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Original article

Intra- and interannual variations of transpiration, leaf area index and radial growth of a sessile oak stand (*Quercus petraea*)

N Bréda, A Granier

Équipe bioclimatologie et écophysiologie forestière, Unité d'écophysiologie forestière, Centre de Nancy, Inra, 54280 Champenoux, France

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Summary — Bud-burst, leaf area index (LAI), transpiration, soil water content and radial growth of a 35-year-old *Quercus petraea* stand were measured during 5 successive years (1989–1993). At the beginning of 1992, half of the stand was thinned. The increase of stand transpiration during spring was linearly correlated to the development of LAI. During the second part of the season, although LAI continued to increase because of rhythmic shoot development, transpiration was strongly reduced as soil water content decreased. The transpiration/potential evapotranspiration (T/PET) ratio decreased sharply as soon as relative extractable water (REW) dropped below 0.4. Likewise, cumulated stand transpiration varied among years because of variability in soil water availability, LAI and canopy structure. A linear relationship, similar to the one observed for weekly variations, was noted between T/PET and LAI; maximum LAI ranged from 3.3 to 6 in this ring-porous species. Seasonal circumference measurements showed that 43% of the annual increment was achieved before leaf development, hence before canopy transpiration and CO_2 assimilation were started. Tree ring area was significantly correlated to the cumulated transpiration; a water-use efficiency variable was defined at both tree and stand level.

transpiration / leaf area index / drought / circumference increment / *Quercus petraea*

Résumé — Variations intra- et interannuelles de transpiration, d'indice foliaire et de croissance radiale d'un peuplement de chêne sessile (*Quercus petraea*). *Le débourrement, l'indice foliaire (LAI), la transpiration, la teneur en eau du sol et la croissance en circonférence d'un peuplement de* Quercus petraea *âgé de 35 ans ont été mesurés pendant 5 années successives (1989 à 1993, fig 6). Au début de l'année 1992, la moitié du peuplement a été éclaircie. L'augmentation de la transpiration du peuplement au printemps était linéairement corrélée à LAI (fig 2). Au cours de la seconde partie de la saison, même si LAI continuait à augmenter en raison de la croissance rythmique des pousses, la transpiration était fortement réduite par la sécheresse édaphique. Le rapport transpiration/ETP diminuait rapidement dès que la fraction disponible de l'eau du sol chutait en dessous de 0,4 (fig 3). De même, la transpiration cumulée du peuplement variait entre les années avec la disponibilité en eau du sol, le LAI et la structure du couvert. Une relation linéaire similaire à celle observée à l'échelle hebdomadaire a* *été mise en évidence entre T/ETP et LAI pour une gamme de LAI s'étendant de 3,3 à 6,0, selon les années et la densité des traitements (fig 8). Les mesures d'accroissement en circonférence au cours de la saison ont montré que 43 % de l'accroissement annuel était réalisé avant le développement des feuilles (fig 4), donc avant la reprise de transpiration et d'assimilation du carbone. La surface de chaque cerne était significativement corrélée à la transpiration cumulée au cours de la saison de végétation (fig 10). Une variable d'efficience d'utilisation de l'eau a été définie à la fois à l'échelle de l'arbre et du peuplement.*

***transpiration / indice foliaire / sécheresse / croissance en circonférence /* Quercus petraea**

INTRODUCTION

Fundamental requirements in modelling forest ecosystem processes are the rates and control of energy, carbon, water and nutrient exchange by forested surfaces, and the responses of these surfaces to natural or silvicultural perturbations such as canopy opening, or to precipitation deficits or excess. Moreover, production depends on leaf area and may be influenced by canopy structural characteristics (canopy stratification and coverage, leaf area index) (Roberts et al, 1993) as well as ambient weather conditions (Jarvis and McNaughton, 1986; Running, 1986). Therefore, an analysis of the growth and health of forest stands needs a good description of crown condition and an accurate estimate of drought-induced stress on both a daily and annual basis.

Leaf area index (LAI, the ratio of leaf area per unit ground area) was often found to be a powerful parameter for the analysis of stand structure. A high LAI is an indication of high site fertility and optimal stand health and productivity. In many models, it is the main independent variable for determining canopy interception, transpiration, respiration, photosynthesis, carbon allocation and litterfall (Running and Coughlan, 1988). LAI varies from stand to stand. Among variables regulating leaf area, soil water availability, as determined by climate and soil properties, is by far the most significant. The effect of water deficit on leaf growth may even be more important to stand productivity than its effect on photosynthesis (Gholz et al, 1990). Leaf area, climate and soil should then interact and one may assume that an ecological equilibrium links these parameters. This assumption has been directly verified at regional scale and for coniferous stands (Grier and Running, 1977).

In another way, transpiration integrates soil water availability and the atmospheric evaporative demand, and has a great influence on physiological processes that determine carbon fixation and growth (Nemani and Running, 1989). As shown by simultaneous measurements of water vapour and carbon dioxide fluxes from a deciduous forest by eddy correlation method, canopy photosynthesis and transpiration are strongly and linearly correlated (Baldocchi et al, 1987). There is much evidence that biomass production is correlated with water use (Legg et al, 1979; Schulze and Hall, 1981; Baldocchi et al, 1987; Honeysett et al, 1992). However, these observations were mainly reported at the stand level and on an annual basis. Little information concerning the magnitude and the timing of intraannual variations of transpiration, LAI, drought and growth exists. Many agricultural studies have shown that transpiration approaches a maximum at a LAI less than 3, the point of canopy closure (Brun et al, 1972; Saugier and Katerji, 1991). Almost no data are available for trees, and one may assume that the high canopy stratification may lead to different canopy behaviour for forest stands.

