

MODELLING NET PHOTOSYNTHETIC RATE OF TEMPERATE DRY GRASSLAND SPECIES AND WINTER WHEAT AT ELEVATED AIR CO₂ CONCENTRATION

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Abstract. A number of C₃ temperate dry grassland species and winter wheat plants were grown in open top chambers either at 365 µmol mol⁻¹ (AC) or at 700 µmol mol⁻¹ (EC) air CO₂ concentrations. Gas exchange measurements were made at several air CO₂ concentrations. When measured at higher CO₂ concentrations, net photosynthetic rate was higher in plants grown at EC than at AC. The widely accepted Farquhar net photosynthesis model was parameterized and tested using several observed data. After parameterization the test results corresponded satisfactorily with observed values under several environmental conditions.

Keywords: temperate grasses, winter wheat, photosynthesis, modelling

Introduction

Many authors use simulation models, in addition to experimental work, to describe plant development and plant production responses to several environmental factors such as higher temperature, drought stress and elevated air CO₂ concentrations (EC). Simulation models describing carbon balance of leaves, whole plants, and ecosystems use a biochemical model of the net photosynthetic rate (P_N). The most popular model is the biochemical model of Farquhar *et al.* (1980), Farquhar and Caemmerer (1982), and their modified versions [9, 4]. In general, the parameterization of a simulation model is not an easy task. Most plants respond to their environment in different ways. As a result, parameter values may differ depending on the plant species and possibly even the plant variety being used. Simulation models are important for describing the effects of EC on photosynthesis. They allow P_N to be predicted without having to carry out measurements.

Abbreviations: AC = ambient [CO₂]; [CO₂] = air CO₂ concentration; C_i = partial pressure of CO₂ in the intercellular space; EC = elevated [CO₂]; M = average deviation; OTC = open top chamber; P_N = net photosynthetic rate; r^2 = determination coefficient.

Materials and methods

Plants and CO₂ fumigation

The experiments were carried out in perspex open top chambers (OTC) (130 cm in diameter and 100 cm in height) at the Global Climate Change and Plant Research Station in Gödöllő, Hungary. The climate of the region is temperate-continental with hot, dry summers. The annual mean temperature is 11 °C and the annual precipitation is 500 mm. [CO₂] was kept at the present-day concentration, AC (365 µmol mol⁻¹) for the control and at 700 µmol mol⁻¹ for the EC treatment. The plants were occasionally irrigated as needed and weed control was carried out mechanically.

Winter wheat

Seeds of winter wheat (*Triticum aestivum* L.) were sown in OTC in two different years with two cultivars (cv. Emma in the first and cv. Martonvásári 15, MV-15) in the second experiment) [5, 11]. The seed spacing was 13.0×1.5 cm. The soil was a light moderately calcareous sandy soil. N,P and K fertilisers were applied at rates of 10, 5 and 5 g m⁻² (100, 50, and 50 kg ha⁻¹), respectively before sowing.

Grassland

The studied vegetation was a xeric temperate loess steppe situated on the edge of the Hungarian Great Plain [8]. The parent rock was sandy loess or loess with thick humus and a nutrient-rich A horizon. The original grassland was made up of more than 90 species. Monoliths (size: 50×50×30 cm in depth) were removed from the grassland and transplanted into the open top chambers with four monoliths to a chamber. The soil in the chambers was removed and replaced by soil from the profiles the monoliths had been collected from. Four weeks after transplantation the grass was cut. Following a two-month adaptation period, the monoliths in the EC chambers were gradually exposed, over a 4-week period, to 700 µmol mol⁻¹ [CO₂]. The species studied during the 3-year exposure to EC and AC were the monocot *Festuca rupicola* Heuff. and the dicot *Filipendula vulgaris* Mönch. *F. rupicola*, the dominant species of the grassland, has sclerenchymatous erect leaves with a waxy surface, while *F. vulgaris* has soft, large incised leaves. Both species are perennial and have C₃ photosynthesis.

