Ann Sci For (1996) 53, 537-546

Original article

Modelling canopy conductance and stand transpiration of an oak forest from sap flow measurements

A Granier, N Bréda

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

(Received 13 January 1994; accepted 31 October 1995)

Summary — In this study, transpiration was estimated from half-hourly sap flow measurements in a 35-year-old sessile oak stand (*Quercus petraea*) from 1990 until 1993 under various soil water conditions. The canopy conductance, calculated from the Penman–Monteith equation, was first analysed in relation to climatic variables: global radiation (R_g) and vapour pressure deficit (VPD). The maximum canopy conductance (g_{cmax}) was modelled with a nonlinear multiple regression over a period of non-limiting soil water content, and of maximal leaf area index (LAI) with a $r^2 \sim 0.80$. Limitations of gc due to soil water deficit (relative extractable water [REW]) and canopy development (LAI) were then taken into account in the model by using multiplicative limiting functions of REW and LAI. A general canopy conductance model was then proposed. Finally, this relationship was re-introduced in the Penman–Monteith equation to predict dry canopy transpiration. Simulated transpiration was in good agreement with sap flow measurements during the year following the calibration (r^2= 0.92 in the control plot, 0.86 in the dry plot). The omega decoupling coefficient was close to 0.1 on a seasonal basis, indicating that transpiration was highly dependent on VPD.

canopy conductance / transpiration / sap flow / oak stand / model

Résumé — Modélisation de la conductance du couvert et de la transpiration du peuplement d'une forêt de chênes à partir de mesures de flux de sève. *Dans ce travail, la transpiration a été estimée à partir de mesures semi-horaires de flux de sève dans un peuplement de chênes sessiles* (Quercus petraea) *âgé de 35 ans, entre 1990 et 1993. Différentes conditions hydriques ont été étudiées. La conductance du couvert* (gc)*, calculée à partir de l'équation de Penman-Monteith, a été dans une première étape reliée aux facteurs climatiques rayonnement global (*Rg*) et déficit de saturation de l'air (vpd). La conductance de couvert maximale* (g_{cmax}) *a été modélisée au moyen d'une régression non linéaire multiple sur une période où l'eau du sol n'était pas limitante, et où l'indice foliaire (LAI) était maximal, donnant un* r^2 *de l'ordre de 0,80. Les limitations de* gc *dues au déficit hydrique du sol (exprimé par le contenu en eau relatif du sol REW) et au développement foliaire (LAI) ont été introduites dans le modèle au moyen de fonctions multiplicatives du REW et du LAI. Un modèle général de conductance* *du couvert a alors été proposé. Enfin, cette relation a été réintroduite dans l'équation de Penman-Monteith, pour simuler les variations horaires de la transpiration. Les valeurs simulées ont montré un bon accord avec les valeurs mesurées de flux de sève l'année suivant celle du calibrage (r^2= 0,92 pour le traitement témoin, 0,86 pour le sec). Le facteur de découplage oméga a été proche de 0,1, attestant une forte dépendance entre la transpiration et le vpd.*

modèle / conductance du couvert / chênaie / flux de sève / évapotranspiration

INTRODUCTION

Transpiration of a forest depends on interactions between a number of variables, some being the physical characteristics of the environment and some the biological behaviour of the plants. Global radiation and vapour pressure deficit are widely demonstrated to be the most significant climatic variables controlling transpiration, both on hourly and on daily scales. On the other hand, stomatal control of transpiration is well characterised at the leaf level and differences in stomatal response among species are often pointed out (Meinzer, 1993). However, regulation of water vapour loss at the canopy level has, up to now, mainly been studied in coniferous and tropical forests.

Transpiration of dry and homogeneous vegetation canopies is classically estimated from climatic measurements using the Penman–Monteith equation (Monteith, 1973), which incorporates the influence of aerodynamic and canopy conductances. The former depends on roughness properties of the canopy, and the latter is considered as the sum of the stomatal conductance of all the leaves, according to the 'big-leaf' hypothesis. When stand transpiration is measured (sap flow or eddy correlation), canopy conductance can be calculated by the reverse form of the Penman–Monteith equation (Stewart, 1988). Derivation of canopy conductance from sap flow measurements has been successfully compared to both eddy correlation measurements (Granier et al, 1990, 1996) and field measurements of stomatal conductance (Granier and Loustau, 1994; Lu et al, 1995).