The aim of this study was to analyse the relationships between transpiration and growth in an oak stand, on both seasonal and annual time paces. The modifications of transpiration were successively analysed as a consequence of i) seasonal and annual variations in leaf area index and ii) soil water balance. Finally, tree and stand growth were described in relation to water use.

SITE AND MEASUREMENTS

The study was conducted during 5 years from 1989 in an almost pure *Quercus petraea* stand in Champenoux Forest, France (48°44N, 6°14E, altitude 237 m). The stand was naturally regenerated, following the 1961s acorn production. At the beginning of 1992, half of the stand (0.16 ha) was thinned. Thirty-five percent of the basal area (28% of the sapwood area) was removed, leaving a plot with a basal area of 17.6 $m^2 \cdot ha^{-1}$ and tree density of 3 077 $trees \cdot ha^{-1}$. The unthinned part (control) had 24.6 $m^2 \cdot ha^{-1}$ and 3 352 $trees \cdot ha^{-1}$ (for further details, see Bréda et al, 1993a and 1995).

Radial increment

Seasonal circumference increment at breast height was measured manually every 10 days on a sample of 100 to 175 trees in each treatment, from mid-March to October during the whole experiment. The reference level was marked with a circle painted after smoothing the bark. Readings were made on dry stems to avoid bark swelling. Data were expressed as the mean cumulated increment for four initial circumference classes (< 200, 200–300, 300–400 mm and > 400 mm) or as relative circumference growth (Hunt, 1982). These classes corresponded approximately to trees in suppressed, intermediate, codominant and dominant crown position in the canopy, respectively. The size of each class was related to diameter distribution in the stand.

In addition to this extensive growth record, 25 trees were randomly selected in the control stand to analyse radial increment from tree rings, since the origin of the stand. Two cores per tree were extracted at 1.3 m above ground along the north–south direction. Measurements from the two cores were averaged. Ring width was measured using a semi-automatic device (Becker, 1989), and cross-dated. As the boundary between earlywood and latewood was easily detected (differing by the size of xylem elements), both were separately measured. Annual width and basal area were computed for each year ring.

Leaf area index

The intraannual variation in LAI was monitored from both global radiation interception (thermopyranometers, INRA, France) and LAI-meter (Demon, CSIRO, Australia), according to the procedure described by Bréda et al (1995). Litter collection during autumn provided every year a direct estimate of maximal LAI. The leaf-fall collection was based on 49 trays (0.25 m^2) from 1989 to 1991, and 21 traps in each plot after thinning. LAI was calculated from daily global radiation interception by inverting the Beer–Lambert equation. Light extinction coefficients, as determined from allometric estimates of maximal LAI (sapwood–leaf area relationship) were 0.38 and 0.28 in control and thinned stands, respectively.

Bud-burst observations

Bud-burst observations were recorded from mid-April to end of May on a sample of ten control and 15 thinned trees from each plot on a 2-day time notation. Bud development was described according to a six stage scale (dormant winter buds, swollen buds, broken buds, just-unfolded leaves, unfolded leaves, developed leaves with elongation of twigs). Bud-burst index ranged from 0 to 100 and was computed as the mean notation of the ten or 15 trees. Shoot flushing events were also dated, but no quantitative estimate was performed.

Stand transpiration

Stand transpiration was estimated from sap flow measurements monitored on a sample of four to eight trees (table I). A larger number of trees was measured in the thinned plot where the variability was higher (Bréda et al, 1995). Trees were chosen according to the sapwood distribution in the stand. The radial sap flowmeters (Granier, 1987) were inserted every year before bud-break and removed during October. Sap flow data were collected on a half hour basis. These devices measure sap flow per unit of sapwood area (sap flux density). Since both control and thinned trees exhibited the same linear sapwood–leaf area relationship (Bréda et al, 1995), sap flow density was proportional to vapour flux density per unit leaf area (ie, transpiration) with the same ratio. Sap flow cumulated over the growing season ($l.year^{-1}$) was calculated for each tree as the product of sap flux density by the sapwood area at the sensor level. Stand transpiration (T, $mm.day^{-1}$) was finally computed from individual sap flow density measurements and stand sapwood area per unit of ground area.

At the end of the experiment, two cores were extracted from all the trees used for sap flow (18 trees) to measure precisely radial increment during the 5 studied years as previously described.

Soil water content

Soil water content was monitored during the 5 years of survey using a neutron probe (Nordisk Elektrisk Apparatfabrik, Denmark).

Table I. Experimental design of the 5 years of measurements for control and thinned stands. The network used for neutron probe estimation of soil water content included one 2.80 m long tube at least, others being 1.60 m long. Number of trees sampled for sap flow measurements, bud-burst notation and seasonal radial increment survey.

