ORIGINAL ARTICLE

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Water-use efficiency as a means of modelling net assimilation in boreal forests

Abstract Although the processes governing photosynthesis are well understood, scaling from shoot to canopy in coniferous forests is complex. Development of different sap-flow techniques has made it possible to measure transpiration of whole trees and thereby also of whole canopies. There is a strong link between photosynthesis and transpiration, for which reason it would be interesting to test whether measurements of canopy transpiration could also be used to estimate canopy photosynthesis. As a first step towards this, water-use efficiency (WUE) was studied at branch and canopy scales on the basis of branch gas-exchange measurements, with half-hourly and daily temporal resolution. Half-hourly and daily WUE at both branch and canopy scales showed a strong dependency on vapour-pressure deficit (δe). Branch photosynthesis modelled from branch transpiration and δe mimicked well measured branch photosynthesis. Also, modelled photosynthesis, scaled to canopy and compared to net forest CO_2 exchange measured by the eddy-covariance technique, occasionally showed good agreement. In spite of these seemingly promising results, there was a difference in the response to δe between branches and between years, which needs to be better understood.

Keywords Boreal forest · Transpiration · Photosynthesis · Scaling · Branch chambers

Introduction

Estimation and analysis of the terrestrial source/sink strength for C is a major research topic today. The inter-

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national negotiations on climate change in Kyoto 1997 further emphasised the importance of the assessment of the C balance of forests in particular. New methods for measuring the net C exchange between the earth's surface and the atmosphere have recently been developed (e.g. Verma 1990; Baldocchi et al. 1996; Grelle and Lindroth 1996), which have opened up new possibilities for better understanding both short-term (hourly) and long-term (annual) mechanisms controlling C fluxes in different types of ecosystems. In spite of these methodological advances, there is still a need to estimate the components of the C budget, because the processes involved are highly non-linear, and respond differently to climatic variables (Steffen et al. 1998). Such data are also necessary for building and testing mechanistic models of the system, which is a prerequisite to assessment of the impact of climate change.

In this context, the measurement or estimation of the net assimilation of forest canopies constitutes a special problem. To our knowledge, no method is available for direct measurement of the net assimilation of an entire forest canopy; all methods must therefore rely on scaling of some kind. Although we now know much about the processes that govern photosynthesis, scaling from shoot to canopy level in coniferous forests is complex. One of the main problems is the accurate estimation of light interception, because the canopy cannot be assumed to be uniform and leaves are not randomly distributed. Intense studies of photosynthesis during the 1970s led to a detailed biochemical model (Farquhar et al. 1980), which today is incorporated into most models that operate at the leaf to ecosystem level (e.g. Wang and Jarvis 1990; Leuning et al. 1995; Lloyd et al. 1995; Falge et al. 1996). To parameterise the Farquhar model, photosynthetic parameters at leaf level on deciduous trees, and at shoot level in coniferous trees, must be estimated. On coniferous trees which retain many age-classes of needle, this may become extremely laborious. Furthermore, the photosynthetic capacity of needles varies with age (Troeng and Linder 1982a; Hom and Oechel 1983; Porté and Loustau 1998) and species. Since most natural forests

are mixed, these differences must also be accounted for. Moreover, the height of the canopy of tall trees makes measurement and sampling difficult and time-consuming. Simplification of the procedure for estimating net canopy assimilation is therefore of great interest.

An interesting approach, which we put forward here, is to utilise the strong link between photosynthesis and transpiration. The two fluxes, of CO_2 and water, are closely connected via the stomatal openings; if we can determine one of the fluxes, we should also be able to determine the companion flux. There have also been methodological advances in water-flux measurements, and our ability actually to measure the transpiration of entire trees, and thus of entire canopies, by measuring a number of trees, has improved significantly through the development of sap-flow techniques (e.g. Cermak et al. 1973; Granier 1987).

The goal of this work is to develop a method for the estimation of whole-canopy net assimilation, on the basis of sap-flow measurements of canopy transpiration. As a first step, we begin by exploring the relationship between fluxes of CO_2 and water at branch level in a mixed pine and spruce forest. The ratio between these two fluxes is usually denoted "water use efficiency" (WUE). WUE is considered to be instantaneous when it is estimated from fluxes measured with a time resolution of seconds to minutes. There exists, however, a whole flora of definitions of WUE, of which many are based on various ratios between biomass components and water-use components. In this paper, we confine ourselves strictly to definitions based on gas-exchange properties. The rationale for our suggested method builds on the fact that WUE appear to be a conservative plant property (e.g. Tanner and Sinclair 1983).