We used this procedure to develop a model of canopy transpiration of a temperate deciduous oak forest, that describes the dependence of transpiration on the environmental driving variables (climate and soil water availability) and on canopy structure. In addition, the model takes into account dynamics of leaf area within the canopy over the season.

STAND AND MEASUREMENTS

This study was conducted from 1990 to 1993 in a 35-year-old sessile oak stand (*Quercus petraea*) regenerated from seed. Other species growing in the understorey were removed (mainly *Tilia* and *Carpinus*) in order to maintain a monolayer structure. Mean height and diameter at breast height were 14.8 m and 8.6 cm, respectively. Vertical extension of the crowns was limited (3–4 m), due to the high stand density (3 600 stem.ha^{-1}). A part of the stand was thinned in 1992, while a group of 17 trees was artificially subjected to water shortage (see Bréda et al, 1993).

Interception of global radiation (linear pyranometers, Inra, France) was monitored from bud burst to fall, so that canopy closure was precisely dated. The seasonal pattern of leaf area index (LAI) was estimated from both light transmittance of diffuse solar radiation and periodic LAI measurements (Demon leaf area meter, Assembled Electronics, Sydney, Australia). Year-to-year variation of maximal LAI, as estimated from litter collections, ranged from 4.2 to 6.0 in the control, and 3.3 in the thinned plot.

Meteorological variables (wind speed, global and net radiation, air temperature, vapour pressure deficit [VPD], incident rainfall) were monitored 2 m above the canopy, on a half-hourly basis. Aerodynamic conductance (g_a) was calculated from wind speed measurements from Monteith's equation (1965). The roughness parameters were determined from empirical functions established on coniferous canopies (Thom, 1972; Jarvis et al, 1976).

Tree and stand transpiration were calculated from half-hourly sap flow measurements using continuous heated radial flowmeters (Granier, 1987), assuming that sap flow at the base of the trunk lagged 0.5 h behind canopy transpiration. The nine to 14 trees measured every year were selected to be representative of sapwood and crown class distribution in the stand.

Canopy conductance was evaluated from sap flow and climatic measurements using the Penman–Monteith equation (Monteith, 1973), and assuming that vapour flux was equal to sap flux:

$$\mathrm{TM} = \frac{e'(w)\,(R_n - G) + \rho\, C_p\, \mathrm{VPD}\, g_a}{\lambda\,[\, e'(w) + \gamma\,(1 + g_a/g_c)]} \qquad [1]$$

where:

TM: maximum transpiration (mm.h^{-1})

$e'(w)$: rate of change of saturation vapour pressure (Pa.C^{-1})

R_n: net radiation above stand (W.m^{-2})

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

ρ: density of dry air (kg.m^{-3})

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

VPD: vapour pressure deficit (Pa)

g_a: aerodynamic conductance (cm.s^{-1})

g_c: canopy conductance (cm.s^{-1})

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

γ: psychrometric constant (Pa.C^{-1})

In this study, heat flow in the soil was measured only during a 3 month period and it was shown to be negligible (< 4%). Rate of storage of heat in biomass was calculated from above-ground estimated biomass and from hourly changes in air temperature (Stewart, 1988).

Relative extractable water (REW) was computed from soil water content measured weekly with a neutron probe over ten 200 cm long access tubes; soil water reserve was defined as the difference between maximum (field capacity) and minimum soil water content observed during the 1989–1993 period (see Bréda and Granier, 1996, for a complete description of the experiment).

All these parameters were monitored from bud burst to fall, from 1990 to 1993. Sap flow and climate data of 1990 were used to calibrate the model of transpiration and data of the following years for its validation.

