a few tested conifers: 3.3, 3.7, and $4.0\ \mu mol \cdot m^{-2} \cdot s^{-1} \cdot MPa^{-1}$ for *Picea abies* (L.) Karst., *Abies bornmulleriana* Natt., and *Pinus pinaster*, respectively (Granier et al. 1990). But the definition of g_L based on sap-flux densities in the sapwood probably cannot be used for direct comparisons between conifers and broad-leaved species: in the latter case, sap transport is probably restricted to a few external rings of the sapwood. Using measurements at different depths in oak stems, we observed (unpublished data) that 80% of the total sap flow occurred in the first 11 mm (i.e., in five or six annual rings). Therefore, mean sap-flux densities based on our estimated sapwood area were probably underestimated. In fact, we measured sap-flux densities of about $2.5-3\ dm^3 \cdot dm^{-2} \cdot h^{-1}$, which were surprisingly close to those of conifers: $1.5-2\ dm^3 \cdot dm^{-2} \cdot h^{-1}$ (Granier 1987; Granier and Claustres 1989) in *Pseudotsuga menziesii* and *Picea abies*, and $2.5\ dm^3 \cdot dm^{-2} \cdot h^{-1}$ in well-watered *Abies bornmulleriana* (Granier and Colin 1990) and in *Pinus pinaster* (Loustau et al. 1990). An estimate based on total sap flow related to leaf area yielded in our case values of about $1.2\ \mu mol \cdot m^{-2} \cdot s^{-1} \cdot MPa^{-1}$, which is very close to values obtained for *Quercus alba* L. by Thompson and Hinckley (1977) and for *Quercus rubra* L. by Reich and Hinckley (1989).

The strong decline in g_L we observed during spring until the beginning of July had previously not been described. Two factors could explain such a decrease. (*i*) A reduction of the soil water content in the upper soil levels could have reduced hydraulic conductance of the soil compartment, and as a consequence, g_L. But we observed a good stability of Ψ_{wp} during this period; and the decline in g_L was mainly related to decreasing midday water potentials, associated with increasing total transpiration. Changes in soil water content were therefore probably not the main cause for the observed decreases in g_L. (*ii*) There is a long delay between cambial activation, which rapidly produces rapidly the large and functional xylem vessels of earlywood, and leaf area expansion in ring-porous and deciduous species such as oaks (Lachaud and Bonnemain 1981; Essiamah and Eschrich 1986). In fact, we observed a good concordance between the dates of stabilization of g_L and those for leaf expansion cessation (as shown by radiation interception). The initial decrease in g_L could therefore be the result of a decrease in leaf specific conductance, i.e., in the ratio of sapwood area to total leaf area. An alternative explanation of decreasing g_L from spring to summer could involve a transition of sap flow from earlywood to latewood vessels, but until now no direct measurements have confirmed this hypothesis (Abrams 1990).

The intensity of drought imposed on our trees was rather high. Values of Ψ_{wp} below -2.0 MPa, as were observed here, are very seldom measured under natural conditions. During the dry summer of 1989, Ψ_{wp} never dropped below -1.5 MPa (N. Bréda, unpublished). Measurements made on conifers revealed minimal values between -1.4 and -2.0 MPa during the drought of 1976 (Aussenac and Granier 1978). Some other measurements were made during the period of maximal water shortage in September 1991 (data unpublished) on adult *Pseudotsuga menziesii* and *Picea abies* in a forest close to the oak experiment. Values of Ψ_{wp} were, respec-

tively, -2.0 and -1.6 MPa. Stresses of the same order of magnitude were detected on *Q. alba* in the stand (Dougherty and Hinckley 1981).

Drought induced a slight decline in g_L in addition to the initial decrease during leaf expansion. This decline may be explained by two hypotheses. (*i*) The onset of xylem embolism in twigs and petioles induces a decrease of the hydraulic conductance. But estimates of vulnerability to embolism made on petioles and twigs of *Q. petraea* by Cochard et al. (1992) revealed a remarkable resistance of the xylem to cavitation. Significant embolism appeared only when leaf water potentials dropped below -2.5 MPa. Moreover, measurements of hydraulic conductance in the twigs and petioles of our stressed trees revealed only limited losses of conductance (less than 30%) restricted in 1990 and 1991 to a few individuals (Cochard et al. 1992). We may therefore conclude that the reductions in g_L were probably more related to changes in soil to root hydraulic conductance.

The observed decrease in g_L was analogous to that reported for *Q. alba* by Thompson and Hinckley (1977), and for *Quercus marilandica* and *Q. rubra* by Reich and Hinckley (1989). But *Picea abies* or *Abies bornmulleriana* showed a steeper drought-induced decline in g_L than did our oak trees (Granier and Claustres 1989; Granier et al. 1989). Precise origin of such interspecific differences is still a matter of discussion. Embolism was probably not involved in either case, as minimal leaf water potentials remained in all cases above the thresholds for cavitation induction measured by Cochard (1992) and Cochard et al. (1992). Rooting patterns were very different in both situations. Our oaks showed rather deep rooting, in a soil with two different compartments; the upper layer (0–60 cm) contained 75% of the total number of roots, while the lower one (70–140 cm) bore only 25%, with very fine and strongly ramified rootlets (N. Bréda, unpublished). Water use dynamics in both compartments were also different, water being extracted much more rapidly from the upper than from the lower horizon. In contrast, the conifers measured earlier were growing in a shallow and homogeneous soil limited by a clay layer at 70 cm (Granier et al. 1989). Recent observations (N. Bréda and A. Granier, unpublished) made in the same stand revealed that Ψ_{wp} was close to values of soil water potential measured in the wettest but still rooted soil layers, as reported by Aussenac et al. (1984) for *Pseudotsuga menziesii*. This ability to exploit deep soil layers could be a general property of oak species, which are often reported to be more deeply rooted than surrounding trees of other species (see review by Abrams 1990).

Another feature related to drought tolerance was the maintenance of relatively high daily transpiration rates during stress, implying that stomata remained open at least during parts of the day. In fact, midday stomatal conductance of sun-exposed leaves never dropped below $0.05\ cm \cdot s^{-1}$, and simultaneous measurements of photosynthesis on the same trees revealed maintenance of high rates of net CO_2 assimilation rates in the morning, followed by strong midday declines (Epron et al. 1992). Stomatal conductance of shade leaves probably remained above these values, and total transpiration was less reduced than would have been expected from sun leaf conductance alone.

The absence of strong connections between stomatal conductance and leaf water potential has been frequently discussed. Changes in the soil water content in the environment of upper roots has been shown to induce modifications in

stomatal conductance through root–shoot signalling (Davies and Zhang 1991); in particular, soil impedance, which is a function of soil water content, may control stomatal aperture (Masle and Passioura 1987; Tardieu et al. 1991). A second year of measurements with the same trees, and the search for abscisic acid in the xylem sap, should help us understand how stomata adapt to decreasing soil humidity under stand conditions. But we could hypothesize that early reduction in relative extractable water has no consequence on the bulk leaf water potential of the tree, probably because of the presence of large amounts of deeper roots able to maintain sufficient water supply.

Acknowledgements

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