Trees (1995) 9: 295–301

Structure and Function
Trees

Gas-exchange and sap flow measurements of *Salix viminalis* trees in short-rotation forest

II. Diurnal and seasonal variations of stomatal response and water use efficiency

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Received: 10 February 1994/Accepted: 28 October 1994

Abstract. Water use efficiency was estimated for *Salix viminalis* (L.) trees growing in the field under non-limiting nutrient and soil water conditions. Gas exchange measurements were used to calculate conductances to water vapour and CO_2 fluxes. Sap flow was measured using a tree-trunk heat balance technique. Transpiration and CO_2 uptake were estimated using an open-top ventilated chamber enclosing the whole foliage of a tree. Mesophyll conductance to CO_2 (g_m') was modelled as a non-linear function of global radiation (R_g) and air temperature. Stomatal conductance (g_s) was modelled as a function of R_g and vapour pressure deficit (δe). The models explained 92 and 88% of the variation of g_m' and g_s, respectively. The net photosynthetic capacity of *S. viminalis* was high compared to a number of broad-leaved species. The optimum temperature for photosynthesis was found to be 20.5 °C. The instantaneous water use efficiency (WUE_i) was high: it reached a maximum of 15 g (CO_2) kg^{-1} (H_2O) for small rates of E, and decreased down to 9 g kg^{-1} for peak rates of E. Water use efficiency calculated from above-ground biomass measurements and from net carbon assimilation revealed a specific carbon allocation pattern during the season. The combination of gas exchange and dendrometric measurements was found to be a promising approach of non-destructive estimation of root/shoot allocation of carbon.

Key words: Mesophyll conductance – Stomatal conductance – Allocation – Growth

Introduction

The primary interactions of a terrestrial plant and atmosphere are represented by fluxes of water and CO_2. Understanding how these fluxes are mutually related and how they depend on environmental conditions can assist management practices in forestry and agriculture, particularly with respect to increasing concentrations of CO_2 in the atmosphere and efficient use of available water. Water use efficiency (WUE), defined as the ratio of assimilated CO_2 or C, or dry matter produced per unit of transpired water, serves as an index for comparing plant species at different hierarchical levels and temporal resolutions. For assessment of WUE via gaseous fluxes, the term instantaneous WUE (WUE_i) is used, because the measurements usually have a resolution of seconds or minutes. Long-term WUE (WUE_l) is estimated from growth (expressed mostly as dry weight increment) and water use over longer periods, from days up to years. The assessment of WUE_i involves measurement of transpiration (E) and CO_2-fixation or assimilation (A_n) which include calculation of stomatal and mesophyll conductance. Simultaneous measurement of total carbon assimilation and the above-ground production allows some estimate of below-ground carbon allocation.

Estimated WUE values in the literature are not easy to compare due to the wide range of approaches chosen for measuring the associated fluxes. To compare WUE found for a species in different regions or time, WUE must be compensated for the environmental conditions under which the measurements were made. This is based mainly on the theory that A_n is a function of E and vapour pressure deficit (δe), provided leaf temperature does not depart from the air temperature and the ratio of conductances for CO_2 and water is approximately constant (e.g. Bierhuizen and Slatyer 1965). This approach, together with other ways of treating WUE with respect to climate, is reviewed by Tanner and Sinclair (1983).

In this paper, WUE_l for above-ground production was estimated from measurements of tree diameter increment and sap flow by the tree-trunk heat balance (THB) method. WUE_i was estimated from measurements of gaseous fluxes by a combination of gas concentration measurements with an infrared gas analyser (IRGA) and volumetric flow measurements in an open-top ventilated chamber enclosing a whole tree canopy. WUE_i was also estimated using functions for mesophyll and stomatal conductance for CO_2.

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These functions were used for independent calculation of A_n and related to sap flow measured in seven other dominant trees. Measured and modelled WUE_i were expressed for fixation of C (WUE_{iC}) and averaged so as to be comparable with a long-term estimate of WUE_i. In this way, root-to shoot allocation pattern could be revealed and the partitioning of net assimilated carbon above- and below-ground was computed. The aim of this study was to estimate long- and short-term WUE for *Salix viminalis* (L.) trees and how that relates to weather variables and time. Application of the methods for estimation of carbon allocation to the below-ground parts of a tree was also studied.

Materials and methods

Site, plant material, methods and calculation used with measurements of gas exchange and sap flow have been described elsewhere (Cienciala and Lindroth 1994). Only the calculation of CO_2-assimilation, conductances to water and CO_2 fluxes, and water use efficiency are presented. The analysis of gas exchange will be expressed in terms of conductances instead of units of CO_2 concentration in the air and in the leaf intercellular space (c_a and c_i, respectively; Von Caemmerer and Farquhar 1981). This is for a simpler interpretation of fluxes, to which conductance is directly proportional (Long and Hällgren 1993), because the size and relationships of fluxes were of main interest here. Since the paper deals with issues of interdisciplinary interest, we occasionally use alternative units for easier comparison of the measured values. All the results presented below will refer to trees of the dominant group as distinguished in Fig. 2 in Cienciala and Lindroth (1994).