Measurement	*1989 Control*	*1990 Control*	*1991 Control*	*1992 Control*	*1992 Thinned*	*1993 Control*	*1993 Thinned*
Litter traps	49	49	49	21	21	21	21
Neutron probe access tubes	12	12	9	3	13	3	13
Sap flow	5	4	4	4	6	4	8
Radial increment	175	146	137	91	84	97	88
Bud-burst	10	10	10	10	15	10	15

Measurements were performed every week during the growing season, and monthly during the winter. The actual soil water content (*R*) was computed from soil moisture profiles (0–160 cm) resulting from counts logged every 10 cm (from surface to 1 m deep) or 20 cm (below 1 m). The access tubes network used in each treatment and year is presented in table I. Soil water availability in the rooted zone was expressed as relative extractable water calculated as REW= $(R - R_{min}) / (R_{max} - R_{min})$, where *R* is the actual soil water content (mean value computed from n access tubes), R_{min} the minimum soil water content observed in experimental dry plots, R_{max} the soil water content at field capacity. Total soil extractable water (R_{max} – R_{min}) was 165 mm.

Climate data

Climate data were monitored 2 m above the canopy and logged every 30 min with a Campbell (CR7) from May to October. The weather station included a pyranometer (Kipp & Zonen [Delf, Holland] or Cimel [Paris, France]), a ventilated psychrometer with platinum sensors (model INRA) and an anemometer (Vector Instruments [Rhyl, UK]). Evapotranspiration was computed according to the Penman equation.

RESULTS

Seasonal fluctuations of leaf area index, transpiration and growth

Transpiration increased in the spring as soon as leaf expansion began (fig 1). The dynamics of foliage development were so rapid that day-to-day increases in leaf area were detected by changes in transmitted global radiation. On 10 May (day 130), the time-course of sap flow and hence of transpiration was only 20% of potential evapotranspiration (PET). Transpiration reached 50% of PET after 8 days, while the first flush was expanded and 80% of the maximal LAI was completed. It should be noted that sap flow first lagged behind PET during the morning of the first days at the beginning of May. This time lag disappeared after 1 week and may have involved stored stem water.

This increase in stand transpiration during the spring was linearly correlated with LAI until complete expansion of the first flush (fig 2). The scatter around this regression

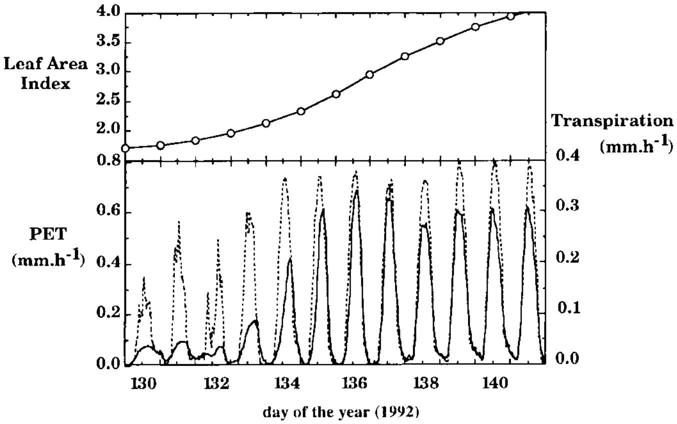

Fig 1. (top) Daily increase of leaf area index calculated from continuous measurements of global radiation transmittance (thermopyranometers) during spring 1992 (10 to 21 May); (bottom) Daily time-courses of stand transpiration estimated from sap flow measurements (solid line) and potential evapotranspiration (PET, dotted line).

was related to differences in soil water availability and/or in PET conditions among weeks. Nevertheless, some differences among years were detected, the main one being observed in 1990 with higher transpiration rates than the following year. In 1989 and 1991, sap flow measurements started too late to monitor the spring increase of transpiration. An increase of T/PET in the thinned as compared to control was observed in 1993, while a single regression had been observed for both treatments in 1992.

Leaf area index reached at least 80% of maximum before soil moisture deficits began. As a consequence, drought effects could be analysed without large fluctuation of LAI. The effect of soil water depletion on transpiration during the summer is shown in figure 3. The ratio of transpiration over PET was affected when soil water content dropped below 40% of REW. This threshold for regulation of transpiration was also detected from reductions in canopy conductance (see Granier and Bréda, 1996).

The carbon allocation patterns during the growing season have been indirectly assessed from phenological and growth observations. Seasonal measurements of circumference showed that about 43% (on average over the 5 years) of the annual increment was achieved before any significant leaf development (figure 4), hence before transpiration and CO_2 assimilation had started. In particular, the whole anatomical earlywood (wood zone including large vessels), representing 19% of the annual tree ring, was completely established by the end of April, that is, 1 month before leaf emergence (end of May). It may be concluded that earlywood was formed from carbon resources accumulated during the previous years. At the end of spring (21 June), and hence before summer drought, the main part of cumulated circumference increment was achieved. A larger sample of ring widths of sessile oaks from this stand demonstrated that the annual increment of earlywood was independent of soil water deficit (fig 5). Soil water deficit was computed from a daily water balance model, using climatic data to

