

Photosynthesis of a temperate fallow C₃ herbaceous ecosystem: measurements and model simulations at the leaf and canopy levels

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Abstract

The objectives of the study were to characterize photosynthesis of temperate fallow C₃ herbaceous species and examine the performance of a simple photosynthesis model (based on the Farquhar's equations) to simulate carbon fluxes at the leaf and canopy levels. The maximum rate of carboxylation at 25 °C (V_{m0}) was estimated for sunlit leaves using *in situ* gas exchange data under saturating irradiance. Throughout the seasons, leaf measurements indicate that values of V_{m0} were similar for the four major species of the fallow. The rate declined from March (100 $\mu\text{mol m}^{-2} \text{s}^{-1}$) to July (50 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and remained almost constant until November. The maximum quantum yield estimated for *Potentilla reptans* L. (dominant species) was 0.082 mol(CO₂) mol⁻¹(photon absorbed), similar to values already published for C₃ species. Leaf area index (LAI) increased from winter (less than 0.2 m² m⁻²) to spring (up to 4 m² m⁻²). Rates of canopy photosynthesis (measured with a canopy chamber) strongly depended on LAI and temperature, in addition to irradiance. They reached a maximum of 25 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and were intermediate between those published for C₄ grassland or cultivated species, and on woody species. At leaf level, simulations gave realistic predictions. At canopy level, the model had the ability to reproduce the effects of environmental and seasonal conditions. However, simulations underestimated the photosynthetic activity of the fallow canopy.

Introduction

Ecological processes and biogeochemical cycles are currently disturbed by various human activities. Consequently, it has become necessary to improve the scientific knowledge concerning a wide range of ecosystem responses (including carbon balance) to climatic change. One of the main issues for carbon cycling is to assess whether an ecosystem will act like a source or a sink. Vegetation is a central player in the carbon cycle and photosynthetic activity of the ground cover makes up a key process for carbon flux in the soil-plant-atmosphere continuum. Models of vegetation processes are powerful schemes for simulating photosynthesis and forecasting the impact of environment alterations (Collatz *et al.* 1991; Terashima and Hikosaka 1995; Sellers *et al.* 1996a; Wohlfahrt *et al.* 2001).

The coupled photosynthesis – stomatal conductance

model of the land surface process model called *SiB2* (*Simple Biosphere Model*) is able to function at spatial scales ranging from individual leaves to the stand level (Sellers *et al.* 1996a). Photosynthesis and net assimilation are computed using equations based on the models of Farquhar *et al.* (1980) and Collatz *et al.* (1991). This simple model treats carbon fluxes from a single-layer canopy without discriminating sunlit and shaded leaves (big-leaf model), and it assumes a constant quantum yield and a fixed relationship between the maximal capacity of carboxylation (V_m) and leaf dark respiration. Detailed testing of *SiB2* in contrasting vegetation types is useful before it can be applied with confidence on a global scale (Sellers *et al.* 1996a,b; Hanan *et al.* 2005). Until now, as far as we have known, the model of Collatz *et al.* (1991) and Sellers *et al.* (1996a,b) was not used with C₃

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Abbreviations: A – net photosynthesis; A_N – net assimilation; C_a – ambient CO₂ partial pressure; C_i intercellular CO₂ partial pressure; ϵ – quantum efficiency for CO₂ uptake; h_s – relative humidity; K_c and K_o – Michaelis constants for CO₂ and O₂ of Rubisco; LAI – leaf area index; PAR – photosynthetic active radiation; R_D – dark respiration; *SiB2* – Simple Biosphere Model; Γ – CO₂ compensation point; τ – relative specificity of Rubisco to CO₂ relative to O₂; V_m – maximal capacity of carboxylation; V_{m0} – maximal capacity of carboxylation at 25 °C; W_c – rubisco-limited rate of photosynthesis; W_e – light-limited rate; W_s – sink-limited rate.

herbaceous wild species found in abandoned fields. Moreover, we used the fallow land as a model vegetation for two reasons. First, land use in Western Europe changed dramatically during the last part of the 20th century as a result of the Common Agricultural Policy, and within agro-ecosystems, fallow vegetation growing mainly in abandoned crop fields became widespread now. During the past ten years, the amount of abandoned field exceeded regularly 15 % of total crop fields. In France in 2001, abandoned fields made up 7.3 % of arable land (over 1.5 Mha). A lot of ecological studies emphasized the contribution of grasslands or abandoned fields to enhance biodiversity in the landscape although they can promote weed spreading and other agronomical problems (Broll 1995; Marshall and Moonen 2002). However,

despite the wide areas covered by fallows, their functioning (seasonal primary production, biomass dynamics, soil-plant-atmosphere fluxes at the plot and field scales) has hardly been studied and is not well-documented. In addition, the vegetation of the fallows (C_3 grasses and forbs) is active over a long period of the year covering spring, summer and autumn so that it can play a particular role in the carbon cycle among agro-ecosystems.