Measurements

The C_i dependence of light-saturated P_N (P_N/C_i curves) was measured in the flag leaves of winter wheat at the beginning of flowering and on the grassland species *F. rupicola* and *F. vulgaris* two and 36 months after the beginning of exposition. Measurements were made using an LCA2-type IRGA system (ADC, Hoddesdon, UK), operated in differential mode and a Parkinson LC-N leaf chamber with an airflow of 5 cm³ s⁻¹. [CO₂] values of 30, 100, 200, 330, 540, 730 and 900 µmol mol⁻¹ were produced using a gas diluter (GD 600, ADC, Hoddesdon, UK). The photosynthetically active radiation (PAR) and the leaf surface temperature were kept constant at 1 000±100 µmol m⁻² s⁻¹ and 20.5±1.5 °C for winter wheat cv. Emma, 800±100 µmol m⁻² s⁻¹ and 20±1 °C for winter wheat cv. MV-15 and 1 200 µmol m⁻² s⁻¹ and 23±1.5 °C for grassland.

Farquhar model

The gas exchange measurements were used to set the parameters and validate the biochemical model described by Farquhar *et al.* (1980) and Farquhar and Caemmerer (1982), and the modified version elaborated by Sharkey (1985) and Harley and Sharkey (1991) (referred to as the Farquhar model in this work).

P_N can be expressed by the Farquhar model (for detailed description, see Appendix):

$$P_N = V_c - 0.5V_o - R_{\text{day}} = V_c \left(1 - \frac{0.5O_i}{\tau \cdot C_i}\right) - R_{\text{day}}, \quad (\text{Eq. 1})$$

where the rate of carboxylation, V_c , is assumed to be limited by one of three factors: the activation state and kinetic properties of Rubisco, the regeneration of RuBP in the Calvin cycle, or the rate of phosphate release during triose phosphate utilization (starch and sucrose production). The micrometeorological variables included temperature, irradiance and [CO₂], which were measured and calculated with the IRGA equipment. Determination coefficients (r^2) were calculated to compare and analyze the relationship between observed and simulated P_N , and average deviation (M) to calculate the difference between observed and simulated P_N .

Results

The parameterization of the Farquhar model was performed on winter wheat cv. Emma, using P_N measurements on flag leaves at seven different air CO₂ concentrations at the beginning of flowering for plants grown at AC or EC. After parameterization, the Farquhar model gave a good estimation of the P_N of winter wheat cv. Emma in both treatments (*Fig. 1 A*). The determination coefficients and average deviation between observed and simulated net photosynthetic rates were $r^2 = 0.9$, $M = 0.98$ for plants grown at AC and $r^2 = 0.98$, $M = 0.34$ for plants grown at EC. The simulation results were not affected by irradiation because of the light saturated conditions. In both treatments P_N was limited by the rate of phosphate release during triose phosphate utilization at higher [CO₂]. The CO₂ saturation concentration and the saturated P_N were smaller for AC plants than at EC.

To validate the model the data set from the other experiment was used. Using the same parameter values as in the first experiment the model simulated P_N accurately, as shown by the r^2 and M values in *Fig. 1 B*.

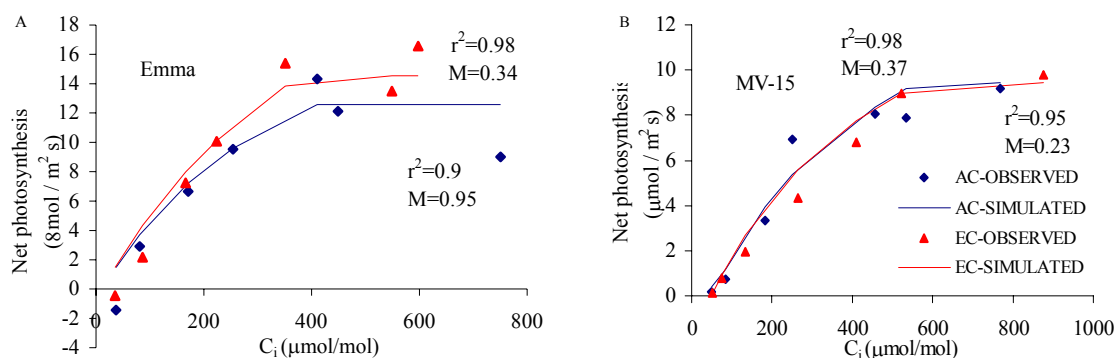


Figure 1. Measured and simulated net photosynthetic rate of flag leaves of winter wheat (*c. Emma A*, *MV-15 B*) grown from germination at ambient, AC (control), or enhanced, EC CO₂ concentration. r^2 denotes determination coefficient and M denotes average deviation between observed and simulated values.