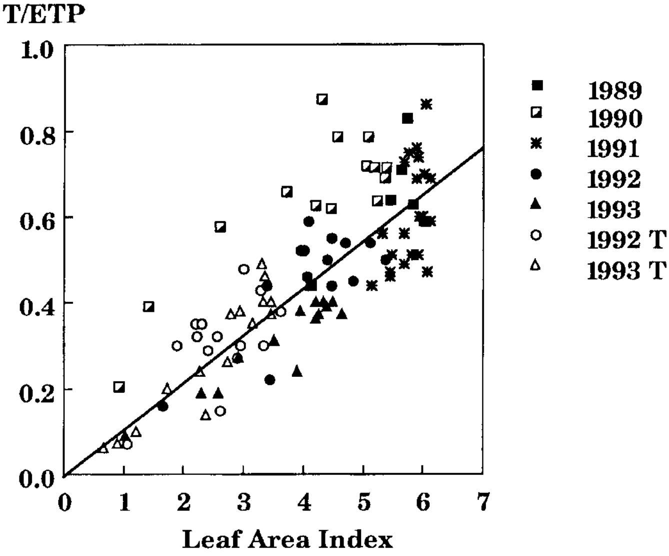

Fig 2. Mean value of transpiration (T) over potential evapotranspiration (PET) calculated over 10 day periods from bud-burst to end of the first flush expansion (mid-June) plotted against leaf area index estimated from radiation transmittance (thermopyranometers from 1989 to 1991 and Demon in 1992–1993). In 1992 and 1993, data were collected in control (closed symbols) and thinned (open circles and triangles) plots. Best fit linear regression was: T/PET = 0.106 * LAI + 0.029, r^2 = 0.67.

drive transpiration, interception and evaporation (Bréda, 1994). In contrast, a significant, negative effect of soil water deficit was observed on latewood thickness. Spring frost during the previous year contributed to residual variation.

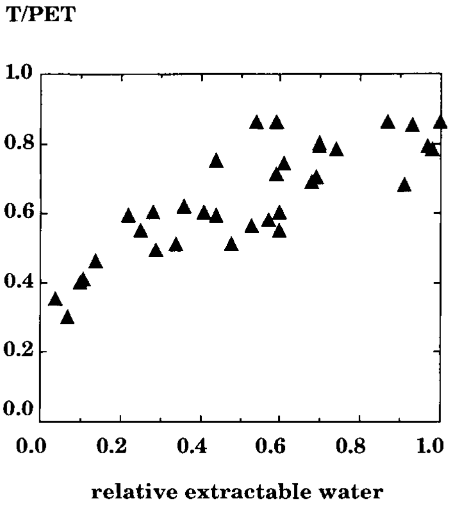

Fig 3. Effect of soil water depletion of the T over PET ratio during the summer, after full expansion of the spring leaf flush.

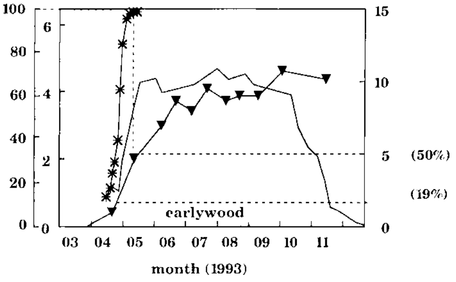

Fig 4. Example of seasonal dynamic of phenological development including bud-burst (asterisks) and leaf area index (solid line), and circumference growth (inverted triangles) of the control oak stand (1993). The bud-burst index ranged from 0 to 100. The threshold for earlywood (ie, wood bearing large vessels) is shown.

Year-to-year variations in transpiration and leaf area index

Figure 6 compares the annual time-courses of T/PET, LAI, circumference increment and relative extractable water observed during the 5 years of survey. It shows that maximal transpiration, maximal LAI and minimal soil water content varied from year to year. These annual characteristics are also reported in table II. Leaf area index increased from spring to autumn in relation to the rhythmic shoot growth of the oaks (three flushes were usually observed). The increase of LAI resulting from the second and third flushes was not always followed by an increase of transpiration, because i) juvenile leaves exhibited low stomatal conductance and ii) they appeared during periods of high PET- inducing stomatal closure. The different transpiration rates among years were accompanied by different circumference increments. The annual cir-

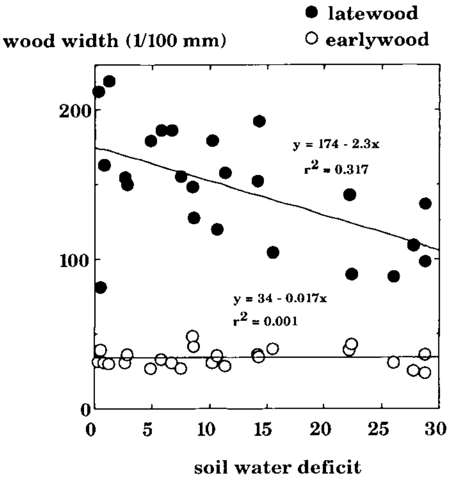

Fig 5. Effect of soil water deficit on earlywood (open circles) and latewood (solid circles) increment as a function of soil moisture deficit computed for an extractable water of 165 mm. Each point represents the mean increment (25 sessile oak cores) of 1 year from 1961 to 1993. Only years exhibiting a period of soil moisture deficit were reported.

Table II. Climatic and phenological characteristics of the 5 studied years: precipitations and potential evapotranspiration (PET) during the growing season (from May to October), summer drought duration (number of days during which relative extractable water [REW] < 0.4), intensity of the drought (minimum REW), and mean bud-burst date and maximum leaf area index (LAI) as computed from litter collection.