RESULTS AND DISCUSSION

Effect of global radiation and vapour pressure deficit on maximal g_c

The canopy conductance (g_c) was first analysed in relation to global radiation (R_g), and vapour pressure deficit (VPD). In order to extract drought and LAI effects, this analysis was conducted over a period of nonlimiting soil water content (manual irrigation), of maximal leaf area index and in dry canopy conditions. A threshold of VPD was taken as 1 hPa to eliminate wettest air conditions when the calculation of g_c was too imprecise. Figure 1 shows that canopy conductance was strongly reduced when VPD increased: 50% of reduction occurred when VPD increased from 10 to 20 hPa. These data were fitted with a nonlinear multiple

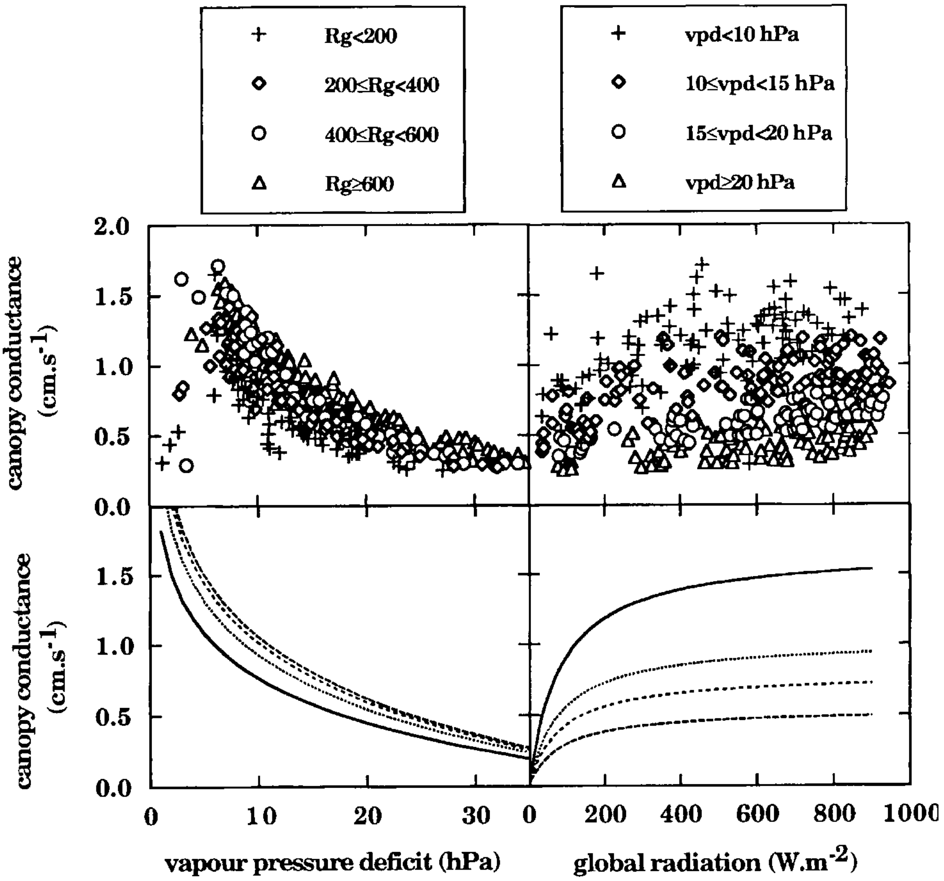

Fig 1. Effect of air vapour pressure deficit and global radiation on calculated canopy conductance of an oak forest (top); data were split up into four classes of global radiation or four classes of vapour pressure deficit. Data are obtained from sap flow measurements during a period of high water supply, for a maximum leaf area index (= 6.0 $m^2.m^{-2}$). Curves are fitted from these data set (bottom). R_g: global radiation; VPD: vapor pressure deficit.

regression programme where maximal canopy conductance (g_{cmax}) was depending on global radiation in a hyperbolic way and on VPD in a logarithmic one:

$$g_{cmax} = f_1\,(R_g, \mathrm{VPD}) = [R_g\,/\,(\,R_g + 82\,)]\;.\;[\,2.803 - 0.704\,Ln\,(\mathrm{VPD})\,] \qquad [2]$$

$$r^2 = 0.75$$

Hence, canopy conductance is an increasing function of global radiation and reaches 50% of its maximum for a global radiation of 82 $W.m^{-2}$. Ogink-Hendriks (1995) found 166 $W.m^{-2}$ in a *Quercus rubra* stand. These values are quite low, as compared with values obtained on coniferous stands (370 $W.m^{-2}$ in Lu et al, 1995 for a Norway spruce forest;