Materials and methods

Site description

This study was carried out in a managed forest at Norunda (60°5′N, 17°29′E, altitude 45 m) about 30 km north of Uppsala, Sweden, during the summers of 1995 and 1996. The forest consists of a mixture of stands, made up of various proportions of Scots pine and Norway spruce, in which stand age varies from ca. 50 to 150 years. In 1994, a 100-m-tall measurement tower was built, for continuous monitoring of the vertical mass and energy exchange of the ecosystem. Eddy-covariance systems were installed at 35, 70 and 100 m (Grelle and Lindroth 1996; Grelle 1997). A footprint analysis, based on the simplified model by Schmid (1994), showed that the 35-m instrument had its source areas within the forested fetch, and was thus most representative of the forest. The studied stand was ca. 70 years old and was situated about 350 m south-west of the 100-m measurement tower. The stand basal area was 29 m² ha⁻¹ and average stand height 23 m. The crown stratum of the stand consisted mainly of Norway spruce [*Picea abies* (L.) Karst.; 66% of the stand basal area] and Scots pine (*Pinus sylvestris* L.; 33%). A sparse lower canopy consisted mainly of acidophilous dwarf shrubs (*Vaccinium myrtillus* L.). The soil was a deep, boulder-rich sandy glacial till.

At Uppsala, the mean annual temperature is 5.5°C (1961–1990), the mean annual precipitation is 527 mm and the mean Penman open-water evaporation is 459 mm (1973–1998). July is normally the warmest and wettest month and April the coolest and driest month (records of Ultuna Meteorological Station).

Branch CO_2 and water-exchange measurements

At the experimental plot, a scaffold tower was raised between a spruce and a pine tree, to gain access to their branches. Measurements were performed on one pair of trees in the summer of 1995 and on a second pair of trees in the summer of 1996. An open-chamber system (In Situ, Sweden) was used to measure water-vapour and CO_2 gas exchange on one spruce (10 May–23 June) and one pine branch (29 June–8 August) in 1995, and two spruce (23 May–11 July, 11 July–17 August) and one pine branch (31 May–23 July and 17 August–9 September) in 1996. The system consisted of chambers made from transparent polyethylene film, mounted on supporting metal plates, a pump unit and a control and measuring unit. Each chamber was connected to a fan via a flexible tube, on which a 2-m-long, 20-cm-diameter metal tube was attached. About 50 cm from the end of the metal tube, a propeller anemometer was mounted, to measure the flow of air through the chamber. The flow, which was kept constant, gave a wind speed of 0.1 m s⁻¹ near the wall and ca. 0.7 m s⁻¹ in the middle of the chamber. It was estimated that the average wind speed was 0.4–0.5 m s⁻¹ which, depending on chamber length, gave an air-exchange rate of 8–12 times min⁻¹. Air was sampled via two (6-mm) high-density polyethylene tube segments placed across the inlet and outlet of the chamber. The tubes were perforated with small holes to sample the entire profile of the air stream in the chamber. Two pumps drew air through the sampling tubes to a gas analyser (IRGA LI-6262; Li-Cor, USA) at approximately 2.5 l min⁻¹. The system, together with calculations of fluxes and gas concentrations, was described in detail by Morén and Lindroth (1999), and modelling of branch conductance and geometry by Morén (1999a).

Climatic variables were recorded close to each measured branch. Ambient temperature and relative humidity were measured with a temperature and relative humidity probe (Rotronic Instrument, USA) placed in a ventilated radiation shield (In Situ). The photosynthetically active radiation was measured with a quantum sensor (LI-190SZ; Li-Cor) ca. 50 cm above each branch. In the later part of the growing season of 1996, this sensor was replaced by a line quantum sensor (LI-191SA; Li-Cor).

After measurements, each branch was cut off and dried in a ventilated oven at 85°C for 48 h to facilitate removal of needles. The needle area of each branch was found by applying the relationship between needle length and total and projected area of a single needle (cf. Morén et al. 2000). All values reported here are on a projected needle area basis.

Analysis, modelling and scaling of branch CO_2 exchange

For the sun-exposed branch chambers, temperature and relative humidity measured outside the chambers were recalculated, to better represent conditions within the chambers [cf. Results, and Morén and Lindroth (1999)]. To avoid problems associated with condensation, measured water exchange data were omitted at night, when relative humidity exceeded 85% and when it was obvious that condensed water was evaporating.

The CO_2 exchange at branch level was analysed in terms of instantaneous WUE (WUE_i). WUE_i is given by (e.g. Bierhuizen and Slatyer 1965):

$$WUE_i = F_C / F_W = kR / \delta e \qquad (1)$$

where F_C is the instantaneous net CO_2 exchange rate, F_W the net water-vapour exchange rate, k is a constant, R is the ratio of resistances to transport of CO_2 and water vapour, and δe is the vapour pressure deficit. It has been proposed that R can be regarded as constant (see e.g. Tanner and Sinclair 1983; Verma et al. 1986; Baldocchi et al. 1987), which means that WUE_i is a function only of δe, and F_C can be expressed as:

$$F_C = k_0 F_W / \delta e \qquad (2)$$

where R is included in k_0.