The acclimation of P_N to EC varied both between species and over the course of the period of exposure. After two months of exposure upward acclimation was exhibited by all EC plants, the degree of which was greater in the dicot species. After 36 months of exposure the monocot species *F. rupicola* showed a downward acclimation in Rubisco capacity and its P_N/C_i curve did not reach saturation. The dicot species *F. vulgaris* showed upregulation for both Rubisco capacity and RuBP regeneration capacity.

Simulations were done for both grassland species studied. The parameter values used in the model were set the same after two and 36 months of CO₂ exposure but differed in the two species. The model simulated P_N accurately in all cases when the plants were grown at AC (for both species and after both exposure times). After two months of exposure the model did not adequately simulate P_N when the plants were grown at EC, but after 36 months the simulation results were accurate.

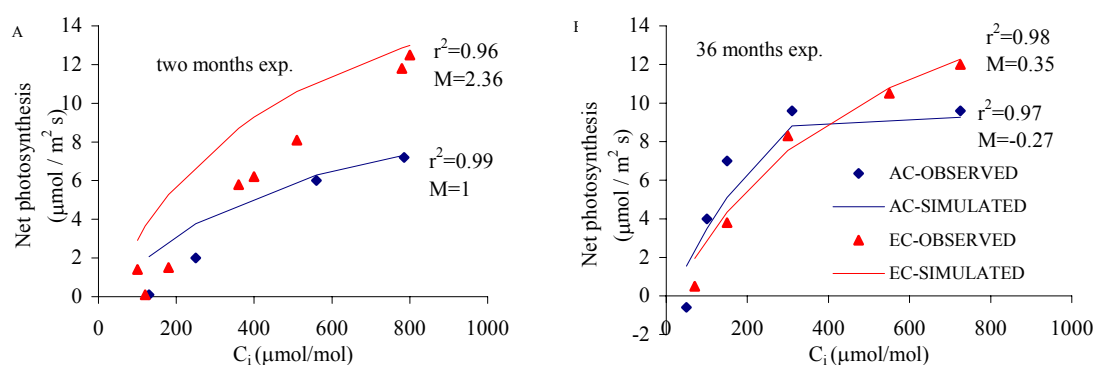


Figure 2. Measured and simulated net photosynthetic rate of leaves of *F. rupicola* grown at AC or at EC after two (A) or 36 (B) months of exposure. r^2 denotes determination coefficient and M denotes average deviation between observed and simulated values.

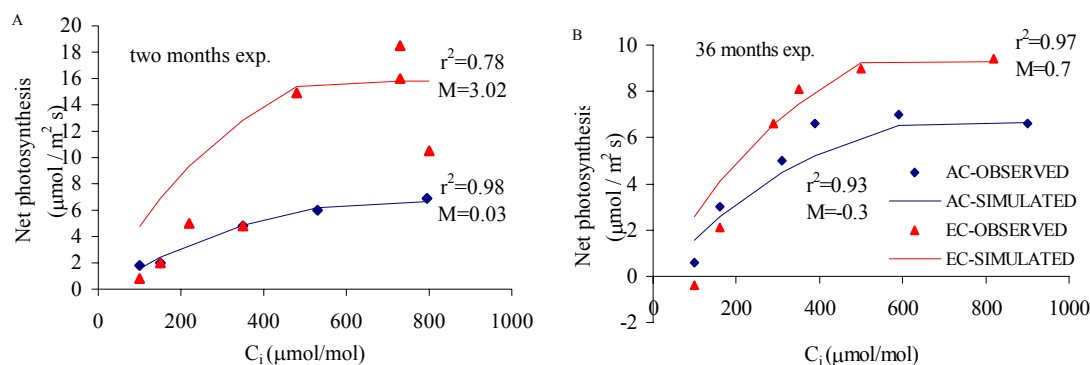


Figure 3. Measured and simulated net photosynthetic rate of leaves of *F. vulgaris* grown at AC or at EC after two (A) or 36 (B) months of exposure. r^2 denotes determination coefficient and M denotes average deviation between observed and simulated values.