The purpose of the experiments was thus to quantify the photosynthetic activity of the dominant natural species of a C_3 herbaceous fallow at the leaf and canopy levels and to test the ability of a “classical” photosynthesis model to simulate carbon fluxes over the seasons of this wild particular vegetation.

Materials and methods

Study area: The study was performed in a fallow field located near Toulouse, south-western France. Both at the leaf and canopy scales, the study was conducted on the MUREX fallow site (43°24'N, 1°10'E; 240 m a.s.l.) which has been extensively described by Calvet *et al.* (1999). The field, involving an experimental area 700 m long and 250 m wide, has been left fallow for 5 years. It is a rather flat plot, on the middle terrace of the Garonne valley, gently sloping down to the edge of a plateau dominating the valley of the Touch river, 30 m below. Mean annual rainfall and temperature were 680 mm and 13 °C, respectively. Rainfall was distributed fairly equally throughout the year but with occasional summer droughts. The vegetation canopy of the site consisted primarily of a dense C_3 herbaceous canopy whose height ranged from 1 m when vegetation was fully developed to 0.1 m in winter. The vegetation of the fallow site consisted of grasses and forbs which occupied about 42 and 58 % of the site, respectively. The main plant species were *Potentilla reptans* and *Elytrigia repens* (L.) Desv. ex Nevski, and to a lesser extent *Erigeron Canadensis* L. and *Rumex acetosa* L. Their growing cycles overlapped, contributing to maintaining a rather dense, evergreen canopy. This kind of herbaceous canopy represents the first stage of a plant succession leading to a *Quercus pubescens* Willd. forest climax. The soil was a typical deep ‘luvisol’: the mean texture of the 1 m surface soil layer was a silt-loam (the sand and clay fractions were 14 and 28 %, respectively). A compact layer around 50–70 cm depth generated dry soil conditions in summer and hydromorphic conditions in winter.

Measurements

This study used data obtained in the field on herbaceous vegetation at the leaf or canopy scale. Measurements at the leaf level were performed from summer 1998 to autumn 2003: over the course of the 1998 and 1999 vegetation periods for V_{m0} determination (Fig. 1), in June

and July 2000 for measurements under controlled conditions (Fig. 2), and in March, May, June, July and September 1999 and 2003 for measurements under field environmental conditions (Figs. 3, 4). Measurements at the canopy level were performed on 12 selected days covering an annual cycle from summer 1997 to spring 1998 (Figs. 5, 6 and 7).

Leaf: Gas measurements were performed *in situ* using a fully climate-controlled portable infra-red gas analyser system for CO_2 (CIRAS-1, PP-Systems, Hitchin, Herts, UK). The system was operated in open flow mode with a 2.5 cm² leaf cuvette and an integrated gas CO_2 supply system. Measurements were made in the field on young, fully-expanded and attached leaves (top leaves). All gas exchange rates are reported on an area basis. CO_2 partial pressure was 36 Pa except for 1) quantum yield estimation where CO_2 partial pressure was 90 Pa and 2) for A_N/C_i curves. For controlled conditions, experiments were carried out in the morning, photosynthetic active radiation (PAR) was imposed, the relative humidity was around 50 % and the leaf temperature was around 24 °C. Other measurements were performed over the diurnal period and the environmental conditions were those of the field.

Leaf temperature was measured by the thermistor of the CIRAS apparatus. Leaf absorptance to PAR was measured with an integrating sphere and was, on average, 70 % for *Elytrigia repens* and *Potentilla reptans* (Demarez *et al.* 2000). This value was used for all species. Intercellular concentration of CO_2 (C_i) used for CO_2 response curves and for V_m estimation was calculated using the internal program of the CIRAS-1 gas exchange system which uses the equation derived from von Caemmerer and Farquhar (1981).

Canopy: The assimilation rate was measured *in situ* with a canopy chamber, repeatedly at about 1–2 h interval from early morning to sunset on selected days.

Measurements were taken on clear or partially cloudy days. Just before performing measurements, the chamber (diameter: 0.5 m; height: 0.5 m, steel frame wrapped with lay-flat tubing) of the *CIRAS-1*, *PP-Systems* was pushed firmly down onto the soil giving a seal. Then, the gas exchange measurements enable estimation of ecosystem (undisturbed canopy + soil) net assimilation (A_N). Ecosystem respiration (R_D) was measured with the screened chamber through the CO₂ flux obtained with the chamber darkened using an opaque cover (negative value). Canopy net photosynthesis (A) was estimated through the difference between ecosystem net assimilation and respiration [$A = (A_N) - (R_D)$]. It has been shown that the first term (A_N) was consistent with the atmospheric flux measured by the eddy-correlation method (Calvet *et al.* 1999). The duration of the measurement never exceeded 2 min. Immediately after, the chamber was removed from the soil until the next measurement. At the end of the day, vegetation enclosed in the canopy chamber was harvested for determination of the green leaf area index (LAI) by planimetric measurements.