Branch net assimilation was modelled by applying a slightly modified version of Eq. 2 (see Results and Discussion). Both measured and modelled branch transpiration was used for F_W. Branch transpiration was modelled as a function of δe and photosynthetically active light (see Morén 1999a).

At night, transpiration is effectively zero, while needles and branches lose CO_2 through respiration. Respiration was modelled as an exponential function of temperature. Needle and branch temperatures were assumed to equal air temperature, T_a:

$$F_C = k_1 \exp^{k_2 T_a} \tag{3}$$

where k_1 and k_2 are fitting parameters.

Canopy net assimilation was calculated from scaled canopy transpiration by applying the modified version of Eqs. 2 and 3 (see Results and Discussion). Canopy transpiration was scaled to canopy according to Morén et al. (2000): On the basis of allometric relationships established from destructive sampling, each tree in the stand was assigned a tree height, live crown length and needle area as functions of diameter on bark at breast height (1.3 m). Needle area was distributed along tree stems according to the needle-area distributions on Norway spruce and Scots pine, respectively, and the vertical distribution of canopy needle area was calculated per metre stand height. For each 1-m layer, starting at the top of the canopy, light was calculated according to Beer's law. On the basis of needle area, light and δe in each layer, branch conductance and transpiration were estimated, before being summed to canopy transpiration.

Net stand CO_2 exchange

Net stand CO_2 exchange was obtained by adding the contributions from forest floor, stems and canopy, and was compared with forest CO_2 net exchange measured by eddy-covariance at 35 m. No soil respiration measurements were available for 1995. Therefore, the contribution from the forest floor, soil respiration, reduced by net assimilation of moss and plants on the forest floor, was modelled. The respiration term was modelled as a function of soil temperature, and CO_2 assimilation as a function of light and temperature (cf. Morén and Lindroth 2000). Based on measurements of stem respiration within the experimental stand, stem respiration was modelled as an exponential function of temperature (Morén 1999b).

Results and discussion

The branch chamber measurements represented the total fluxes from needles of different age-classes, which experienced a wide range of light levels, depending on their position within the branch. The response to climate therefore represented a temporal and spatial mean of the contribution from thousands of needles: 70,000–130,000 needles for the spruce branches and 25,000 and 40,000 needle pairs, respectively, for the two pine branches. Although the chambers were designed to maintain near-ambient conditions, chamber temperatures maximally were 5°C higher and relative humidities up to 20% lower than in the air outside the chambers. More typical values were +1°C and –5%, respectively (Fig. 1b, c).

Water and CO_2 fluxes were strongly correlated (Fig. 1d, e). Analysis showed that branch conductance within the growing season was governed mainly by light and water-vapour pressure deficit (Morén 1999a). Moreover, the analysis showed that branch conductance was very sensitive to the light conditions afforded by the branches; i.e. branch structure was crucial to the rate of
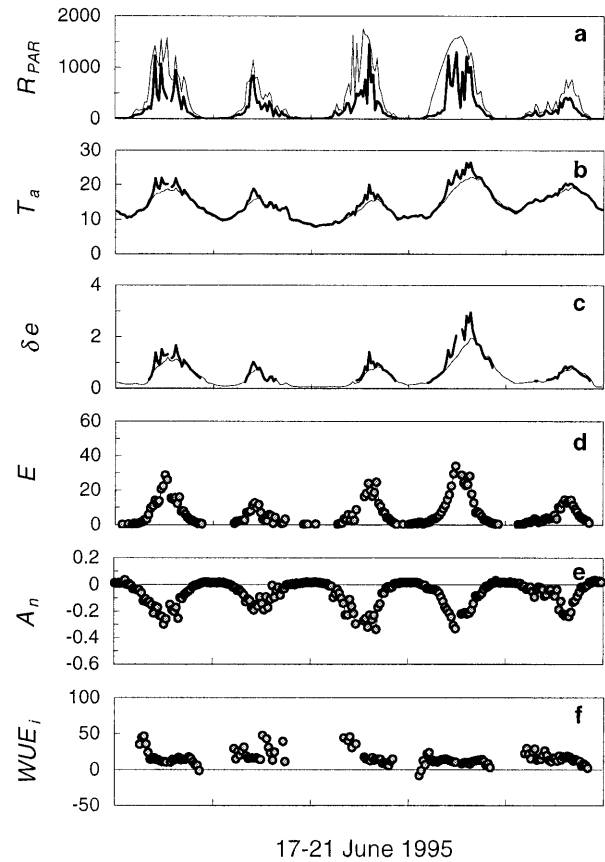