	Control					*Thinned*	
	1989	*1990*	*1991*	*1992*	*1993*	*1992*	*1993*
Precipitations (mm)	268	382	276	338	434	338	434
PET (mm)	609	595	615	558	502	558	502
Drought duration (days)	93	43	35	81	57	0	35
Minimum REW	0.15	0.28	0.19	0.16	0.09	0.45	0.24
Bud-burst date		3 May	25 May	13 May	30 April	7 May	28 April
Duration of leafly period (days)		181	171	174	188	182	194
Maximum LAI	6.0	5.6	6.0	5.1	4.2	3.3	3.3
Accident		Irrigation from day 218	Spring frost				

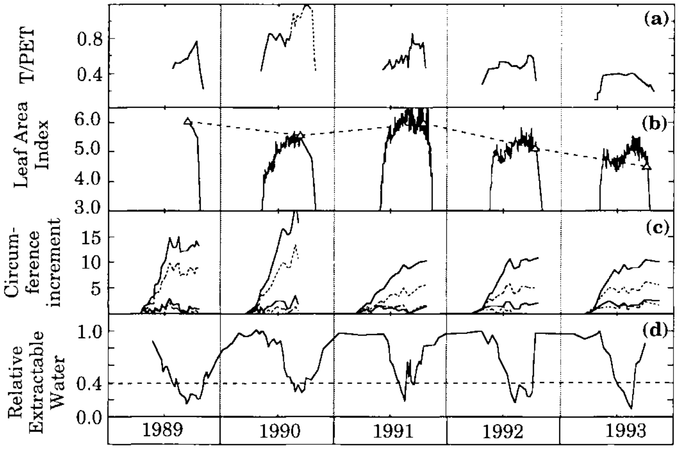

Fig 6. (**a**) Interannual variations in stand transpiration (T/PET): in 1990, trees used for transpiration measurements were irrigated during the second part of the season (dotted line). (**b**) Variations in leaf area index, computed from litter collection (triangles) or from interception of radiation (solid line). (**c**) Cumulated circumference increment, represented for four initial circumference classes (< 200, 200–300, 300–400, > 400 mm). (**d**) Variations in relative extractable water computed from neutron probe measurements. The dotted line represents the threshold for soil moisture deficit (REW < 0.4).

cumference increment curves exhibited the same pattern during the 5 years: a linear part which stopped every year around 15 July, followed by a plateau. The date of this cessation of growth was independent of soil water content and may reflect a pattern of growth mainly determined by day-length and cumulated temperatures. Some fluctuations during the second part of the growing season depended on relative extractable water and may have reflected changes in stem water content rather than growth events. In particular, stem shrinkage appeared when REW dropped below the threshold of 0.4. The final annual increment was therefore mostly dependent on the rate of circumference increment during the spring, calculated from the linear part of the seasonal curve of growth (fig 7). No difference between control and thinned stands appeared and a single regression was calculated without 1991 data ($r^2 = 0.89$). Data from 1991 were excluded because the initial rate of increment was significantly lower in that year, perhaps because of a severe spring frost (–4.2 °C on 24 April). In 1990, both high water supply and LAI led to the highest growth. The last 2 years (1992–1993) exhibited summer droughts and also a lower LAI.

On a seasonal basis, a linear relationship appeared between annual mean T/PET and LAI (fig 8). During the study, maximum LAI ranged between 3.3 and 6, depending on the year and the stand density. In the control plot, LAI and T/PET decreased in proportion from 1989 to 1993. In the thinned plot, T/PET increased between 1992 and 1993 without any modification of LAI as a consequence of i) a greater light use efficiency bacause of better crown exposure and ii) a higher soil water availability (Bréda et al, 1995).

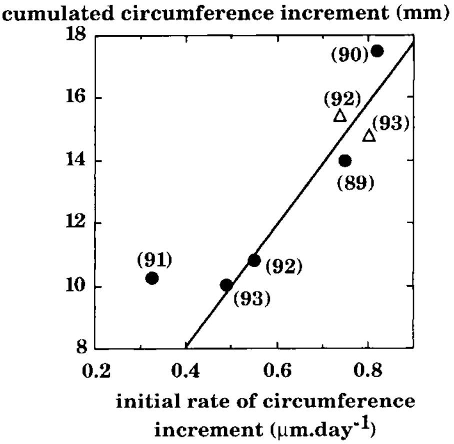

Fig 7. Cumulated circumference increment over the growing season for the biggest trees (initial circumference > 400 mm) as a function of initial circumference increment rate (mm.day^{-1}), calculated as the slope of the linear part of the growth curve, ranging from mid-April to mid-July (d100 to d200). Years are indicated in parentheses; control (solid circles) and thinned (open triangles) stands are reported. The regression calculated without 1991 (spring frost damages) is shown.

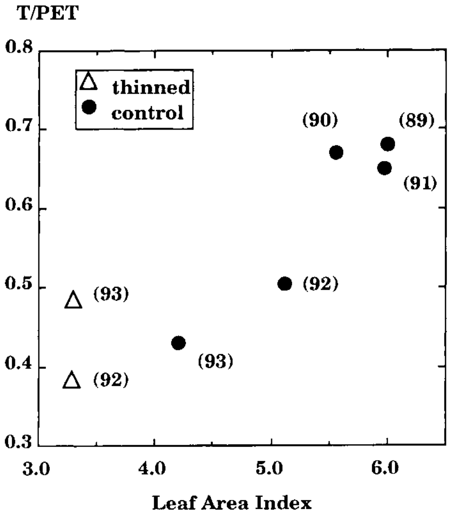

Fig 8. Relationship between annual T/PET ratio and maximal leaf area index as observed by litter collection in control (solid circles) and thinned plots (open triangles). Years are indicated in parentheses. The T/PET ratio in 1990 was calculated before the irrigation mentioned in figure 6.