498 W.m^{-2} in Granier and Loustau, 1994 for a Maritime pine forest).

Effect of leaf area variations on g_c

Canopy conductance variations resulting from the phenological development of the canopy were investigated in spring 1990. During this period, soil water content was close to field capacity. The observed values of g_c during spring were lower than g_{cmax} defined in equation [2], because of partial leaf expansion. The ratio between observed and maximal values of g_c (daily average between 11 and 14 h TU) was plotted against LAI from d118 to d161 (28 April to 10 June) in figure 2. A logarithmic function f_2 limiting maximal g_c was fitted:

$$g_c/g_{cmax} = 0.402 + 0.801 * \log_{10}(\mathrm{LAI}) \quad [3]$$

$$r^2 = 0.75$$

Effect of soil water deficit on g_c

The role of water supply in controlling canopy conductance was investigated from observed values of g_c in both control and dry plots, during a period of constant and maximal LAI. A logarithmic function of g_{cmax} (f_3, fig 2) was calibrated using daily values of relative extractable water (REW):

$$g_c/g_{cmax} = 1.05 + 0.59 * \log_{10}(\mathrm{REW}) \quad [4]$$

$$r^2 = 0.94$$

It can be noted that g_c seemed not to be modified at the beginning of soil drying ($0.6 \leq \mathrm{REW} \leq 1$).

Stewart (1988) proposed a multiplicative model of canopy conductance as the product of elementary functions of radiation, vapour pressure deficit, air temperature and soil moisture. In our work, we assumed that temperature was of minor importance on g_c

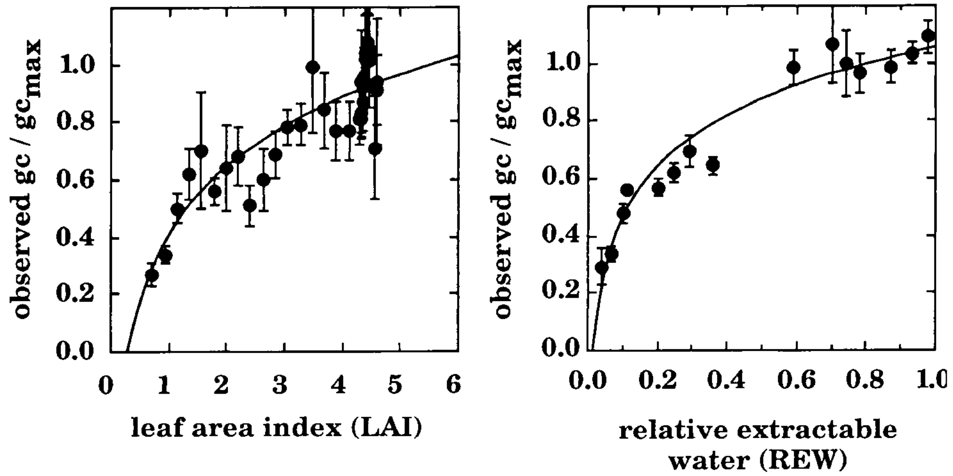

Fig 2. Effect of leaf area index (LAI) and of soil water availability (REW) on the relative canopy conductance of the oak forest, expressed as the ratio of that measured on maximum canopy conductance. Each point is a daily mean of canopy conductance between 11 and 14 h TU and vertical bars are standard deviations. The maximum value was obtained in 1990 during a period without water stress, with a LAI = 6.0. g_c: canopy conductance; g_{cmax}: maximal canopy conductance.

as compared with R_g and VPD. Then the complete canopy conductance model may be written as follows:

$$g_c = g_{cmax} \cdot f_2(\text{LAI}).\ f_3(\text{REW}) \quad [5]$$

where $g_{cmax} = f_1(R_g, \text{VPD})$.