17-21 June 1995

Fig. 1a–f Half-hourly mean values of climatic variables, transpiration, net assimilation, and instantaneous water-use efficiency (WUE_i) measured with a chamber on a sun-exposed brush-type Norway spruce branch. **a** Incident photosynthetically active radiation (R_{PAR}; μmol m^{-2} s^{-1}), measured above the stand (*thin line*) and ca. 50 cm above the branch chamber (*thick line*); **b** temperature (T_a; °C) outside the chamber (*thin line*) and inside the chamber (*thick line*); **c** vapour pressure deficit (δe; kPa) outside the chamber (*thin line*) and inside the chamber (*thick line*); **d** transpiration (E; mg m^{-2} s^{-1}); **e** net assimilation (A_n; mg m^{-2} s^{-1}); and **f** WUE$_i$ (mg g^{-1}). Transpiration and net assimilation on a projected needle area basis

water and CO_2 exchange measured at branch level (Morén 1999a). Branch conductance of both pine and spruce was found to be comparable to stomatal conductance at shoot level, presented in other studies. Reported maximal photosynthetic rates for Norway spruce are ca. 0.5 mg m^{-2} s^{-1} for current-year shoots (Wieser and Havranek 1994; Roberntz and Stockfors 1998), and for Scots pine ca. 0.7 mg m^{-2} s^{-1} for 1-year-old shoots (Troeng and Linder 1982b; Wang et al. 1995). The maximal photosynthetic rates for the five branches in this study were in the range 0.17–0.41 mg m^{-2} s^{-1} for spruce and 0.26–0.40 mg m^{-2} s^{-1} for pine, and thus corresponded with reported values (Morén 1999a).

WUE$_i$ at branch level

WUE$_i$ was slightly higher in the morning than in the afternoon (Fig. 1f). The non-symmetrical pattern was ex-

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Fig. 2a, b WUE plotted versus δe. Values are half-hourly means from 8 May to 24 June 1995 on a sun-exposed brush-type Norway spruce branch; **a** all data, **b** only for R_{PAR} >200 µmol m^{-2} s^{-1}. For abbreviations, see Fig. 1
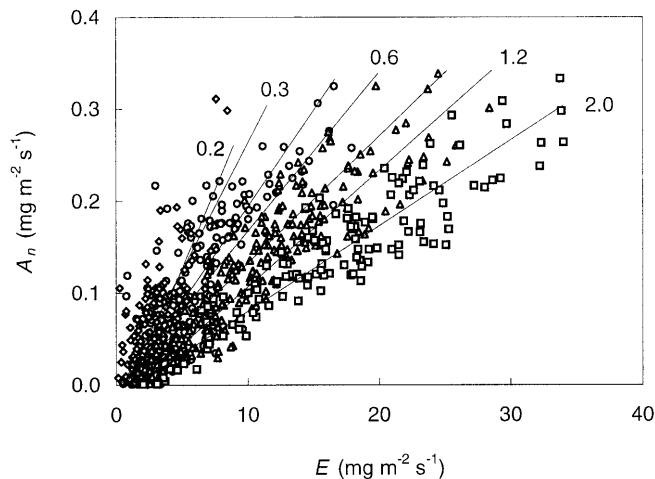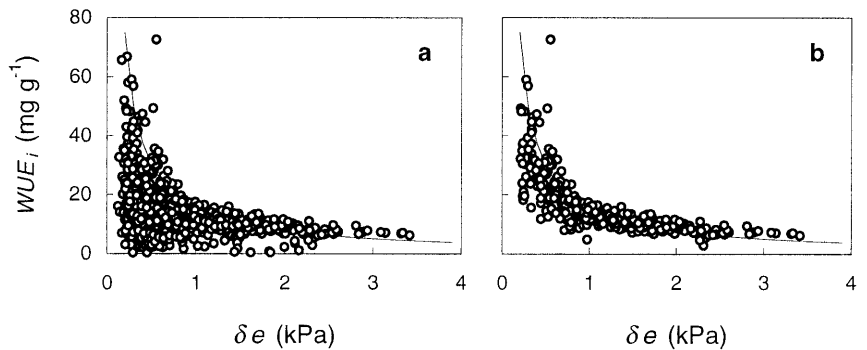

Fig. 3 A_n plotted versus E. Branch and time-period as in Fig. 2. *Lines* are regression lines referring to the data classified according to δe. *Starting from the left*, the intervals were: 0.15–0.25, 0.25–0.35, 0.35–0.50, 0.50–0.75, 0.75–1.00, 1.00–1.50, >1.50 kPa. For clarity, symbols were given for four larger groups only, 0.15<δe<0.50 (*diamonds*), 0.50<δe<0.75 (*circles*), 0.75<δe<1.50 (*triangles*), δe>1.50 (*squares*). For abbreviations, see Fig. 1

Fig. 4 The slopes from the regressions in Fig. 3 plotted versus the midpoint of each δe class. *Circles* refer to data in Fig. 3, $s=0.0148\delta e^{-0.6057}$, $R^2=0.98$, in the text denoted A, whereas *squares* refer to another set of branches, $s=0.0164\delta e^{-0.3800}$, $R^2=0.94$, in the text denoted B. For abbreviations, see Fig. 1

plained by the dependence on δe (Fig. 2). At light levels >200 µmol m^{-2} s^{-1}, WUE$_i$ showed the typical decrease in response to increasing δe as, for example, reported by Lindroth and Cienciala (1996) (Fig. 2b). At light levels <200 µmol m^{-2} s^{-1}, the fluxes were small and the variation increased (Fig. 2a).