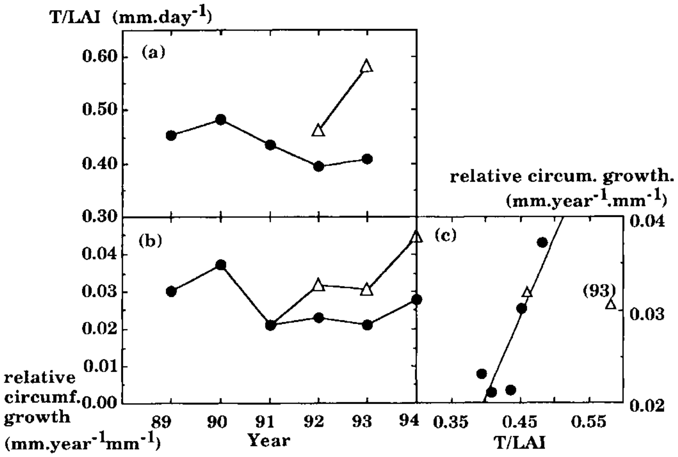

Fig 9. Interannual fluctuations of (**a**) the mean daily transpiration of the stand per unit leaf area index (T/LAI) and (**b**) the mean relative annual circumference increment for the biggest trees of the stand (initial circumference > 400 mm). (**c**) Regression between T/LAI and relative circumference growth at stand level. Control: solid circles; thinned: open triangles.

Annual growth and water use

The similarity between interannual variations in annual circumference increment and transpiration at the stand level is shown in figure 9a, b. Because leaf area index varied among years and treatments, the use of the transpiration/LAI ratio permits a direct comparison. Year-to-year changes in T/LAI and growth varied similarly. The amount of water needed to achieve a given basal increment is the slope of the linear regression between T/LAI and relative growth (r^2 = 0.74) (fig 9c). It represents a stand index of water-use efficiency for growth integrated over the growing season. This index appeared constant among years, and it may be concluded that no change in carbon allocation between stem and other compartments could be detected. The previously mentioned increase of transpiration in 1993 in the thinned (figs 8 and 9a) stand was not accompanied by an improved growth (fig 9b). An improvement of growth was observed during the following year (1994). The thinned stand exhibited a too high transpiration rate as compared to its growth as exemplified by its deviation from the regression between T/LAI and relative growth (fig 9c). This deviation from the line may have reflected changes in carbon allocation patterns within the thinned trees (crown growth, root system development, stemwood respiration).

In the same way, sap flow measurements allow us to analyse the relationship between growth and transpiration at the tree scale.

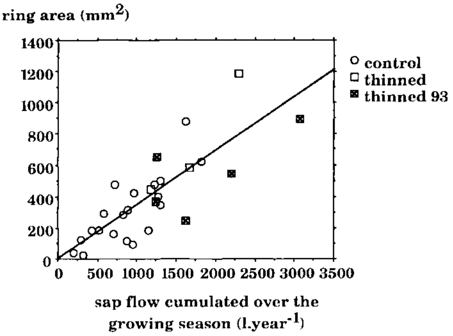

Fig 10. Basal area increment related to the amount of transpired water over the growing season as measured from sap flowmeters. Each point is an individual tree during 1 year, from control (open circles) and thinned (open squares) plots. As differences among years were not significant, years were not distinguished, except data from thinned trees in 1993 (squares).

Yearly basal area increment is also well correlated with the amount of transpiration over the growing season (ring area = 0.339 * $\sum$ SF, $n = 28$, $r^2 = 0.65$; fig 10), and it might be proportional to the amount of fixed CO_2. The slope of this regression may be defined as an index of efficiency for circumference growth at the tree scale. It exhibited only slight (nonsignificant) variations among years. Nevertheless, some of the thinned trees exhibited a lower slope during 1993, as mentioned for the stand level.

DISCUSSION

Long-term monitoring of sap flow and climatic data (from bud-burst to leaf fall) were suitable to analyse the dependence of transpiration on both LAI and PET. The sap flowmeter device allowed us to detect small daily fluctuations of transpiration occurring during leaf flushing (fig 1), owing to its fine time resolution. Prediction of transpiration as a function of LAI has been developed since several years in order to estimate crop water use and to quantify the amount of water needed for irrigation (Brun et al, 1972). As a general conclusion with crop and grassland, a curvilinear relationship was observed between T/PET and LAI on well-watered soils. An almost linear increase was observed until a LAI of about 2.5 (Ritchie and Burnett, 1971). Afterwards, T/PET increased more gradually until it approached an asymptote. Further uncreases in LAI did not result in additional interception of total radiation (Saugier and Katerji, 1991). An increase of transpiration area would induce locally a lower water vapour pressure deficit. In addition, local exchange will be reduced because of wind sheltering and the poor coupling between crop canopy transpiration and the atmosphere (Jarvis and McNaughton, 1986); therefore, transpiration versus LAI would increase less than linearly. Such results are scarce for mature and deciduous forests, because reliable LAI monitoring during leaf flushing has been only recently developed. The linear increase of T/PET with leaf area until a LAI of 6.0 was reached (fig 2) is somewhat surprising as compared to crop canopy behaviour. The absence of a threshold LAI leading to saturation of T may reflect specific properties of the oak canopy: i) The canopy transpiration is strongly coupled with the atmosphere (see Granier and Bréda, 1996) so that the previously mentioned sheltering effect is small (Bosveld et al, 1991). ii) The spatial arrangement of leaves and, in particuliar, the clumping (associated with flushing and a short vertical extension of the crowns) lead to a highly porous canopy. This was also illustrated by the low light extinction coefficient determined for this canopy as compared to a grassland (0.38 and 0.70, respectively). As a consequence, T was proportional to the amount of foliage until a LAI of 6.0 because radiation was still available at the base of the crown. As another consequence of this canopy porosity, slight vertical gradients of vapour pressure deficit were measured inside the crown and only small differences in stomatal conductance were observed between the top and base of the crown (Bréda et al, 1995).