Model of transpiration

This model of g_c was then re-introduced in the Penman–Monteith equation to predict dry canopy transpiration. Simulated transpiration (fig 3) was in good agreement with sap flow measurements during the year fol-

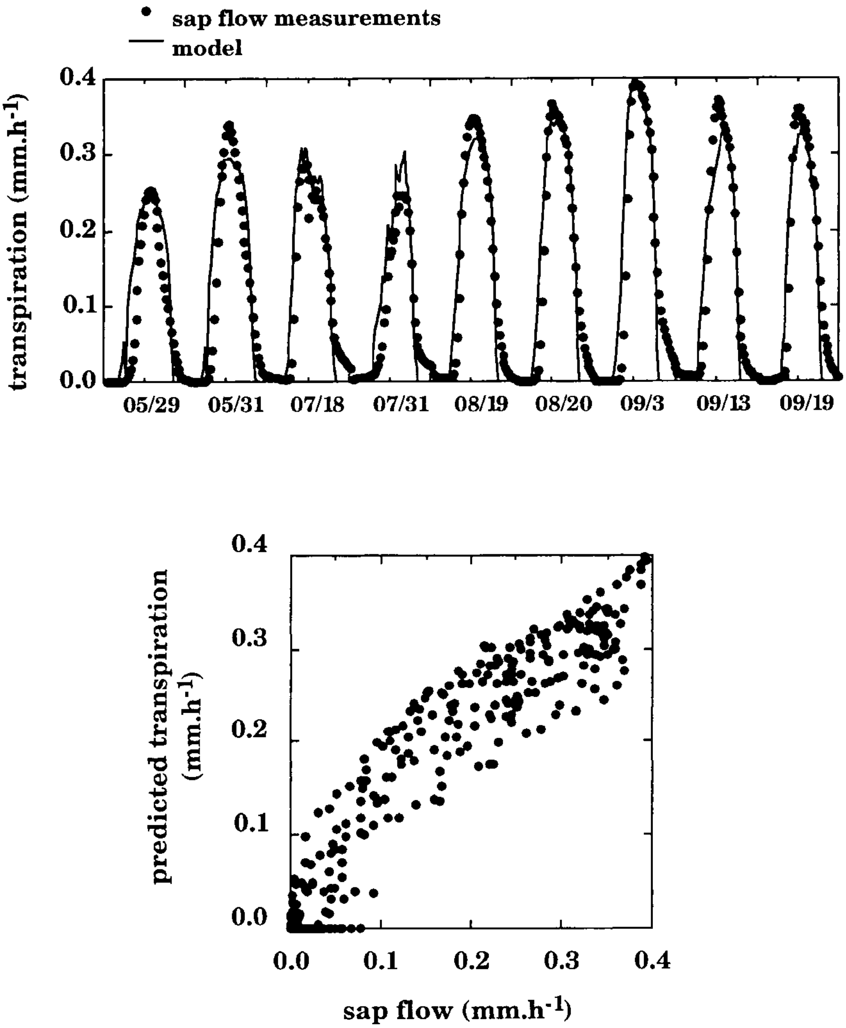

Fig 3. Comparison between sap flow measurements and the model of transpiration (top) including drought and leaf area index functions, for a closed canopy of oaks, during 9 days. Bottom: relationship between measured sap flow and estimated transpiration for the same days. The model was calibrated on 1990 measurements and validated on 1991 data.

lowing the calibration ($r^2 = 0.92$ in the control plot, 0.86 in the dry plot). Nevertheless, differences between sap flow and model were observed in the morning and in the evening, probably due to a dehydration in the morning of the water exchangeable tissues of the trees (Jarvis, 1975), followed by a rehydration in the evening; the best fit ($r^2 = 0.92$) between observed and predicted values was obtained by introducing a 1 h time lag.

During the following 2 years, a good correlation between observed and predicted transpiration was also found, but the model overestimated transpiration, in both the control and the dry plot (+21% in 1992, +34% in 1993). This means that a factor other than environmental variables and LAI had affected maximal canopy conductance. A possible involvement of canopy structure modifications is hypothesized: as a result of the 1991 spring frost, we observed in the following years a more clumped foliage distribution which could lead to a less favourable sun exposure of the leaves.