Model description and parameterisation

Leaf: The combined model used for the estimation of leaf CO₂ assimilation was initially presented in detail by Collatz *et al.* (1991) and Sellers *et al.* (1996a). It consists of coupled leaf photosynthesis – stomatal conductance model. The photosynthesis model is a modified version of that of Farquhar *et al.* (1980) and the stomatal conductance model was derived from Ball *et al.* (1987). The assimilation is a smoothed transition between the minimum of 3 functions: the assimilation rates limited by the efficiency of the photosynthetic enzyme system (W_c), the amount of PAR absorbed by the leaf (W_e) and the capacity of the leaf to export or utilize the product of photosynthesis (W_s).

Results and discussion

Leaf

Measurements: Both ε and V_{m0} are important species-specific parameters of the photosynthetic capacity of the plants. Quantum yield was derived from *in situ* measurements on *Potentilla reptans* in controlled environmental conditions at C_a of 90 Pa. The initial slope of the light response curve (mean of 17 curves) of A_N gave a quantum yield of 0.077 mol(CO₂) mol⁻¹(photon absorbed) (not shown). Under low light and 90 Pa CO₂, C_i was calculated to be around 72 Pa. This partial pressure of CO₂ is not sufficiently high to suppress photorespiration. Under this intercellular CO₂ partial pressure, taken the specificity factor of Rubisco, τ as $V_c O/V_o$, $C_i = 2\,600$ (Collatz *et al.* 1991), and O as 21\,000 Pa, the ratio V_o/V_c was estimated as 0.12. Considering that in the photorespiratory carbon oxidation cycle, 0.5 mol of CO₂ is released, the intrinsic quantum efficiency for CO₂ uptake,

Canopy assimilation was calculated by coupling the leaf stomatal-photosynthesis model with the radiative transfer model of Goudriaan (1977). The coupling procedure is detailed in Sellers *et al.* (1992). The scaling of leaf photosynthesis to the canopy is based on one major assumption: leaf physiological properties vary throughout the plant canopy in response to the radiation-weighted time-mean profile of PAR.

Parameterisation of the photosynthesis sub-model

Estimation of the intrinsic quantum efficiency for CO₂ uptake (ε) was performed from gas exchange rates derived from steady-state measurements of photosynthetic PAR response curves (0–70 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for CO₂ partial pressure of 90 Pa and other controlled environmental conditions.

Estimation of V_{m0} : At ambient external CO₂ concentration and high irradiance, it was assumed that the leaves are substrate-limited allowing estimation of V_m by a one-point method using only the measurements of net assimilation rate (A_N), C_i and a value of R_D (Ni and Pallardy, 1992; Wilson *et al.* 2000a,b; Kosugi *et al.* 2003). Because full A_N/C_i curves seriously constrained the replication needed for statistical inference, and due to the difficulty of controlling leaf conditions in the field while measuring one A_N/C_i curve, V_m was estimated by the one-point method under a PAR of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and ambient CO₂ (and other field environmental conditions). We verified there was a tight relation ($r^2 = 0.90$, $n = 16$) between the value of V_m estimated from the one-point method and the value estimated from full A_N vs. C_i curves although some bias were observed as indicated by the slope of the linear regression ($y = 1.16x + 0.78$).

ε , was estimated to be 0.082 mol(CO₂) mol⁻¹(photon absorbed). This is in the range of values for herbaceous C₃ species. Leaf quantum yield generally does not vary with seasonal changes or canopy positions (Luo *et al.* 2000).

The mean seasonal pattern from spring to autumn of V_{m0} was derived from 180 measurements made in 1998 and 1999 on the four main species of the fallows: *P. reptans*, *E. repens*, *E. canadensis* and *R. acetosa* (Fig. 1). The study of the seasonal changes in V_{m0} indicated that V_{m0} values did not markedly vary among species (grasses or forbs) since standard deviations were reasonably low. Wohlfahrt *et al.* (1999) also observed that grasses and forbs did not differ significantly from each other with respect to V_{m0} in wild species from mountain grassland ecosystems, and Wullschlegel (1993) found no significant differences in V_{m0} between monocot