Calculation of CO_2 flux (A_n)

The net flux of CO_2 between the tree crown and the surrounding air was measured and calculated according to the detailed description given for transpiration by Cienciala and Lindroth (1994) with the following exceptions: (i) M_w was replaced by M_c (molecular weight for CO_2) and $k = 10^6$ (because CO_2 concentration is given as µmol mol^{-1}) in Eq. (2), (ii) it was assumed that the concentration in the reference cell was 360 ppm, i.e., equal to the ambient concentration in the air. The error caused by the deviations from this value was negligible.

Boundary layer and stomatal conductance for water vapour

The average boundary layer conductance to water vapour diffusion (g_b; cm s^{-1}) per unit one-sided leaf area in the chamber was estimated as (e.g. Monteith and Unsworth 1990)

$$g_b = (c_d u_c)/P_d \tag{1}$$

where c_d is a drag coefficient (0.2), u_c is the wind speed inside the cuvette (cm s^{-1}) and P_d is the shelter factor (1.5).

The leaf surface conductance to water vapour diffusion (g_s; cm s^{-1}) per unit leaf area was estimated as

$$g_s = g_b/\{g_b[\rho c_p(e_s-e_a)]/(\lambda E\gamma)-1\} \tag{2}$$

where λ is the latent heat of vaporisation of water (2465 J g^{-1}), E is the transpiration per unit leaf area (g $m^{-2}s^{-1}$), γ is the psychrometric constant (65.5 Pa K^{-1}), ρ is the density of air (1225 g m^{-3}), c_p is the specific heat of air (1.01 J $g^{-1}K^{-1}$), e_s is the saturated vapour pressure (Pa) at "air" temperature and e_a is the actual vapour pressure (Pa).

Conductances to CO_2 flux

The calculation of conductances associated with flux of CO_2 is analogous to that summarised by Bugbee (1985). The total CO_2 flux (A_n; mmol $m^{-2}s^{-1}$) can be written as

$$A_n = \Delta C/\Sigma R \tag{3}$$

where ΔC (mmol m^{-3}) is the CO_2 concentration gradient between the chloroplast and the external atmosphere (360 ppm) and ΣR is the total resistance given by

$$\Sigma R = 1/g_b'+1/g_s'+1/g_m' \tag{4}$$

where g_b', g_s' and g_m' are boundary layer, stomatal and mesophyll conductances for flux of CO_2, respectively. Note, however, that g_m' is a complex variable, which includes both transport and "enzyme" components (e.g. Jones 1992). We treat g_m' as a "rest" term in the resistance (conductance) analogy (Eqs. 3, 4 and below). Thus no attemps are made to elaborate the g_m-concept itself, which may often be ambiguous (see e.g. Parkhurst 1994). CO_2 concentration in the chloroplast is assumed to be equal to the compensation concentration. g_b' was calculated via boundary conductance for water vapour (g_b) as

$$g_b' = g_b/1.387 \tag{5}$$

where the constant of 1.387 is the ratio of diffusivity between water vapour and CO_2, empirically corrected for turbulence (Thom 1968). Since $g_b' >> g_s'$, it has a small impact on the total CO_2 flux and is not discussed further here.

Similarly, g_s' was calculated via stomatal conductance for water vapour (g_s) as

$$g_s' = g_s/1.56 \tag{6}$$

where the constant of 1.56 is the ratio of diffusivity between water vapour and CO_2. The mesophyll conductance (g_m') was calculated by rearranging Eqs. 3 and 4 from measured A_n.

Modelling stomatal and mesophyll conductance

Stomatal and mesophyll conductance data were fitted using non-linear least-square regression analysis. The model was initially analogous to the approach described by Massman and Kaufmann (1991). In the first step, conductance (g, i.e., g_s, g_s' or g_m') was modelled as a function of global radiation (R_g) as

$$g = g_n+g_xR_g/(r_g+p_r) \tag{7}$$

where the three parameters are g_n, the minimum conductance (night-time conductance), g_x, related to maximum conductance and p_r, parameter related to maximum radiation.

For g_s, the response to vapour pressure deficit (δe) was included by incorporating the modifier $f_{\delta e}$ to Eq. 7 as

$$g = (g_n+g_xR_g/(R_g+p_r))f_{\delta e} \tag{8}$$

where $f_{\delta e}$ was in a form analogous to that of Lohammar et al. (1980), namely

$$f_{\delta e} = 1/(1+p_d\delta e) \tag{9}$$

where p_d is the slope parameter.