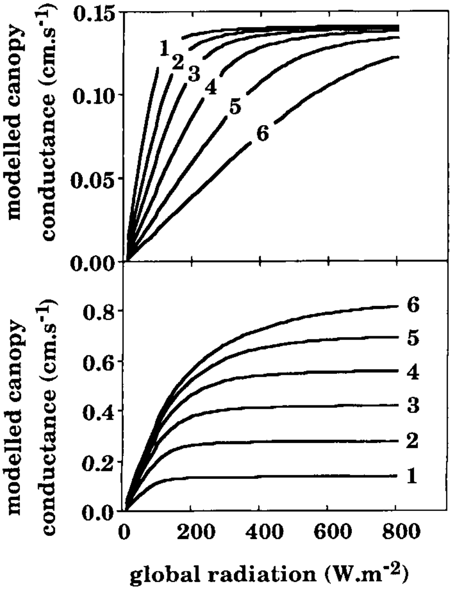

Fig 4. Effect of increasing leaf area index (LAI) (0 to 6) on canopy conductance of an oak forest. Top: elementary canopy conductance for each of the six layers, as a function of incident (above canopy) radiation. Bottom: equivalent canopy conductance for LAI increasing from 0 to 6.

Dependence of canopy conductance on leaf area index

In order to evaluate the effect of leaf area index on the canopy conductance variations, we simulated in figure 4 the response to increasing incident global radiation. A theoretical oak canopy of LAI = 6 was partitioned into six layers of LAI = 1 each. The same response curve of canopy conductance to radiation was applied to each layer (see Appendix and fig 5). From the extinction profile of radiation predicted by the Beer law, using a k extinction coefficient of 0.42 (Bréda, 1994), incident radiation reaching each layer was computed. Then, the canopy conductance of each successive layer was calculated, assuming the same value of VPD for each layer. Finally, from the relationship of conductances in parallel, the sum of the conductances of all the elementary layers was found. This simulation suggested that canopy conductance increased quite linearly with LAI under high radiation (> 500 $W.m^{-2}$) conditions. Calculated g_c for various maximal year-to-year LAI (under non-limiting soil water conditions) were close to this linear response (fig 6); in the same experiment, Bréda and Granier (1996) also found a linear relationship between stand transpiration and LAI as much during leaf expansion as during the leaf fall period.

Coupling of transpiration to the atmosphere

We first tested the sensitivity of the model to g_a in the case of the oak stand using higher

(+50%) and lower (–80%) values of g_a. The comparison with sap flow measurements showed only small differences (< 5%) between observed and simulated transpiration, because g_a was much higher than g_c: the ratio g_a/g_c varied from 30 to 200. The oak canopy appeared therefore well coupled to the atmosphere.

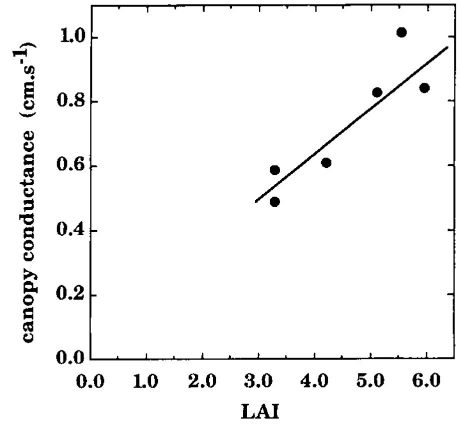

Fig 5. Relationship between canopy conductance and leaf area index (LAI) under nonlimiting soil water conditions. Values are standardized using equation [2] for a global radiation of 500 W.m^{-2}, and for a vapour pressure deficit of 10 hPa. Data are obtained during 1990 to 1993 in the control, and during 1992 and 1993 in the thinned oak stand.

The degree of decoupling with the atmosphere (Jarvis and McNaughton,1986), the so-called *omega coefficient* Ω, is calculated from $e'(w)$ and the ratio g_a/g_c. It quantifies the dependence of transpiration to climate. Calculated Ω for bright days (fig 7) ranged from 0 to 0.1, VPD being the main driving variable of canopy transpiration, which was strongly limited by canopy conductance. A comparison of daily variations of Ω was made with other forest canopies: *Pinus sylvestris* (Granier et al, 1996), *Picea abies* (Lu, 1992) and tropical rainforest (Granier et al, 1995b). Midday value of Ω ranged from 0.05 to 0.1, as much for temperate coniferous and broad-leaved forests as for tropical rainforest. Köstner et al (1992) found a similar diurnal pattern of Ω in a *Nothofagus* forest, but their estimates were slightly higher than ours (morning peak = 0.38, afternoon = 0.20). Canopy conductances were similar in both oak and *Nothofagus* stands, so that differences were due to a higher aerodynamic conductance over the oak forest. Hence, differences in Ω between species (fig 7) may be related to both aerodynamic characteristics of the canopies (roughness) and of the air mass. Only tropical rainforest showed during the morning a high Ω value, when wind speed was low, as also reported by Meinzer et al (1993). Nevertheless, care must be taken that in our experiments the height of measurement