Seasonal fluctuations in transpiration (T/PET) have been related to LAI and soil water availability. Leaf area index appeared as the main parameter governing the T/PET ratio during the first part of the season, when soil water content was not limiting ($0.4 < \text{REW} < 1$). For our site, we never observed spring drought and bud-burst always occurred as soil water content was near field capacity. The studied trees were about 35 years old and the rhythmic shoot elongation was still important, in comparison to the general assessment that such a crown development typically concerns resprouts and young saplings (Longman and Coutts, 1974). Therefore, increases in LAI beyond 6.0 had only a limited impact on T/PET because during this second part of the growing period, T/PET was reduced by stomatal closure resulting from soil water deficits (Bréda, 1993a). A sharp decrease in T/PET was observed as REW dropped below 0.4, a threshold caused by the depletion of water from the soil macroporosity (Bréda et al, 1994). For oaks, midday stomatal conductance was then reduced by half.

During the 5 years of measurements, the stand experienced various climatic and soil moisture conditions that yielded an excellent opportunity to study the interactions between LAI, drought and transpiration on the same site. Such a single site, multi-year approach is interesting because most experimental data is derived from multi-site comparisons of water consumption along soil moisture gradients (Gholz, 1982). As a result of this latter approach, a direct proportionality between LAI and transpiration is assumed, but without experimental support (Nemani and Running, 1989). It is sometimes assumed that mature forest stands with closed canopies support constant amounts (weight or area) of foliage (Jack and Long, 1991). Gholz and Fischer (1982) showed that the amount of foliage may slowly decline over time. Such a reduction in LAI following canopy closure is often associated with a reduction in leaf area efficiency (reduction of both the amount of leaf area and leaf area efficiency; Long and Smith, 1992). In contrast, our results demonstrated that a close canopy represents an instable steady state where biotic or climatic factor may lead to imbalance.

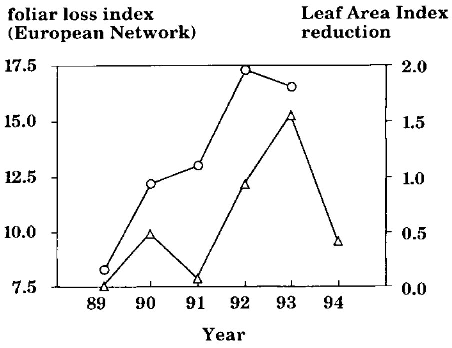

Fig 11. Comparison of foliar loss between the Champenoux stand (leaf area index reduction, open triangles) and northeast sessile oak forests (open circles) as estimated in the European Network (data from Ministère de l'Agriculture et de la Forêt, 1994).

In our stand, LAI varied substantially from one year to the next; however, a decreasing trend has been observed since 1991. This decrease in LAI (without tree mortality) was a general feature in oak stands in northeast France during this period: the foliage loss index observed in the European Network of forest vitality survey (Ministère de l'Agriculture et de la Forêt, 1994) followed the same pattern as our stand (fig 11). The good agreement between measurements of LAI variations and annual assessment of defoliation (as a percentage of leaf loss) has to be mentioned, because it stresses the significance of 'defoliation estimates' generally used for health surveys. We did not observe any variation in individual leaf size among years (data not shown) and the reduction of LAI was thus a consequence of the reduction in the number of leaves. The 1991 spring frost occurred when leaves were just unfolded, and –4.2 °C temperature corresponds to the critical temperature leading to frost injuries for sessile oak (Liepe, 1993). This frost probably had major consequences on water transport and hence on tree vitality; all large vessels of the newly formed earlywood were likely cavitated at least in the terminal shoots (Sperry and Sullivan, 1993). The hydraulic conductance may then be reduced by the late freeze, both during that spring and that summer, as reported by Sperry et al (1994). Indeed, these authors observed that no additional layer of earlywood vessels was produced following the freeze and that the latewood produced had an insignificant effect on hydraulic conductance. The primary carbohydrate and nutrient sources for the initial and then for the replacement leaf flushing were stored reserves. Because the previous year had been wet, one might expect an optimum carbon accumulation. The lack of reduction of maximal LAI in 1991 was somewhat surprising, as it was also an exceptionally dry year. An important consideration regarding this result is the interaction between the two climatic constraints (spring frost and drought). As buds were completely destroyed, the leaf expansion was delayed by 3 weeks, so that water uptake was also delayed. This saving of water allowed an important but somewhat erratic development of lamna shoots, which normally would have been reduced by the drought. The assimilated CO_2 was then allocated to shoots and leaf production rather than stored. As a consequence, LAI of the following year (1992) was reduced. Similar persistent effects of the 1991 spring frost on 1992 and 1993 oak crown conditions in Rheinland were reported (Schröck and Block, personal communication).