Discussion

The aim of the experiment was to obtain information on how the model of Farquhar *et al.* (1980) and Farquhar and Caemmerer (1982) modified by Sharkey (1985) and Harley and Sharkey (1991), described the P_N of Hungarian winter wheat cultivars and grassland species. The results of P_N measurements revealed two important facts: first, there was a large increase in P_N as a result of EC, and second, gas exchange acclimation responses were influenced by the length of exposure to EC.

The study also supports the use of the model for describing the P_N of various C₃ plants under several types of environmental conditions. Separate parameterization and validation for individual plant species is essential, but the results show that the same parameterization can be used for two different Hungarian winter wheat cultivars grown in different years.

In conclusion, the Farquhar model is able to describe the P_N of different plant species under various environmental conditions (irradiance, temperature, CO₂), but parameterization has to be done very carefully in all cases, especially for long-term examinations. Hence, the Farquhar model should be included in various plant growth simulation models.

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Appendix

Symbols and units:

RuBP: ribulose-1,5-bisphosphate

RuBPCO: RuBP carboxylase/oxygenase

P_N [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: net photosynthetic rate of leaf

V_c [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: rate of carboxylation at RuBPCO

V_o [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: rate of oxygenation at RuBPCO

τ : specificity factor for RuBPCO [7]

C_i [Pa]: partial pressure of CO₂ in the intercellular space

O_i [kPa]: partial pressure of O₂ in the intercellular space ($O_i = 30$ kPa)

R_{day} [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: day respiration rate (excluding photorespiration) [1]

W_c [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: RuBPCO (amount, activation state and kinetic properties) limited carboxylation rate

W_j [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: RuBP regeneration-limited carboxylation rate

T [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: rate of phosphate release in triose phosphate utilisation (starch and sucrose production)

W_p [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: T -limited carboxylation rate [4; 9]

V_{cmax} [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: maximum rate of carboxylation

K_c [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: Michaelis constant of C_i for carboxylation

K_o [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: Michaelis constant of O_i for oxygenation

J [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: potential rate of electron transport [10]

I [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: quantum flux density absorbed by the leaf

α : efficiency of light energy conversion on an incident irradiance basis [$\text{mol}(\text{electron}) \text{mol}^{-1}(\text{photon})$]

$J_{\max}$ [$\mu\text{mol m}^{-2} \text{s}^{-1}$]: radiation saturated rate of electron transport

P_N can be expressed by Farquhar model:

$$P_N = V_c - 0.5V_o - R_{\text{day}} = V_c \left(1 - \frac{0.5O_i}{\tau \cdot C_i}\right) - R_{\text{day}},$$

where the rate of carboxylation, V_c , is assumed to be limited by one of three factors:

$$V_c = \min\{W_c, W_j, W_p\}$$

$$W_c = \frac{V_{\text{cmax}} \cdot C_i}{C_i + K_c(1 + O_i / K_o)},$$

where the carboxylation is limited by the amount, activation state and kinetic properties of RuBPCO.

$$W_j = \frac{J \cdot C_i}{4(C_i + O_i / \tau)}$$

In the W_j formula above, it is assumed that four electrons generate sufficient STP and NADPH for the regeneration of RuBP in the Calvin cycle [2]. The radiation dependency in the model is on electron transport [10]:

$$J = \frac{\alpha \cdot I}{\left(1 + \frac{\alpha^2 \cdot I^2}{J_{\max}^2}\right)^{1/2}},$$

and

$$W_p = 3T + 0.5V_o = 3T + \frac{V_c \cdot 0.5O_i}{C_i \cdot \tau \cdot C_i \cdot \tau}$$

Temperature dependence of K_c , K_o , R_d , τ , $J_{\max}$, V_{cmax} , and T are:

$$\text{parameter } (K_c, K_o, R_d, \tau) = e^{c - \frac{\Delta H_a}{R \cdot T_k}}$$

and

$$\text{parameter } (J_{\max}, V_{\text{cmax}}, T) = \frac{e^{c - \frac{\Delta H_a}{R \cdot T_k}}}{1 + e^{\frac{\Delta S \cdot T_k - \Delta H_d}{R \cdot T_k}}}$$

[6], where c is a scaling constant, ΔH_a is an activation energy, R is the gas constant ($R = 0.00831 \text{ kJ K}^{-1} \text{ mol}^{-1}$), T_k is leaf temperature [K]. τ is a declining function of temperature whose activation energy is negative. ΔH_d is the energy of deactivation, and ΔS is an entropy term.