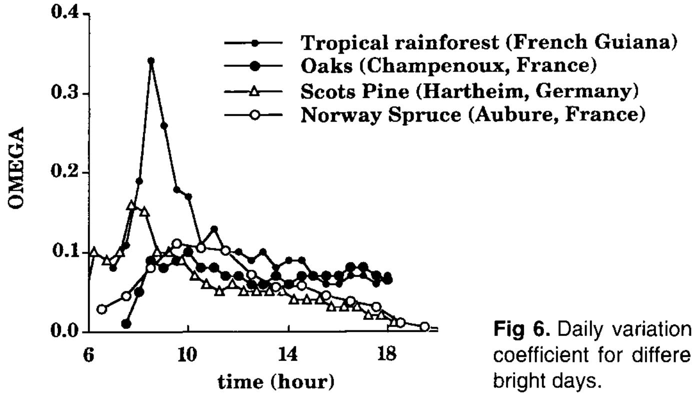

Fig 6. Daily variation of the omega decoupling coefficient for different forest canopies, during bright days.

of air temperature and vapour pressure deficit was only 2 m above canopies, ie, not at the top of the boundary layer.

CONCLUSION

A mechanistic model has been developed to evaluate stand transpiration from the analysis of interactions between stand structure and microclimate. This model provides a convenient analytical framework. The effects of leaf area on canopy conductance and hence on stand transpiration can be examined in relation to environmental conditions and aerodynamic characteristics of the stands. A water balance model, including the present model of transpiration, has already been used for long-term simulation of drought and its influence on tree growth (Bréda, 1994).

APPENDIX

The relationship between elementary conductance (for one layer of LAI=1) and global radiation (R_g) reaching this level was assumed to be of the form:

$$g_c = \frac{1 + 0.01\,R_g - [(1+0.01R_g)^2 - 4\,t\,0.01\,R_g]^{1/2}}{14\,t} \qquad [6]$$

Different response curve shapes can be obtained by changing the value of the parameter t: $t = 1$ corresponds to a broken line, $t = 0.2$ to a curvilinear relationship, and $t = 0.9$ to an intermediate curve (see fig 5). These three cases were tested

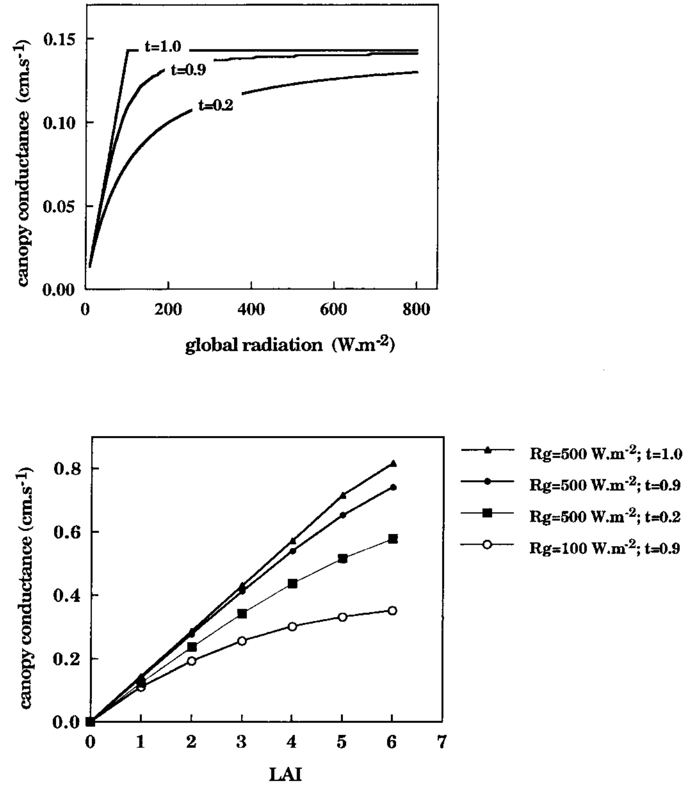

Fig 7. Relationship between canopy conductance, leaf area index and global radiation. Top: variation of the canopy conductance/global radiation function for one elementary layer (LAI = 1). The different shapes are obtained by changing the value of the t-parameter in equation [6]. Bottom: When varying the shape of the elementary function, the relationship between equivalent canopy conductance and LAI remains almost linear for global radiation = 500 W.m^{-2}. For a low global radiation (100 W.m^{-2}), this relationship is nonlinear.