and dicot agricultural crops. V_{m0} declined gradually from ca $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ in March to ca $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ in July and then remained almost constant until November. The reasons for this seasonal change have been discussed elsewhere (changes in leaf nitrogen per unit area, in fractional allocation of leaf nitrogen to Rubisco and in mesophyll resistance, and Rubisco inactivation (Wilson *et al.* 2000a,b). Medlyn *et al.* (2002) illustrated the fact that values of V_m derived from gas exchange data depend strongly on the assumed values of K_c and K_o and hence they are not readily comparable between studies. Nevertheless, our values of V_{m0} are in the range of values for C_3 herbaceous species (Wullschlegel 1993). From these data, a relation giving V_{m0} at any time of the vegetation season was deduced using nonlinear least squares curve fitting: $V_{m0} = 1392 x^{-0.6}$, $r^2 = 0.94$, where x means a day of year (Fig. 1). This relation was used thereafter for calculating seasonal V_{m0} values used in the simulations. Because grasses and forbs did not differ significantly from each other with respect to V_{m0} , this allows to use the same relation for the seasonality of V_{m0} for dominant types of natural C_3 herbaceous species (fallow), at least in the context of reduction of the model's complexity to a level appropriate for large-scale application. It is noteworthy that due to the temporal modulation of this parameter, the time-invariant value of V_{m0} provided by Sellers *et al.* (1996b) for agriculture/ C_3 grassland ($100 \mu\text{mol m}^{-2} \text{s}^{-1}$) was similar to our field estimates only in early spring. Over the entire growing season (from day 75 to day 320), the mean value for V_{m0} was around $62 \mu\text{mol m}^{-2} \text{s}^{-1}$. In a survey of general functional properties of several vegetation classes, Baldocchi and Meyers (1998) estimated V_{m0} to be equal $58 \mu\text{mol m}^{-2} \text{s}^{-1}$ for temperate grassland.

When values A_N obtained from *in situ* observations (natural light, temperature and h_s) on major species of the fallow field (*P. reptans*, *E. repens*, *E. canadensis* and *R. acetosa*) are plotted against irradiance, there is a

marked dispersion of the data (Fig. 2). The strong variability of A_N is illustrated by the fact that under saturating irradiance, A_N ranged from $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $17 \mu\text{mol m}^{-2} \text{s}^{-1}$. Which environmental parameter can account for the very large variability in experimental A_N observed at high irradiance? As already claimed in Materials and methods, there was no severe drought stress on any observation day. Thus, we rejected the hypothesis that the biochemical properties of the leaves were strongly affected by drought when low values of A_N were observed under saturating irradiance. The main environmental factor affecting *in vivo* CO_2 assimilation under saturating irradiance (*i.e.* for Rubisco-limited photosynthesis) is often assumed to be temperature (Bernacchi *et al.* 2001). Indeed, when A_N (205 measurements excluding the data with a PAR lower than $800 \mu\text{mol m}^{-2} \text{s}^{-1}$) are plotted against temperature, it is shown that A_N decreased strongly above a maximum around $18\text{--}22^\circ\text{C}$ (Fig. 3).

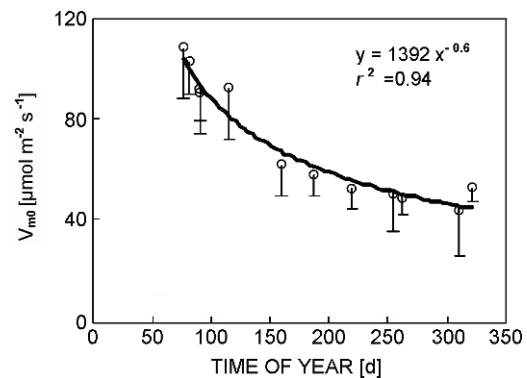


Fig. 1. Mean and standard deviations of the seasonal maximum rate of carboxylation at 25°C (V_{m0}) driven from measurements made on *P. reptans*, *E. repens*, *E. canadensis* and *R. acetosa*. Values were derived from leaf gas exchange analysis under saturating light and atmospheric CO_2 (one point method). $n = 180$.

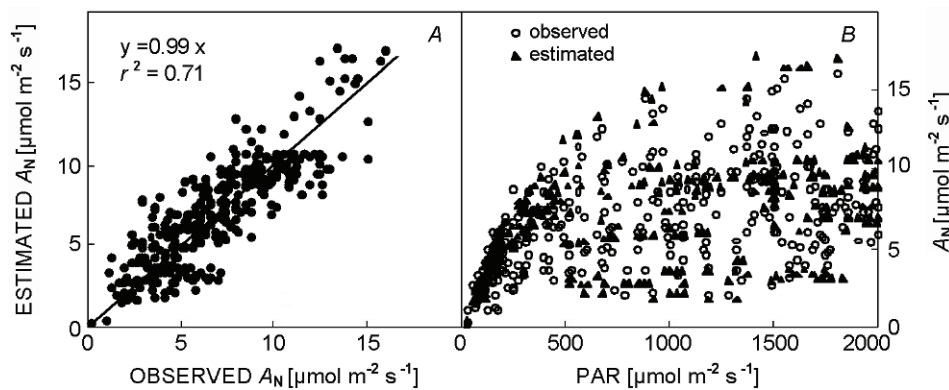


Fig. 2. Comparison between estimation of net leaf CO_2 assimilation (A_N) by the model and experimental A_N . A: Relationship between estimated and observed A_N , solid line represent linear regression forced through the origin. B: Response of estimated and observed A_N to PAR. Measurements ($n = 366$) were performed in fallow fields under environmental conditions on sunlit leaves of the dominant species (see the legend of Fig. 1).