For g_m', the temperature response was applied by adding the modifier f_T to Eq. 7 as

$$g_m' = g_n+g_xR_g/(R_g+p_r)f_T \tag{10}$$

where f_T was analogous to function applied for g_s by Jarvis (1976) as

$$f_T = [(T_a-T_n)/(T_o-T_n)]\{[(T_x-T_a)/(T_x-T_o)]^a\} \tag{11}$$

where T_a is air temperature, T_n is related to the lowest temperature for carbon assimilation (set to 0 here). T_o is the parameter to be fitted and it represents the optimum temperature for carbon assimilation. The exponent a, which equals $(T_x-T_o)/(T_x-T_n)$, was fixed (= 0.5). Thus, T_x, the maximum assimilation temperature, is determined solely by T_o (Massman and Kaufmann 1991).

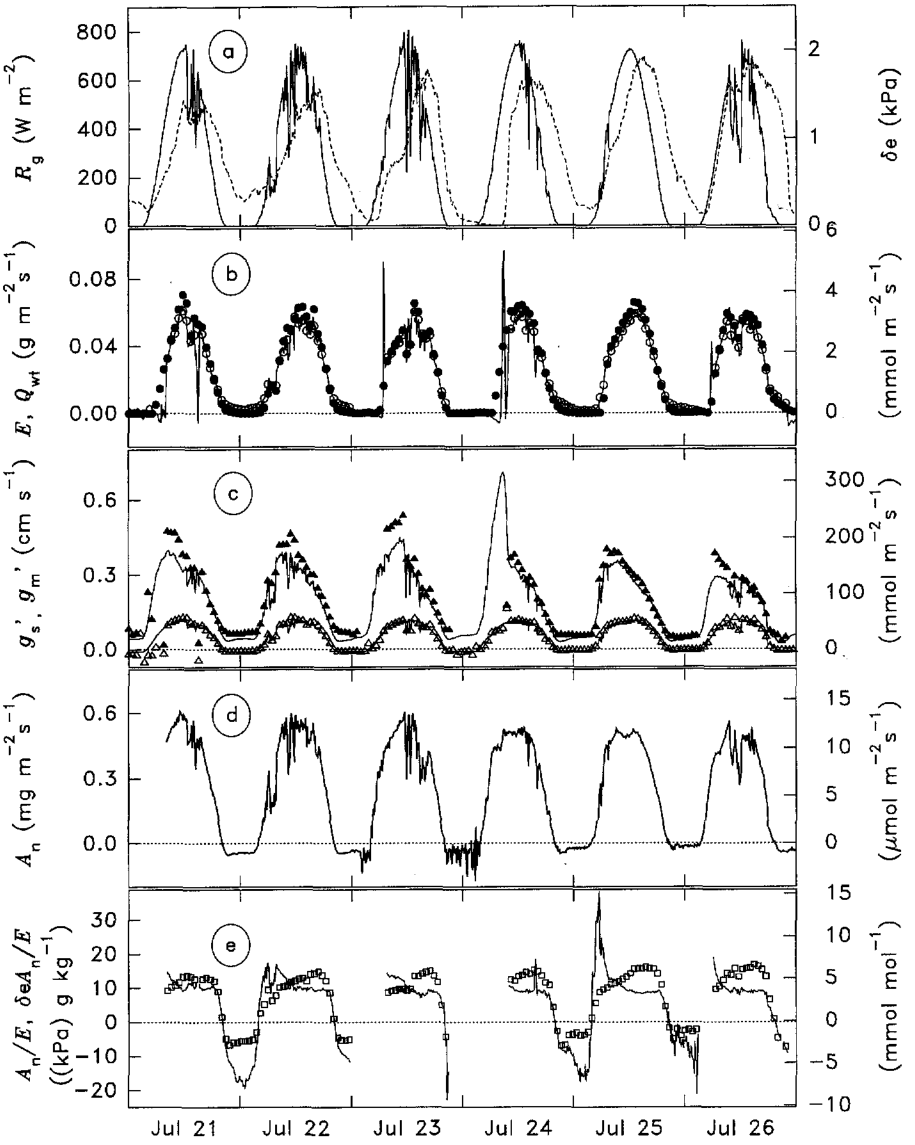

Fig. 1a–e. Six successive days with some of the measured and/or calculated climatic and physiological variables: **a** global radiation (R_g, solid line), vapour pressure deficit (δe, *dashed line*); **b** transpiration (E, *solid line* and *open symbols*) and sap flow (Q_{wt}, *filled symbols*) – the peaks in E observed for 23–24 July are an example of erroneous data due to condensation in the gas-exchange system; **c** measured stomatal and mesophyll conductance to CO_2 flux (g_s' and g_m', *filled and open symbols*, respectively) and the fitted values of g_s' and g_m' according to Eqs. 8 and 10, respectively (*solid lines*); **d** measured net assimilation of CO_2 (A_n, *solid line*); **e** water use efficiency given by A_n/E (*solid line*) and compensated by δe ($\delta eA_n/E$, *symbols*). Note: for clarity, the symbols in **b**, **c** and **e** show every 5th reading of the series of values

The conductance data used to fitting Eqs. 7–11 excluded those obtained during rain and when condensation occurred in the gas-exchange system (see Cienciala and Lindroth 1994).