for LAI increasing from 1 to 6, for a fixed value of $R_g = 500$ W.m^{-2}. The case of $R_g = 100$ W.m^{-2} is also shown in figure 5.

REFERENCES

Bréda N (1994) Analyse du fonctionnement hydrique des chênes sessile *(Quercus petraea)* et pédonculé *(Quercus robur)* en conditions naturelles ; effet des facteurs du milieu et de l'éclaircie. PhD Thesis, University of Nancy I, France, 59 p + annexes

Bréda N, Granier A (1996) Intra- and interannual variations of transpiration, leaf area index and radial growth of a sessile oak stand. *Ann Sci For* 53, 521-536

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

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

Granier A, Loustau D (1994) Measuring and modelling the transpiration of a maritime pine canopy from sapflow data. *Agric For Meteorol* 71, 61-81

Granier A, Bobay V, Gash JHC, Gelpe J, Saugier B, Shuttleworth WJ (1990) Vapour flux density and transpiration rate comparisons in a stand of Maritime Pine (*Pinus pinaster* Ait) in Les Landes forest. *Agric For Meteorol* 51, 309-319

Granier A, Huc R, Barigah TT (1995) Transpiration of natural rainforest and its dependence on climatic factors. *Agric For Meteorol* 78, 19-29

Granier A, Biron P, Köstner B, Gay LW, Najjar G (1996) Comparison of sap flow and vapour flow at stand level and derivation of canopy conductance for Scots pine. *Theoret Apl Climat* (in press)

Jarvis PG (1975) Water transfer in plants. In: *Heat and Mass Transfer in the Plant Environment. Part 1* (DA de Vries, NG Afgan, eds), Scripta Book Company, Washington DC, USA, 369-374

Jarvis PG, McNaughton KG (1986) Stomatal control of transpiration: scaling up from leaf to region. *Adv Ecol Res* 15, 1-49

Jarvis PG, James GB, Landsberg JJ (1976) Coniferous forest. In: *Vegetation and the Atmosphere* (JL Monteith, ed), Vol II, Academic Press, New York, 171-240

Köstner B, Schulze ED, Kelliher FM, Hollinger DY, Byers JN, Hunt JE, McSeveny TM, Weir PL (1992) Transpiration and canopy conductance in a pristine broadleaved forest of *Nothofagus:* an analysis of xylem sap flow and eddy correlation measurements. *Oecologia* 91, 350-359

Lu P (1992) Ecophysiologie et réaction à la sécheresse de trois espèces de conifères (*Abies alba* Miller, *Picea abies* (L) Karsten et *Pinus sylvestris* L) ; effet de l'âge. PhD Thesis, University of Nancy I, France, 116 p

Lu P, Biron P, Bréda N, Granier A (1995) Water relations of adult Norway spruce trees under soil drought: water potential, stomatal conductance and canopy transpiration. *Ann Sci For* 52, 117-129

Meinzer FC (1993) Stomatal control of transpiration. *Trends Ecol Evol* 8, 289-294

Meinzer FC, Goldstein G, Holbrook NM, Jackson P, Cavelier J (1993) Stomatal and environmental control of transpiration in a lowland tropical forest tree. *Plant Cell Environ* 16, 429-436

Monteith JL (1965) Evaporation and environment. *Symp Soc Exp Bot* 19, 206-234

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

Ogink-Hendriks MJ (1995) Modelling surface conductance and transpiration of an oak forest in the Netherlands. *Agric For Meteorol* 74, 99-118

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

Thom AS (1972) Momentum, mass and heat exchange of vegetation. *QJR Meteorol Soc* 98, 124-134