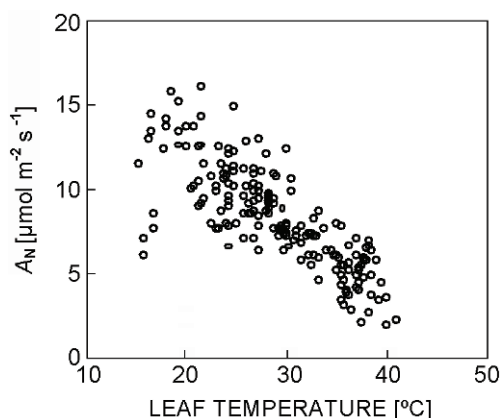


Fig. 3. Response of CO₂ net leaf assimilation (A_N) to leaf temperature. A_N was observed on leaves of the dominant species of fallow fields. Only data of Fig. 2 for which PAR > 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ were used. ($n = 205$)

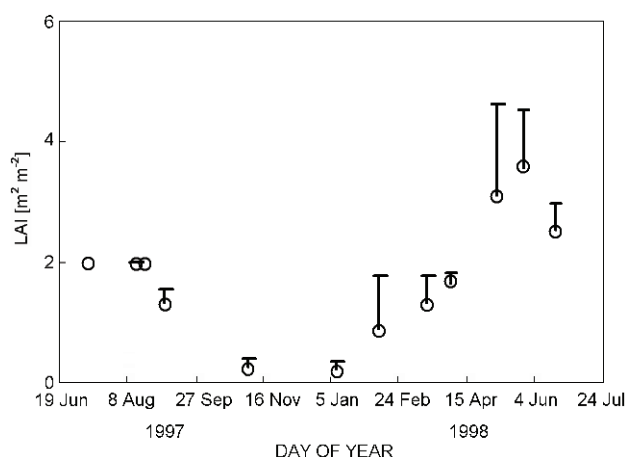


Fig. 4. Changes in the green leaf area index (LAI) of the fallow canopy during the simulation period (1997–1998).

Simulations: The behaviour of the models was compared with the data sets obtained from *in situ* observations on major species of the fallow field (Fig. 2). Good agreement was obtained between measurements and simulations ($y = 0.99x$, $r^2 = 0.71$). Therefore, it is demonstrated that the *SiB2* model of photosynthesis – stomatal conductance (without soil moisture stress factor) is suitable for estimating instantaneous leaf CO₂ assimilation (younger expanded leaves) for various herbaceous plants and seasons. In other respects, the good agreement between observed and simulated data suggests that the seasonal evolution of V_{m0} is correctly described here. Thus, it has been shown that i) a single time-related pattern of V_{m0} appears to be sufficient to get accurate flux estimates for various species of the fallow (grasses and forbs) and, ii) as already demonstrated with other species, parameterization using *in situ* gas exchange data (single point method) and not complete A_N/C_i curve for V_{m0} determination is a useful method (Wilson *et al.* 2000a).

Canopy

Measurements: Fig. 4 shows the measured values of LAI over an annual cycle from July 1997 to June 1998. The maximum LAI was lower in 1997 (about 2 $\text{m}^2 \text{m}^{-2}$) than in 1998 (about 3.6 $\text{m}^2 \text{m}^{-2}$) which is consistent with the differences in rainfall regime: 1997 was characterised by a spring and autumn drought (Calvet *et al.* 1999) and 1998 was a wet year with evenly distributed precipitation (data not shown).

We made 376 observations of the diurnal and seasonal changes in CO₂ fluxes of the fallow canopy. Measurements of the ecosystem CO₂ fluxes were conducted by the canopy chamber method under natural light or in darkness (ecosystem respiration) allowing calculation of canopy photosynthesis (A) and net assimilation (A_N) as for leaf level. Ecosystem respiration increased exponentially with air and soil temperature (Fig. 5). Time series of canopy photosynthesis for 12 days through one annual cycle (covering 1997–1998) are shown in Fig. 6. During late autumn or winter, assimilation remained very low. This was associated with low temperature and LAI. For sunny spring days, assimilation advanced and declined symmetrically around noon when it reached the highest values. These values were associated with temperatures of around 25 °C and high values of V_{m0} , light and LAI (following spring growth). Later in spring or in summer, assimilation reached intermediate values and the shape of the diurnal curves was less “ideal” showing some midday and afternoon saturation or depression. This was likely due to some deterioration of plant water relations during midday as often evoked (Collatz *et al.* 1991; Tuzet *et al.* 2003). The values of photosynthesis for well developed herbaceous fallow field canopies were intermediate between those observed on C₄ grassland or cultivated species, and on woody species (Kim and Verma 1991; Olioso *et al.* 1996; Dugas *et al.* 1997; Leuning *et al.* 1998; Thorgeirsson and Soegaard 1999; Kelly *et al.* 2002; Saigusa *et al.* 2002).