Year-to-year variations in growth were high, as observed for LAI. It was suspected that low leaf area may become the limiting factor for carbon gain and growth. As a consequence of substantial variations of LAI from one year to the next due to either natural factors or thinning, maximal T/PET under optimum water supply (REW > 0.4) may have varied from 0.5 to 0.8 in proportion to LAI. The amount of foliage is then the most important origin of annual transpired water and hence of canopy photosynthesis (Baldocchi et al, 1987), because it determines the transpiration rate during the period of high water consumption. Besides, as the annual T/PET was closely correlated to LAI ($r^2 = 0.82$), residual variation being correlated to soil moisture deficit. Annual basal increment was strongly related to transpiration, which depends on both LAI and soil water availability during the summer. In fact, growth rate is proportional to the amount of radiation intercepted by the canopy. As intercepted light is mainly determined by the amount of foliage, LAI expresses the growth potential of the stand (Jarvis and Leverenz, 1983). Inversely, LAI seemed to depend on growth from the previous year, thus giving LAI an intermediate position between two successive annual growths. The current growth rate (slope of the growth curve) may be influenced by the previous year's soil water availability (which determines the amount of carbohydrates stored) and the current year's spring frost. A direct effect of spring frosts on circumference growth has been cited for broad-leaf species (oak, hickory, beech; Liu and Muller, 1993; Santini et al, 1994). The study of tree growth by analysis of annual growth rings allowed us to consider a longer temporal period and has revealed the differential effect of soil moisture deficit on early- and latewood increment. The earlywood was independent of soil moisture deficit but its development (April) was strongly influenced by temperature, as observed by Hinckley et al (1976) or Becker et al (1994). In contrast, the latewood growth appeared related to soil water deficit Hinckley et al (1976) called this phase of stem growth "the oil moisture limited phase". This result is also consistent with the climatic model of interannual variation in growth developed by Becker et al (1994): stemwood growth appeared to be related to fluctuations in precipitation in May, June and August.

The monitoring of both cumulated circumference growth and water transport during several complete growing seasons has provided new information about the functional interaction between foliar phenology and tree water relations. A large part (43% on average in the 5 years) of the annual diameter increment takes place during the spring before leaf expansion; this proportion includes more than the earlywood (= only 19% of ring width). Hinckley and Lassoie (1981) also mentioned that approximately 30% of the total stem increment is added before bud-burst in ring-porous hardwood. Our observation is also consistent with Dougherty et al's (1979) early measurements of photosynthesis on white oak. They showed that most of the early growth processes were either completed or well underway before the establishment of significant rates of net photosynthesis. They observed that when leaves were rapidly expanding, stem (but also root) cambial growth virtually ceased; this transition phase may correspond to the beginning of latewood production. Leave expansion acts as a sink of stored photosynthetates. Spring cambial growth is therefore independent of the re-activation of buds and is not affected by current drought. As large vessels of oaks exhibited high vulnerability to frost-induced embolism (Cochard et al, 1992; Bréda et al, 1993b), and as only rings of the more recent years are functional (Granier et al, 1994), a new layer of xylem must be developed to ensure water supply of young leaves (Essiamah and Eschrich, 1986; Sperry et al, 1994). Stored carbohydrates from the previous year are then involved during spring in both xylem differentiation and leaf expansion. This phenological cycle in which cambium re-activation precedes leaf development usually characterises ring-porous species (Hinckley and Lassoie, 1981; Wang et al, 1992) and has been observed on *Castanea sativa* (Boutin, 1985) and on *Sorbus torminalis* (Lachaud and Mansouri, 1993). Lachaud and Bonnemain (1981) observed in 30-year-old oaks that cambial re-activation occurred at least 3 weeks before bud-burst. We also observed that this time lag between cambial growth and leaf expansion leads to an exceptionally high hydraulic conductance from soil-to-leaves during spring, which was strongly reduced after a few weeks as leaves expanded (Bréda et al, 1993a). In contrast, cambium re-activation and bud-burst occur simultaneously as observed in *Fagus* by Lachaud and Bonnemain (1981) or growth follows bud-burst in diffuse porous species in which vessels function for several years (Gasson, 1987; Anfodillo et al, 1993).

We computed an index of water-use efficiency integrated over the season at both stand and tree level, and it was expressed as the ratio of annual basal increment over cumulated sap flow. This index is only an indicator because i) we used basal area instead of volume production, ii) respiration was not taken into account and iii) no attempt was made to partition biomass to components other than the stem. The latter point has certainly to be involved to explain the apparent lower water-use efficiency of trees from the thinned plot, where crown development was higher than in control trees. Nevertheless, the water-use efficiency for growth, as defined, was constant among years, probably because the stand balances (via control of transpiration, adjustment of LAI) to maintain this constant efficiency. This balance may be a characteristic of the species at this stage of development and on this site. Unfortunately, our direct measurements of carbon assimilation were not suitable to investigate the intrayear variation in intrinsic water-use efficiency (assimilation versus transpiration at leaf scale). Measuring carbon isotope composition in the annual growth rings will allow assessing indirectly a time-integrated value of water-use efficiency.

CONCLUSION

The data collected during the 5 years of survey at Champenoux, France exhibit large year-to-year variations in LAI and soil moisture, which gave an accurate parametrization of both seasonal and interannual trends of T/PET. The mechanism involved in the interactions between intensity and duration of drought, LAI, transpiration and basal area increment have been presented. Our results provided strong evidence that taking into account year-to-year fluctuations in LAI will improve water balance and growth modelling. Nevertheless, the understanding of interannual variations of LAI needs further research, including the collection of longer temporal series of LAI to quantify delayed effects of this parameter on long-term trends in growth.

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