A plot of net assimilation versus transpiration for the measurements made on the spruce branch in 1995, gave a seemingly curvilinear relationship with a large scatter (Fig. 3). Grouping of data according to δe explained most of the scatter and the curvilinear shape of the relationship. A plot of the slope of the regression line for each class, s, versus the midpoint of the δe class, gave a negative power function to replace $k_0/\delta e$ in Eq. 2 (A in Fig. 4):

$$s = a\delta e^{-b} \tag{4}$$

where a and b are fitting parameters. All of the regression lines (Fig. 3) had an intercept less than zero, and thus the modified version of Eq. 2 took the form:
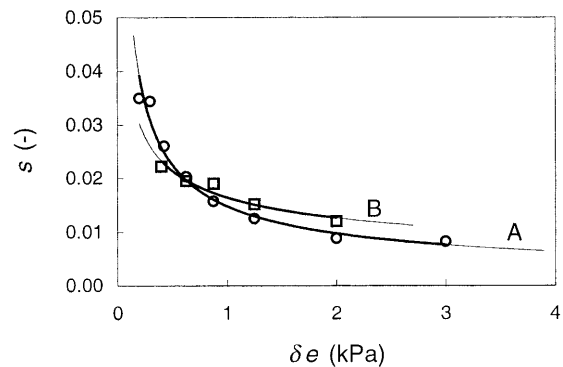
$$F_C = sF_W + i \tag{5}$$

where i is the average of the intercept of the regressions lines.

Equation 5, with parameters according to Fig. 4, A and i=0.025, was applied to the spruce branch on which the model parameterisation was made. The combination of measured transpiration and modelled net assimilation mimicked the diurnal variation of measured net assimilation, except occasionally at noon where the model overestimated net uptake (Fig. 5a). For the period 28 May–3 June, the model explained 89% of the variation in net assimilation, and for the whole period of measurements on this branch (n=811), the model explained 80% of the variation (Fig. 5b). When measured transpiration was replaced by transpiration estimated from modelled branch conductance, the model similarly explained 75% and 66% of the variation, and showed a tendency to overestimate net assimilation at mid-day (Fig. 5c, d). Why measured and modelled fluxes deviated more when transpiration was also modelled, is explained by the fact that the effect of shoot development during the measuring period was not accounted for in the branch conductance model [see Morén (1999a): Fig. 7]. This parameterisation also worked well for the gas-exchange measurements on the pine branch in 1995. Here, the model explained 90% of the variation in net assimilation (n=1069). For the measurements of gas exchange on branches in 1996, on the other hand, this model parameterisation caused

Fig. 5 Measured and modelled branch A_n (**a**) and (**b**) modelled A_n, based on measured E and δe, (**c**) and (**d**) modelled A_n based on E calculated from branch conductance, in turn, modelled from light and δe. In **a** and **c**, *circles* refer to modelled, and *thin lines* to measured A_n. In **b** and **d** *black dots* refer to data shown in **a** and **b**, whereas *grey dots* refers to the period covered by measurements on that branch, 8 May–24 June 1995. *The lines are one-to-one lines.* For abbreviations, see Fig. 1
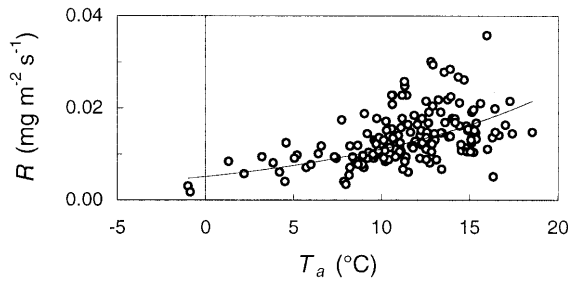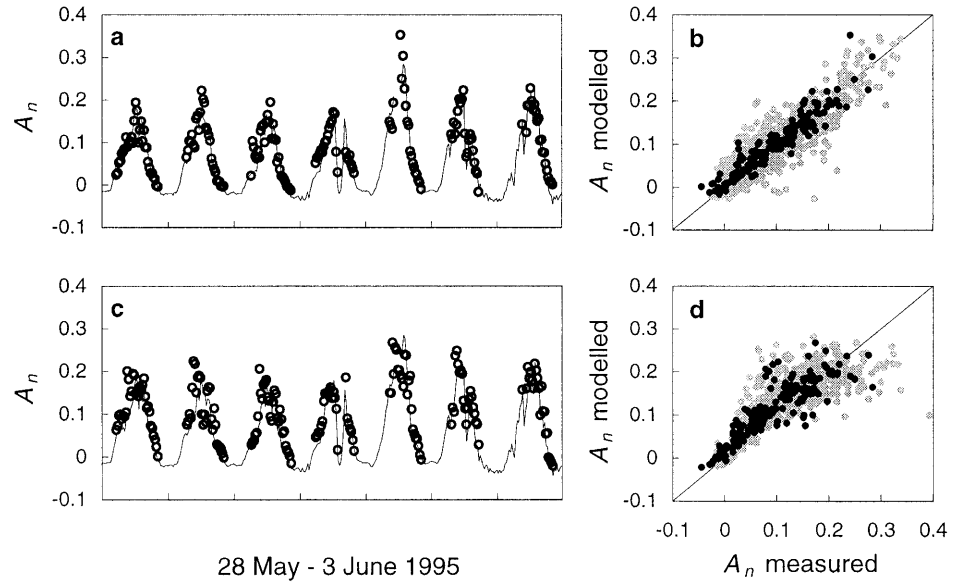
28 May - 3 June 1995