Simulations: Considering the data on A all together (Fig. 7), the model provided a reasonable fit to the experimental responses of herbaceous canopy over a wide range of seasons, plant species, quantum flux density, temperature, relative humidity, *etc.* but there is a tendency for simulations to underestimate observations ($y = 0.76x$, $r^2 = 0.60$).

We made the hypothesis that the chamber method can be used because it has been previously demonstrated that atmospheric net CO₂-flux obtained by chamber measurements or eddy-correlation measurements are in a good agreement (Calvet *et al.* 1999). Therefore, how can we explain the discrepancy between simulations and measurements? First, the simplifying assumptions on which the model is based (*see* Introduction section), particularly those associated with scaling-up the leaf level

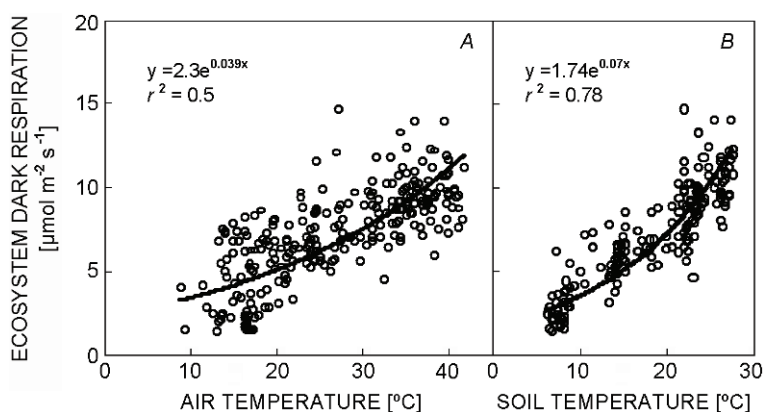


Fig. 5. Response of ecosystem dark respiration (R_D) to air (A) or soil (B) temperature in fallow fields. Measurements were conducted over an annual cycle from summer 1997 to summer 1998 by the canopy chamber method.

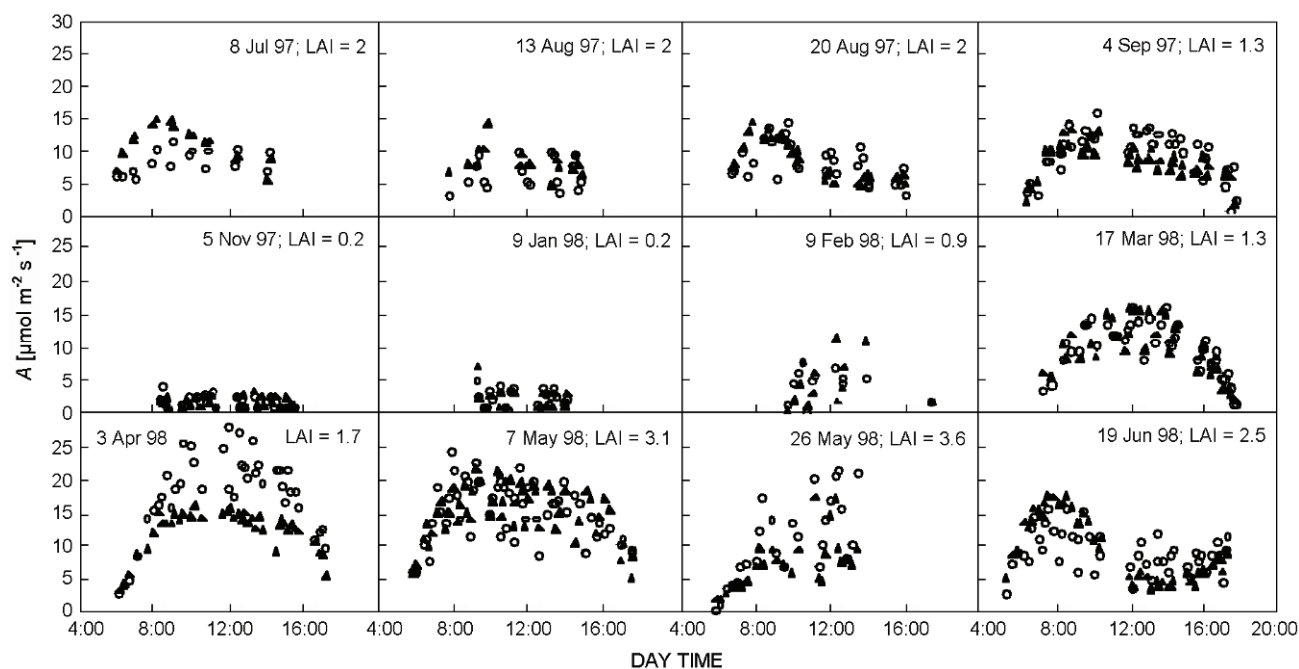


Fig. 6. Modelled (○) and measured (▲) rate of diurnal photosynthesis (A) of herbaceous fallow field canopies. Measurements were performed on selected days covering the seasonal cycle of 1997–1998.