Water use efficiency

The instantaneous water use efficiency (WUE$_i$; g kg^{-1} or μmol mmol^{-1}) was given by

$$WUE_i = A_n/E \tag{12}$$

where A_n (mg m^{-2}s^{-1} or μmol m^{-2}s^{-1}) is the net photosynthetic rate (assimilation rate of CO_2) and E (g m^{-2}s^{-1} or mmol m^{-2}s^{-1}) is transpiration.

The long-term water use efficiency (WUE$_l$; g kg^{-1}) was estimated as

$$WUE_l = DW/Q_{wt} \tag{13}$$

where Q_{wt} (kg) is sap flow integrated over a specific period (approx. 2 weeks) and DW (g) is the dry weight of the above-ground parts of the tree, estimated as 2-parameter power function of trunk-diameter measured at a height of 50 cm (d_{50}; mm)

$$DW = b(d_{50})^c \tag{14}$$

where parameters b = 0.0869 and c = 2.7 were estimated from destructive biomass measurements from 30 sample trees (Theo Verwijst, unpublished data, 1992). For comparison of WUE$_i$ and WUE$_l$, values were also expressed in terms of assimilated carbon (C) per unit of transpired water and denoted as WUE$_{iC}$ and WUE$_{lC}$, respectively. The conversion factor of Linder and Axelsson (1982) was used for WUE$_{lC}$, giving the carbon content of the dry weight of biomass as 50.5%.

The term "modelled WUE$_{iC}$" used in this work means estimates of water use efficiency based on calculated "instantaneous" net assimilation integrated for daily carbon uptake and then divided by daily water use. A_n was computed using modelled g_s' (g_s; $g_s' = g_s/1.56$) and g_m', and then expressed in terms of daily accumulated carbon. For E, the average of the measured Q_{wt} per day of 5–7 dominant trees was used (relationship between E and Q_{wt} – see Cienciala and Lindroth 1994).

Results and discussion

Modelling conductances to CO_2

Mesophyll (g_m') and stomatal (g_s') conductance to CO_2 differed in magnitude and diurnal dynamics. g_m' was

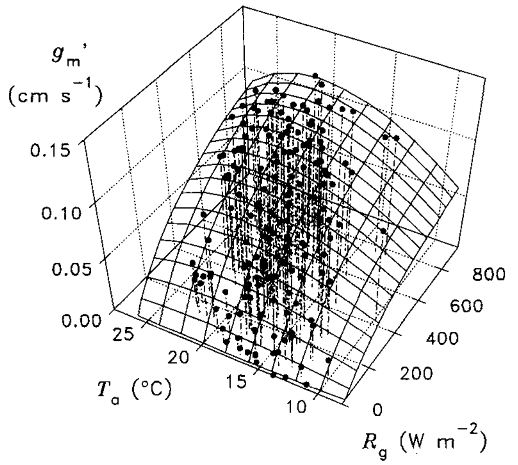

Fig. 2. Modelled mesophyll conductance to CO_2 (g_m') as a function of global radiation (R_g) and air temperature (T_a), (Eq. 10; surface) and the actual g_m' values (*filled circles*). For clarity, only every 15th point is shown ($r^2 = 0.92$)

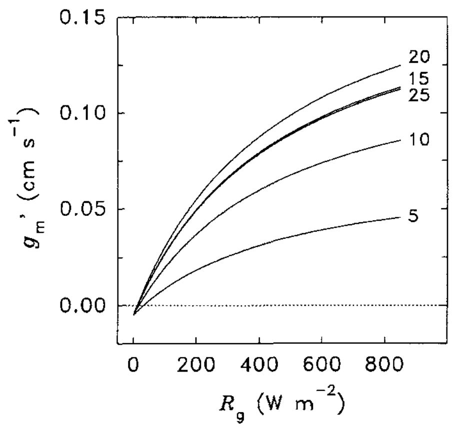

Fig. 3. Modelled mesophyll conductance to CO_2 (g_m') as a function of global radiation (R_g) for a range of temperatures (T_a; the responses for 15 ° and 25 °C coincide)