Fig. 6 Nocturnal branch respiration (R) as a function of T_a, $R=0.0051\exp(0.0774T_a)$, $R^2=0.34$. *Each circle* represents one nocturnal average respiration value (*see text*)

6-10 July 1995

Fig. 7 a Branch A_n scaled to canopy ($F_{C,C}$), forest floor CO_2 efflux ($F_{C,FF}$), and stem respiration ($F_{C,S}$), scaled to stand level (mg m^{-2} s^{-1}); **b** the sum of the components in **a** (*continuous line*), in comparison with net forest CO_2 exchange as measured by means of the eddy-covariance technique (*dotted line*; mg m^{-2} s^{-1}), **c** R_{PAR} measured above the stand (*solid line*; µmol m^{-2} s^{-1}), and δe within the stand (*dotted line*; kPa), and **d** T_a within the stand (*solid line*; °C) and wind speed above the stand (*dotted line*; m s^{-1}). All data are half-hourly mean values. For abbreviations, see Fig. 1

significant underestimation of net assimilation. It was found that the response to δe of these branches was less strong (parameter B in Fig. 4). When net assimilation was modelled with parameters according to Fig. 4, B, and $i=0.015$, the model explained 76, 82 and 83% of the variation in net assimilation of these three branches (n in the range 886–1438). In spite of the strong relationship between model and measurements, the model, most of the time, underestimated net assimilation for one of the three branches, the spruce branch measured during 23 May–11 July, indicating a third type of response to δe. Thus it is evident that WUE can be used to model net assimilation, but the cause of the different responses to δe must be clarified.

Scaling to canopy and stand levels

Equation 5 was applied to scale half-hourly net assimilation to canopy level during daytime, whereas at night, needle, twig and branch respiration was modelled as a function of air temperature (Eq. 3). Half-hourly data for the temperature-respiration relationship showed a wide scatter. Therefore, an average value for each night of
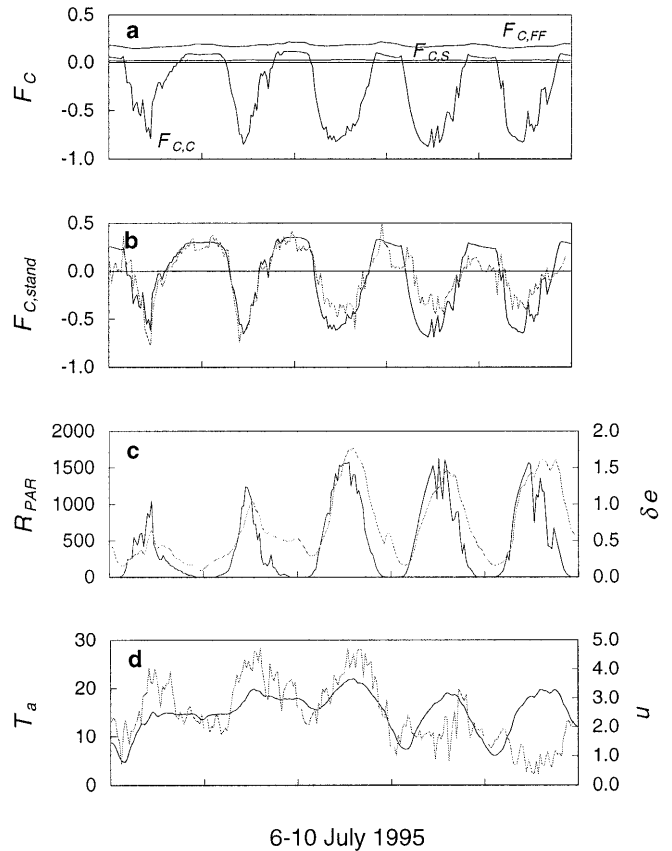
measurements and each branch was established, which resulted in a weak temperature response (Fig. 6).