to the canopy one, reduce the model complexity to a level appropriate for a large-scale application. These assumptions are only approximately true in real plant canopy and they may of course largely contribute to discrepancies between measurements and simulations (especially the absence of separation into sunlit and shaded leaves). However, the underestimation of the rates of canopy photosynthesis was unexpected because we did not apply the standard SiB2 soil moisture stress factor which can decrease V_m values and thus A , and because big-leaf models tend rather to overestimate instantaneous canopy photosynthesis (De Pury and Farquhar 1997). Second, uncertainties in estimates of air temperature and relative humidity for the enclosed canopy may also contribute to discrepancies between measurements and

model simulations. For example, it is possible that our measurements of the air temperature in the canopy chamber were not relevant due to air chamber heating with solar radiation during the duration of CO_2 flux measurements. Indeed, measurements of air temperature may give values up to 5 °C higher inside the chamber than outside (for air in the chamber at 25 °C). The temperature of the air inside the chamber would be higher than the canopy temperature because flux measurements were too rapid (120 s) to allow complete equilibrium between canopy biomass and air inside the chamber. This underlines the difficulties associated with the prediction of canopy CO_2 fluxes due to uncertainties in local environmental conditions within the canopy (Wohlfahrt *et al.* 2000). If temperatures above 20 – 25 °C were

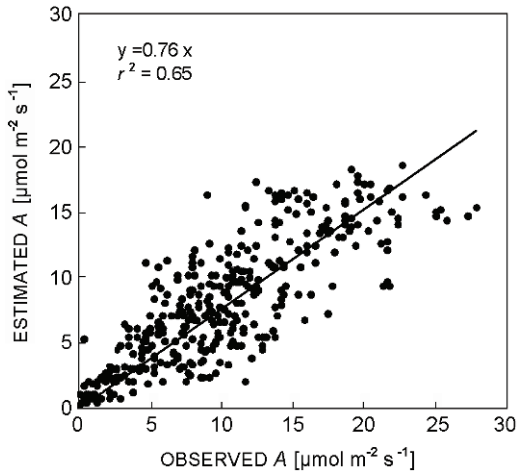


Fig. 7. Relationship between estimated and observed photosynthesis (A) of herbaceous canopies. Fallow field measurements (canopy chamber method) were carried out spanning seasonal cycles from summer 1997 to summer 1998. Solid line represent linear regression forced through the origin. ($n = 376$).

overestimated, model predictions would have been an underestimation of canopy photosynthesis (Fig. 4).

To extend from the leaf to the canopy in a species mixture inevitably requires many assumptions. Despite the already mentioned biases in the simulations at the canopy level, the results in Fig. 6 show that the daily and seasonal trends in herbaceous assimilation could be reproduced by the model.

Appendix

Model description and parameterisation

Leaf

Photosynthesis sub-model: The rate of photosynthesis is calculated from three potential rates: W_c , the Rubisco-limited rate of photosynthesis, W_e , the light-limited rate, and W_s , the sink-limited rate.

$$W_c \text{ is calculated as: } W_c = V_m \frac{C_i - \Gamma}{C_i + K_c(1 + P_{a(0)} / K_o)} \quad (1)$$

where V_m is the capacity of Rubisco for CO₂ fixation per unit leaf area [$\mu\text{mol m}^{-2} \text{s}^{-1}$], K_c and K_o are the Michaelis constants for CO₂ and the competitive inhibition constant for O₂ with respect to CO₂ in the Rubisco reaction, respectively. $P_{a(0)}$ (assumed constant) and C_i are O₂ and CO₂ partial pressures in the intercellular space, respectively. Parameter C_i is given by

$$C_i = C_s - 1.6 P A_N r_{s(\text{H}_2\text{O})} \quad (2)$$

where P is the mean atmospheric pressure, $r_{s(\text{H}_2\text{O})}$ is the stomatal resistance for water and C_s is the leaf surface CO₂ partial pressure (Collatz *et al.* 1991). The parameter Γ is the CO₂ compensation point due to photorespiration and is calculated as: $\Gamma = P_{a(0)}/2\tau$, where τ is the relative specificity of Rubisco to CO₂ relative to O₂.

W_e describes the response of photosynthesis to photosynthetically active radiation (PAR) as:

$$W_e = \varepsilon(1 - \omega) PAR \frac{C_i - \Gamma}{C_i + 2\Gamma} \quad (3)$$

where $(1 - \omega)$ is leaf absorbance of radiation and ε is the intrinsic quantum efficiency for CO₂ uptake.