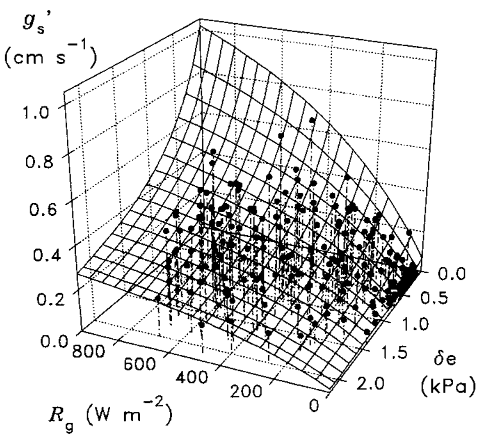

Fig. 4. The modelled stomatal conductance to CO_2 as a function of global radiation (R_g) and vapour pressure deficit (δe) (Eq. 8; surface) and the actual g_s' values (*filled circles*). For clarity, only every 15th point is shown ($r^2 = 0.88$)

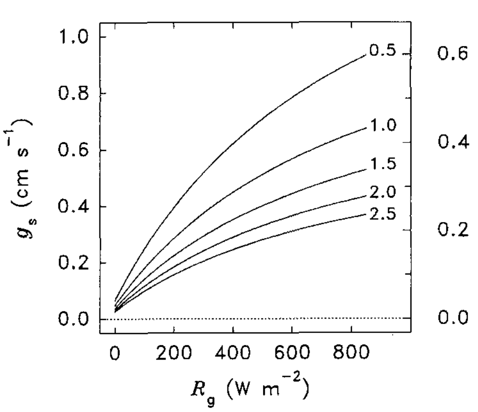

Fig. 5. Modelled stomatal conductance to CO_2 diffusion (g_s'; *right*) or to water vapour (g_s; *left*) as a function of R_g for a range of vapour pressure deficit (δe; kPa) values

Table 1. Dependence of g_m' on R_g and T_a according to Eq. 10: parameter values, standard error (SE) and coefficient of variation (CV, %) of the individual parameters are given ($r^2 = 0.92$, $n = 3260$)

Parameter	Value	SE	CV (%)
g_n (cm s^{-1})	-5.08e-3	4.60e-4	7.58
g_x (W m^{-2})	0.186	3.03e-3	1.58
p_r (W m^{-2})	473.94	17.37	3.43
T_o (°C)	15.24	0.129	8.45

usually one-third to one-quarter of g_s', and reached a maximum of about 0.1 cm s^{-1} during warm clear days with high global radiation (R_g). The diurnal pattern for g_m' was symmetrical and correlated with R_g. In contrast, g_s' rose sharply in the morning, reached the maximum of about 0.4 to 0.45 cm s^{-1}, and then gradually decreased (Fig. 1c).

During night-time, g_s' was commonly above zero, i.e. stomata did not close entirely and significant levels of transpiration were measured during periods of high vapour pressure deficit e.g. for the nights of July 21/22, 24/25 (Fig. 1a–c). Night-time transpiration from the same stand was also reported by Iritz and Lindroth (1994) who measured stand evaporation by micrometeorological methods. On the other hand, g_m' was normally negative because of respiratory losses.

Fitted relationships confirmed the observations above. R_g and T_a (Eq. 10, Table 1, Figs. 2, 3) explained 92% of the variation in g_m'. g_m' was sensitive to temperature and approximately doubled when temperature increased from 5 °C to 12 °C. It reached its optimum at 20.5 °C. Native plants usually have optima similar to the daytime temperatures at which they normally grow (Salisbury and Ross 1992). The light response of g_m' did not reach saturation even at maximum irradiance. This is a common feature for many species when net photosynthesis is measured for a whole shoot (Salisbury and Ross 1992). The leaves deeper down in the canopy do not reach light saturation even at maximal irradiance above the canopy. Single leaves of *Salix aquatica* (Smith) showed a clear light saturation response while the response of the shoot was similar to that found in this study (McDonald 1989).