Scaled net stand CO_2 exchange showed, in general, poor agreement with net forest CO_2 exchange, measured by means of the eddy-covariance technique. Therefore, only a short period was selected for comparison of scaled and measured fluxes. This period was selected when variation in the nocturnal respiration rates of the two independent methods appeared to be fairly similar, and the level of scaled nocturnal respiration was adjusted to fit measured forest respiration. When based on half-hourly data, the highest canopy net photosynthetic rates were ca. 0.8 mg m^{-2} s^{-1} (Fig. 7a). At stand level, soil CO_2 efflux became important, whereas the contribution from stems to respiration was almost negligible. (Fig. 7a). Modelled soil respiration and net assimilation by forest-floor vegetation gave a rough estimate of the contribution from the forest floor to net CO_2 exchange. Forest-floor efflux rates were highest during the night and lower during the day, because of net assimilation by the forest-floor vegetation (cf. Morén and Lindroth 2000).

The selected period started with two nights during which the friction velocity (u^*) was ca. 0.4 m s^{-1}, implying that air in the canopy was well mixed with the air layers above the canopy. Here, modelled and measured net exchange agreed well (Fig. 7b). During the following two nights, u^* was <0.2 m^{-2} s^{-1} and respired CO_2 was stored within the canopy, rather than being transported to the air above the forest (e.g. Lee 1998). During the day, the modelled net ecosystem exchange agreed well with measured fluxes on 6 and 7 July, whereas the model overestimated CO_2 exchange on 8–10 July (Fig. 7b). It is difficult to give a simple explanation of the observed differences. One plausible explanation is the observed variability in net ecosystem exchange (NEE) with wind direction (Grelle 1997). The forest surrounding the flux tower consists of a mixture of stands, varying in density and species composition. It is therefore not surprising that the NEE of an individual stand will differ considerably, as compared with the average NEE as seen and measured by the eddy-covariance system in the tower. A comparison is further complicated by the fact that NEE is a sensitive balance between two large terms and thus, is sensitive to small differences in these separate terms (Goulden et al. 1998; Lindroth et al. 1998). Nevertheless, during the first 3 days of the chosen period, 6–8 July, the wind direction was in the sector 200–260°, implying that the present stand, at least, was in the source area sector of the eddy-covariance system, while it was not in that sector during 9–10 July. To avoid inappropriateness in scaling models, in particular for heterogeneous forests, being overshadowed by difficulties in interpreting the source of measured ecosystem fluxes, a considerably improved forest-floor efflux model or continuous measurements for longer periods, inclusion of the CO_2 storage within the stand and some kind of footprint analyses will be required to ensure that ecosystem fluxes represented the experimental plot.
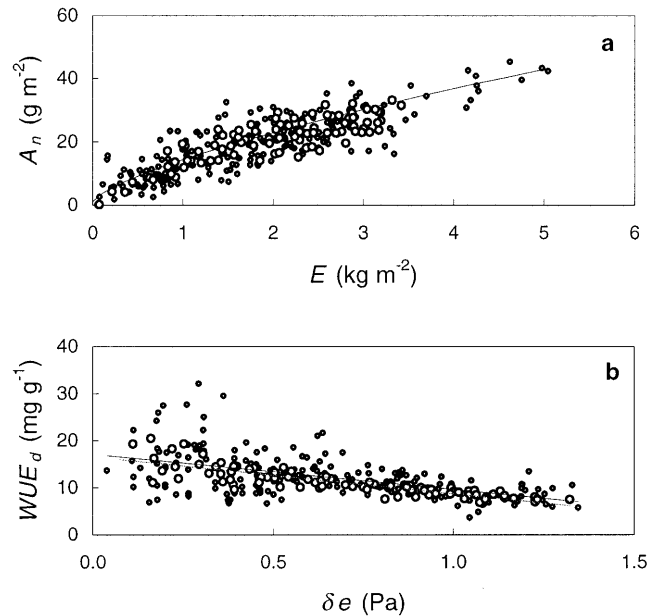

Fig. 8 a Daily sums of measured branch A_n, plotted against measured branch E for all branches in this study (*black circles*), and similarly scaled canopy CO_2 and water exchange for the period 1 June to 31 August 1995 (*grey circles*). **b** Diurnal WUE (WUE_d) (i.e. the ratio of daily sums of net assimilation and transpiration in **a**) plotted versus δe. Symbols as in **a**. Regression lines: WUE_d based on measured gas exchange (*solid line*), and based on scaled fluxes (*dotted line*). For abbreviations, see Fig. 1

Daily and long term WUE

The seemingly curvilinear shape of the relationship between net assimilation and transpiration was preserved when summed to daily WUE (WUE_d) values (Fig. 8a). This was valid both for the branch-chamber measurements, transferred to ground surface area by multiplying with the leaf area index of the stand, and scaled fluxes. The δe response denoted A (Fig. 4) was used for the scaling. As compared to WUE_d at branch level, scaled canopy net assimilation was underestimated for high transpiration rates (Fig. 8a). The response denoted B (Fig. 4) gave, on the contrary, an even larger overestimate of net assimilation at high transpiration rates.