W_s is the capacity for the export or utilisation of the product of photosynthesis, it was taken as:

$$W_s = V_m/2 \quad (4)$$

Changes with temperature (T) of the kinetic parameters were described by the Q_{10} function:

$$\begin{aligned} K_c &= K_{c298} Q_{10}^{(T-298)/10} \\ K_o &= K_{o298} Q_{10}^{(T-298)/10} \\ \tau &= 2600 Q_{10}^{(T-298)/10} \end{aligned} \quad (5)$$

where K_{298} is the parameter value at 25 °C and Q_{10} is the relative change in the parameter for a 10 °C change in temperature. In addition for V_m , a gradual temperature inhibition was introduced using the function:

$$V_m = \frac{V_{m0} Q_{10}^{(T-298)/10}}{1 + \exp[0.3(T - 308)]} \quad (6)$$

Respiratory CO₂ production (R_D) was scaled to the V_m as $R_D = 0.015 V_m$ (Collatz *et al.* 1991) and A_N (net assimilation) is then defined as $A_N = A - R_D$ where A is the leaf photosynthetic rate. We measured CO₂ efflux in the dark at 25 °C and verified the accuracy of the above expression of R_D .

To allow a more realistic and gradual transition from one limitation to another when co-limitation occurs between

W_c , W_e and W_s , the actual rate of photosynthesis is calculated by solving two quadratic equations for their smaller roots. The first quadratic equation is solved for an intermediate variable, W_p , which is an estimate of photosynthetic rate under the co-limitation of electron transport and Rubisco capacity:

$$\Theta W_p^2 - W_p (W_c + W_e) + W_e W_c = 0 \Rightarrow W_p = \text{Min}(W_c, W_e) \quad (7)$$

where Θ is an empirical constant describing the transition between the two limitations. Estimates of Θ from experimental responses have generally yielded values in the range of 0.8 – 0.99 while under unusual conditions lower values for Θ may be observed (Collatz *et al.* 1991). Here, we used the classical value of 0.8. Next, W_p and W_s are introduced into a second quadratic equation, the smaller root of which is an estimate of the actual rate of net photosynthesis:

$$\beta A^2 - A (W_p + W_s) + W_p W_s = 0 \quad (8)$$

where β is an empirical constant describing the transition between W_p and W_s .

Stomatal conductance sub-model: Stomatal conductance (g_s) was modelled according to Ball *et al.* (1987) :

$$g_{s(H_2O)} = m \frac{A_N}{P_{s(CO_2)}} h_s P + b \quad (9)$$

where m (9) and b ($0.01 \text{ mol m}^{-2} \text{ s}^{-1}$) are empirical constants and h_s is the relative humidity at the leaf surface. Although slight fluctuations in parameter m may have a significant physiological meaning related to intrinsic water use efficiency, there is an evidence that the value of m occupies a relatively narrow range (around 9) for all C_3 species (Baldocchi and Meyers, 1998; Kosugi *et al.* 2003).

Values of parameters: τ , K_c , K_o , Q_{10} (τ , K_c , K_o and V_m), m and b defined by the biochemistry of photosynthesis at an intercellular O_2 partial pressure of 20.9 kPa, were derived from Collatz *et al.* (1991). The values of parameters ε and V_{m0} were estimated from the gas exchange data described in the following section.

The system of equations (7) and (8) is solved by an iterative approach based on the calculation of C_i . C_i is first initialized by an *a priori* value of 34 Pa. The resulting A_N and g_s calculated using this value are used to calculate a new value of C_i . This iterative processes ends when the values of C_i , A_N and g_s satisfy equation 2 for a specific minimum error.

Canopy

Canopy PAR transmission: The PAR flux transmission is calculated following the Goudriaan (1977) expression:

$$PAR_t = PAR_o \exp(-k \text{ LAI})$$

where PAR_t is the PAR flux at leaf area index LAI in the canopy, PAR_o is the PAR flux above the canopy and k is the extinction coefficient for PAR within the canopy :

$$k = (G(\Theta)/\cos\Theta) (1-\omega)^{1/2}$$

where ω is the leaf albedo (0.3) and $G(\Theta)$ is the effective leaf area projection along a direction with a zenith angle Θ . It strongly depends on leaf angle distribution (LAD). Θ is the zenith angle of the incident illumination. Similarly to Sellers *et al.* (1992), we assumed a spherical LAD which implies $G(\Theta) = 0.5$.

Integration of the coupled leaf stomatal-photosynthesis model over canopy was done considering the profile of leaf nitrogen and hence V_{m0} within the plant canopy are distributed according to the radiation-weighted time-mean profile of PAR:

$$V_{m0} = V_{m0} \exp(-k \text{ LAI})$$

where V_{m0} is the value for top leaves (*i.e.* the value estimated from Fig. 1 since young fully expanded leaves are at the top of the canopy). Sellers *et al.* (1992) assume that the ratio $G(\Theta)/\cos\Theta$ is equal to 1 which implies that the mean solar zenith angle is equal to 60° . This assumption simplifies the expression of k to $(1-\omega)^{1/2}$.

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