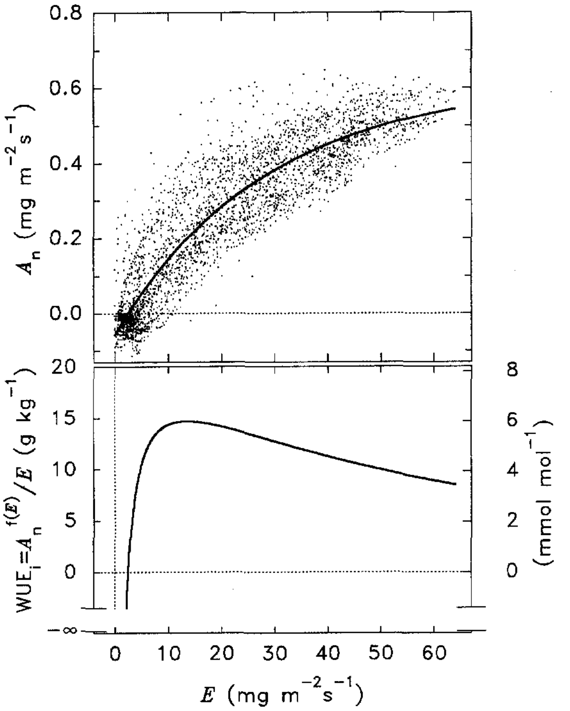

Fig. 6. *Top:* the instantaneous water use efficiency (WUE$_i$ = A_n/; 10-min cases shown by *dots*) approximated by the least-square fitted function according Eq. 15 (*solid line*). *Bottom:* instantaneous water use efficiency (WUE$_i$) against transpiration rate (E). Alternative units noted on respective y-axes

Table 2. Dependence of g_s' (g_s) on R_g and δe according to Eq. 8: parameter values, standard error (SE) and coefficient of variation (CV, %) of the individual parameters are given ($r^2 = 0.92$, $n = 3260$). For g_s, multiply parameters g_n and g_x by 1.56, as well as the corresponding values of SE

Parameter	Value	SE	CV (%)
g_n (cm s^{-1})	0.066	2.5e-3	3.77
g_x (W m^{-2})	1.803	0.072	3.98
p_r (W m^{-2})	847.2	42.22	4.98
p_d (kPa)	1.242	0.037	2.95

R_g and δe explained 88% of the variation in stomatal conductance to CO_2 or water vapour (g_s' and g_s, respectively; Eq. 8, Table 2, Figs. 4, 5).

The values for g_s were in reasonable agreement with porometer measurements on individual leaves in the same stand (unpublished data) which gave maximum conductances of about 1.5 cm s^{-1}.

The function for stomatal conductance was chosen according to the experience by Massman and Kaufmann (1991). In their study, the function of Lohammar et al. (1980) performed well in comparison with some other models even though it contained only three free parameters to be estimated by the least square procedure. The economy of the parameters was also the reason for including the Lohammar equation in the SPAC model when parameterising water fluxes for spruce trees by Cienciala et al. (1994). Here, however, we had to introduce a fourth parameter (g_n; Eq. 8), which would account for the observed significant stomatal opening during night-time.

Diurnal CO_2 assimilation and instantaneous WUE

Net assimilation of CO_2 (A_n) reached the maximum of 0.6 mg m^{-2}s^{-1} (13.6 μmol m^{-2}s^{-1}). At night, A_n typically fell to negative values (i.e. respiration) of about −0.05 mg m^{-2}s^{-1} (Figs. 1d, 6a). In an extensive review on photosynthesis in trees, Ceulemans and Saugier (1991) summarised the 'photosynthetic capacity', defined as "maximum CO_2 exchange rates at saturating light, 20–25 °C and 330 ppm CO_2" of a large number of deciduous broad-leaved species. Most of the data included were based on single-leaf measurements rather than a whole tree canopy which results in low values of saturated A_n. The values found here belong to the upper range of 'photosynthetic capacities'.

The relationship between A_n and E was non-linear and there was a relatively large scatter in the data (Fig. 6, top). The following 3-parameter ($p_{1,2,3}$) equation

$$A_n = p_1[1-\exp(-p_2E)]+p_3 \qquad (15)$$

was fitted ($r^2 = 0.85$, $n = 3260$). Using this function, the "mean" instantaneous water use efficiency (WUE$_i$ = A_n/E) was plotted against transpiration rate (Fig. 6, bottom). WUE$_i$ increased rapidly from negative values to a maximum of 15 g kg^{-1} for transpiration rates of 12–15 mg s^{-1} m^{-2} and then decreased slowly to about 9 g kg^{-1} at a maximal transpiration rate of 60 mg s^{-1} m^{-2}.

The pattern of the response shows that *S. viminalis* utilised water more efficiently when transpiration rates were well below maximum. Bassman and Zwier (1991) investigated the gas exchange of different *Populus* clones grown in greenhouse. They found that WUE$_i$ decreased with increasing "vapour density difference" (VDD), mainly at low density differences. At maximum VDD (about 18 g m^{-3}), WUE$_i$ was almost constant. For an increase of VDD from 3 to 18 g m^{-3}, WUE$_i$ of *Populus* dropped by about 50%. For a similar increase in δe, WUE$_i$ of *S. viminalis* dropped by about 65% (not shown). For high values of δe (2.4 kPa) or VDD (18 g m^{-3}) where the curves level out, WUE$_i$ of *S. viminalis* was about 3.2 mmol mol^{-1} compared to 1.25–2.65 mmol mol^{-1} found for the different *Populus* clones. This suggests that *Salix* has a higher water use efficiency than *Populus*. However, the differences in measurement methods (e.g. single leaf vs whole tree, greenhouse vs field, etc.) and limited material prevent really conclusive comparison of absolute values.