On a diurnal basis, measured branch net assimilation and transpiration reached maximum rates, of ca. 45 g m^{-2} and 5 kg m^{-2}, respectively. Scaled to canopy level, corresponding figures were ca. 35 g m^{-2} and 3.3 kg m^{-2} (Fig. 8a). WUE_d showed a similar decrease with increasing water vapour pressure as did WUE_i. On average, the range in WUE_d was 7–17 mg g^{-1} for the δes encountered, implying that the relationship with δe cannot be ignored on a diurnal basis (Fig. 8b).

On a seasonal basis, WUE is denoted long-term (WUE_l) (cf. Lindroth and Cienciala 1996). For the branches in this study, WUE_l showed a large variation, the lowest values being 5 mg g^{-1} and the largest 32 mg g^{-1} (Fig. 9a). The mean (±SD) over the 2 years for the five branches was 12.3±4.6 mg g^{-1}. For *Salix viminalis*, Lindroth and Cienciala (1996) reported WUE_l of
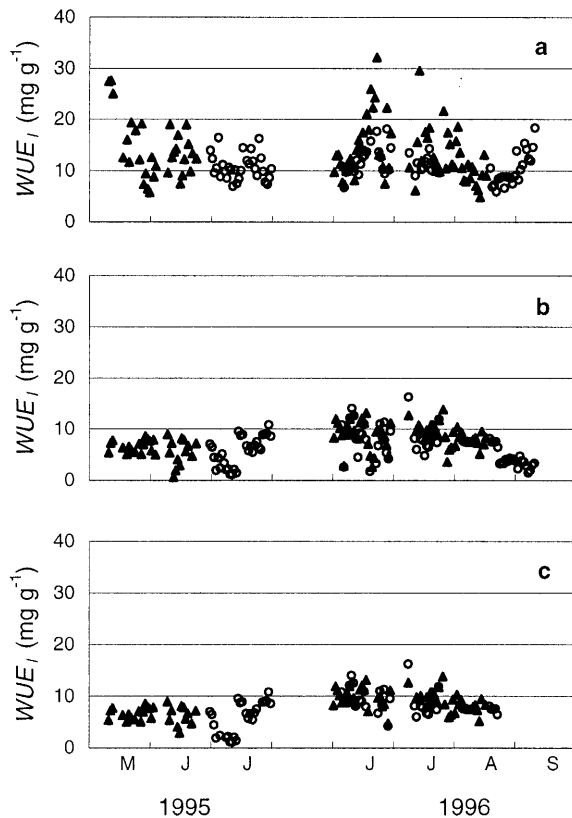
Fig. 9a–c Long-term WUE (*WUE$_l$*). **a** WUE$_d$ based on branch chamber measurements with data from Fig. 8b plotted on their respective day of measurements, **b** WUE$_d$ weighted for δe, all data, and **c** data only for mean daily R_{PAR} above the stand >320 μmol m^{-2} s^{-1}. *Filled triangles* refer to the spruce branches, while *open circles* refer to the two pine branches. For abbreviations, see Figs. 1, 8

11.3±4.1 mg g^{-1}, and Rayment (1998) an average for four Black spruce branches over 230 days of 13 mg g^{-1}. When weighted by δe, the variation was considerably reduced (7.13±3.0 mg g^{-1}; Fig. 9b). Furthermore, when considering only days on which the diurnal mean of photosynthetically active radiation, measured above the canopy, was >320 μmol m^{-2} s^{-1}, the lowest values of the normalised WUE were excluded and the variation further reduced (8.0±2.7 mg g^{-1}). A plausible cause for the low values was that the relative importance of needle, twig and branch respiration increased at low assimilation rates. Therefore, it would probably be more appropriate only to establish the WUE relationship on the basis of branch chamber measurements for those periods during which respiration only constitutes a small part of the CO_2 exchange of the branch.

In May and June 1995, the mean normalised long-term WUE of the spruce branch was ca. 7 mg g^{-1} (Fig. 9c). At the end of June, the branch chamber was moved to a pine branch, and normalised WUE proved to be fairly unstable. In the summer of 1996, two chambers operated in a spruce and a pine tree. In contrast to 1995, values were higher. In June, the normalised WUE was on average 10 mg g^{-1}, and decreased through July to August to ca. 8 mg g^{-1}, thus approaching the mean value for 1995.

In conclusion, this paper has shown that WUE can serve as a means of modelling net assimilation. The measurements made in this study, however, indicate that the response of WUE to δe needs to be better understood, and this holds also for the seasonal differences in absolute values.

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