The underlying causes of non-linearity between A_n and E has been considered by Bierhuizen and Slatyer (1965). WUE$_i$ can be described as a function of the ratio between conductances (R) and leaf vapour pressure deficit (δe_L):

$$\mathrm{WUE_i} = A_n/E = \mathrm{k}R/\delta e_L \qquad (16)$$

where

$$R = (1/g_s'+1/g_b'+1/g_m')/(1/g_s+1/g_b) \qquad (17)$$

and k is a constant. If R is regarded as a constant WUE$_i$ is a function only of δe_L (e.g. Tanner and Sinclair 1983; Verma et al. 1986; Baldocchi et al. 1987). Normalising A_n for δe ($\delta e \approx \delta e_L$ assuming negligible differences between air and leaf temperatures) it can be seen that the relationship between A_n and E for *S. viminalis* remained curvi-linear only at low values of E (Fig. 7).

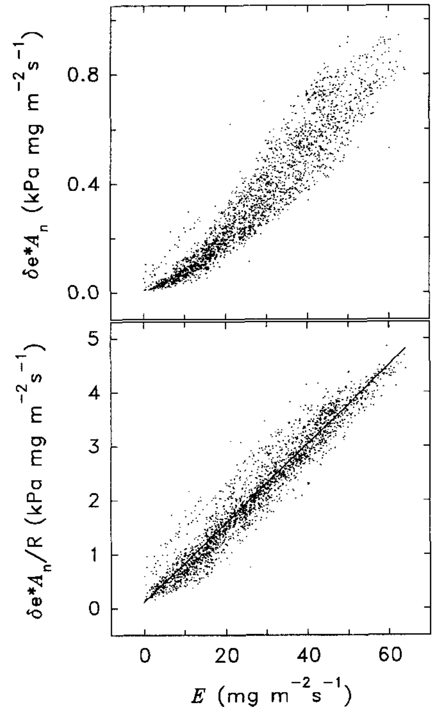

Fig. 7. Scatter diagram of the relationship between net assimilation (A_n) and transpiration (E) normalised for vapour pressure deficit (δe, *top*) and weighted by the ratio of conductances (R; *bottom*) – 10-min readings

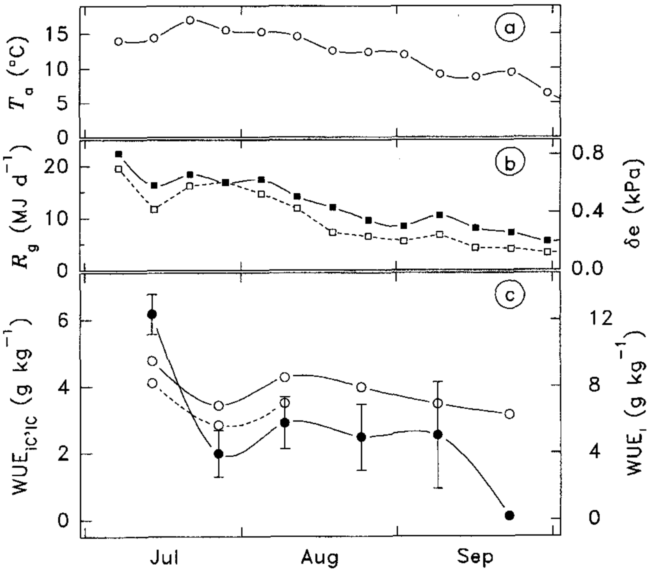

Fig. 8. **a** Weekly means of air temperature, **b** Weekly values of global radiation (R_g; *solid line and filled symbols*) and of vapour pressure deficit (δe; *dashed line and open circles*), **c** The actual long-term water use efficiency estimated for above-ground production (*filled symbols*; standard error shown by *bars*) on the basis of assimilated carbon (*WUE$_{lC}$*; *left axes*) or dry weight (*WUE$_l$*; *right axes*); the measured and modelled WUE$_{iC}$ for assimilation of C (*open symbols*; *solid and dashed line*, respectively). Data are averaged for identical periods of 10–14 days

The normalisation of A_n for δe also changed the diurnal pattern of WUE$_i$: the maximum was shifted from morning to late afternoon and δeWUE$_i$ became less variable (Fig. 1e). Using Eqs. 8 and 10 to calculate R and then weighting A_nδe by R further improved the linearity of the relationship with reduced scatter (Fig. 7). Variations in δe and R explained practically all of the non-linearity between A_n and E.

WUE and allocation of carbon (long-term)

The long-term water use efficiency (WUE$_l$) determined for above-ground production varied considerably during the season (Fig. 8). WUE$_l$ was slightly over 12 g kg^{-1} in early July, decreased below 4 g kg^{-1} in the end of the month, rose again to about 5 to 5.8 g kg^{-1} and then decreased to 0.2 g kg^{-1} at the end of the season. The average value of WUE$_l$ during the period 10 July–1 October was 5.0 g kg^{-1} (g dry biomass per kg transpired water).

WUE expressed in terms of carbon estimated for above-ground biomass (WUE$_{lC}$) initially showed higher values than that based on net assimilation (WUE$_{iC}$), i.e. WUE$_{lC}$ > WUE$_{iC}$ for mid-July. For the rest of the season, however, WUE$_{lC}$ < WUE$_{iC}$ with increasing difference in late September. The measured and modelled WUE$_{iC}$ differed in magnitude by 14–18%, with lower measured values. Higher modelled compared with measured WUE$_{iC}$ (Fig. 8c) are expected because of the differences in the data sets used for calculation. Measured values for periods when transpiration measurements were affected by condensation and rain were omitted (see Cienciala and Lindroth 1994). Thus measured WUE$_{iC}$ contains relatively more data at high δe. There was also the effect of increased air temperature (and δe) in the chamber (see below).

Average modelled WUE$_{iC}$ was 3.8 g kg^{-1} for the period 10 July to 1 October. For the same period, WUE$_{lC}$ calculated for above-ground biomass, was 2.6 g kg^{-1}. Total assimilated carbon and that accumulated for above-ground parts were 440 and 321 g, respectively, for the same period. Assuming the respiration of the biomass outside the chamber (mostly below ground) was 15% of the net assimilation (cf. Dickmann and Pregitzer 1992), 86% of C was allocated to above-ground biomass and 14% to the stool and root system. The stand was both irrigated and fertilised and trees were grown on 8-year-old stumps: thus the 14% fraction is fairly reasonable compared to results from other root studies (e.g. Santantonio et al. 1977).

The seasonal temporal differences of WUE$_i$ compared with those of WUE$_l$ show that changes in the pattern of allocation occur in *S. viminalis*. When WUE$_{iC}$ < WUE$_{lC}$, it is assumed that tree uses carbon from a pool in the stump and roots as well as current assimilate (Lindroth et al. 1994).

Enclosure and errors associated with extrapolations to open-grown trees

The enclosure by the chamber imposed changes of environmental conditions and this must be considered when extrapolating these measurements to open-grown trees. In chamber, R_g decreased by 5%, diffuse light increased by 10%, air temperature increased linearly with net radiation, typically by 1 °C for clear-sky midday conditions, and continuous ventilation held wind speed inside the chamber at 0.5 m s^{-1} (Cienciala and Lindroth 1994).

The effect of R_g was taken into account in parameterisarion of g_m and g_s (g_s'). No compensation was made for changes in diffuse light; it is believed that diffuse light promotes assimilation and thereby WUE (e. g. Denmead et al. 1993). In our study this is expected to have no significant impacts because of the small light fraction involved. The influence of the increased T_a in the chamber on g_m and g_s' was calculated for five warm sunny days 22–26 July (Fig. 1 a). The increased T_a gave 0.7% decrease of the mean in g_m-model and 2.9% decrease in g_s' (g_s)-model (T_a acts via δe in this model). Finally, the ventilation rate in the chamber matched the average windspeed in the canopy, the effects based on aerodynamic properties (aerodynamic conductance) were neglected. It is thus reasonable to expect, that the total error associated with extrapolation of conductance data for CO_2-flux from chamber- to open-grown trees was less than 5%.

Conclusions

The variation in g_m' was largely explained ($r^2 = 0.92$) by a simple non-linear model with R_g and T_a as independent variables. Most of the variation in g_s was explained ($r^2 = 0.88$) by a model with R_g and δe as independent variables. This model included night-time which was non-negligible. The net photosynthetic capacity, as defined by Ceulemans and Saugier (1991), of *S. viminalis* was high compared to a large number of broad-leaved species. WUE_i was maximal at low transpiration rates. During the period of measurement, the pattern of carbon allocation for above- and below-ground parts varied considerably. The combination of gas exchange and dendrometric measurements provides a unique approach for the non-destructive estimation of allocation of carbon to root and shoot.

Acknowledgements. We are obliged to Jerry Leverenz and James McDonald for their constructive comments on the manuscript and to Theo Verwijst for providing the parameters for estimation of dry weight of the shoots. This research was funded by the Swedish Natural Science Research Council under contracts G-GU 09382-320 and G-Gu 09382-321.

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