PHOTOSYNTHETICA 40 (2): 293-300, 2002

Modelling net photosynthetic rate of winter wheat in elevated air CO_2 concentrations

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Abstract

Winter wheat plants were grown in open top chambers either at 365 μmol mol^{-1} (AC) or at 700 μmol mol^{-1} (EC) air CO_2 concentrations. The photosynthetic response of flag leaves at the beginning of flowering and on four vertical leaf levels at the beginning of grain filling were measured. Net photosynthetic rates (P_N) were higher at both developmental phases in plants grown at EC coupled with larger leaf area and photosynthetic pigment contents. The widely accepted Farquhar net photosynthesis model was parameterised and tested using several observed data. After parameterisation the test results corresponded satisfactorily with observed values under several environmental conditions.

Additional key words: acclimation; carotenoids; chlorophyll; intercellular CO_2 concentration; leaf area; net photosynthetic rate; ribulose-1,5-bisphosphate carboxylase/oxygenase capacity; temperature; *Triticum aestivum*.

Introduction

In the last 30 years there has been growing concern about anthropogenic CO_2 emissions into the earth's atmosphere (Keeling *et al.* 1976a,b, Haszpra 1995, Hofmann and Peterson 1996). As a result, increased number of experiments have been carried out to understand the effects of elevated air CO_2 concentration (EC) on important crops, *e.g.* wheat (Krenzer and Moss 1975, Tuba *et al.* 1994, Wheeler *et al.* 1996, Ghildiyal *et al.* 2001). Plants grown at higher [CO_2] than at present-day [CO_2] have an increased photosynthetic rate and a decreased transpiration rate that leads to better water use efficiency (Tuba *et al.* 1994, 1996). Plants grown at EC have greater biomass and higher yields (Harnos *et al.* 1998). EC also alleviates the effects of various stresses, *e.g.* drought stress (Sionit *et al.* 1980, Ferris *et al.* 1998, Pospíšilová and Čatský 1999) or high temperature (Ingram *et al.* 1995, Ferris *et al.* 1996). The net photosynthetic rate (P_N) of C_3 plants increases at EC under both radiation limited and radiation saturated circumstances (Jauhiainen and Silvola 1999). EC increases both P_N and growth of C_3 plants, however, the magnitudes of these increases are very difficult to predict.

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 EC. Simulation models describing carbon balance of leaves, whole plants, and ecosystems use a biochemical model of P_N. The most popular model is the biochemical model of Farquhar *et al.* (1980), Farquhar and Caemmerer (1982), and their modified versions (Sharkey 1985, Harley and Sharkey 1991) called FACASHA model in this study. In general, parameterisation of a simulation model is not an easy task. Most crops respond to their environment in different ways. As a result, parameter values may differ depending on the crop and possibly even the crop cultivar 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 the measurements.

Received 9 April 2002, *accepted* 17 June 2002.

Abbreviations: AC = ambient [CO_2]; C_i = partial pressure of CO_2 in the intercellular space; Chl = chlorophyll; [CO_2] = air CO_2 concentration; EC = elevated [CO_2]; FACASHA = model of net photosynthetic rate described by Farquhar *et al.* (1980) and Farquhar and Caemmerer (1982) and modified by Sharkey (1985) and Harley and Sharkey (1991); K_c = Michaelis constant of C_i for carboxylation; OTC = open top chamber; P_N = net photosynthetic rate; r^2 = determination coefficient; T = rate of phosphate release in triose phosphate utilisation; V_{cmax} = the maximum rate of carboxylation.

Acknowledgements: This work was supported by the MEGARICH Project, EU contract ENV4-CT97-0503, the Hungarian Scientific Research Fund (OTKA, Nos. F020704, T18595, T22723), and the Research Development of Higher Education (FKFP0472/97). Dr. T. Janda and Dr. Z. Nagy are gratefully acknowledged for their help and useful comments.

The purpose of this study was to analyse the effects of EC on P_N of Hungarian winter wheat cv. Emma grown in open top chambers (OTCs), and to parameterise and test the FACASHA model.

Materials and methods

Plants and CO_2 fumigation: The experiment was carried out 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. The soil is a light moderately calcareous sandy soil. NPK fertilisers were applied respectively at rates of 10, 5, and 5 g m^{-2} (100, 50, and 50 kg ha^{-1}) before sowing. Seeds of winter wheat (*Triticum aestivum* L. cv. Emma) were sown on 10 October 1996. Spacing of seeds was 13.0×1.5 cm. Wheat plants for the [CO_2] treatment were transferred into perspex open top chambers (130 cm in diameter and 100 cm in height) from the beginning of germination. [CO_2] was kept at present-day concentration, AC (365 μmol mol^{-1}) for the control and at 700 μmol mol^{-1} for the EC treatment. [CO_2] and ventilation in EC and AC chambers were maintained as described by Tuba *et al.* (1994). The plants were occasionally irrigated as needed and weed control was by mechanical means.

Measurements: C_i dependence of photon saturated P_N (P_N/C_i curves) were measured in the flag leaves at the beginning of flowering. 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 cm^3 s^{-1}. [CO_2] of 30, 100, 200, 330, 540, 730, and 900 μmol mol^{-1} were produced by a gas diluter (*GD 600*, *ADC*, Hoddesdon, UK). Photosynthetically active radiation (PAR) and leaf surface temperature were kept constant at 1 000±100 μmol m^{-2} s^{-1} and 20.5±1.5 °C, respectively. At the beginning of ear filling four different leaf levels of treated and control plant leaves were measured at 350 and 700 μmol(CO_2) mol^{-1} and at a temperature of 35 °C within the canopy under *in situ* irradiance.

Leaf area was measured at the beginning of flowering and at the beginning of ear filling by a leaf area meter (*LAM 001*, *Delta T Devices*, Cambridge, UK). The photosynthetic pigments—chlorophyll (Chl) (*a*+*b*) and total carotenoids (*x*+*c*)—of flag leaves were quantitatively determined at the beginning of flowering and at the beginning of grain filling, in 100 % acetone extract solution by spectrophotometer (*Shimadzu UV-6000*, *Shimadzu Co.*, Kyoto, Japan) using the re-determined extinction coefficients (Lichtenthaler 1987). Gas exchange measurements were made simultaneously on the same leaves at the same time.

Model parameterisation, validation, and testing: The gas exchange measurements made on flag leaves at the beginning of flowering were used to set the parameters of the biochemical model described by Farquhar *et al.* (1980), Farquhar and Caemmerer (1982), and the modified version by Sharkey (1985) and Harley and Sharkey (1991) (FACASHA model in this work). A short description of the model can be found in the Appendix. The study of Harley *et al.* (1992) was used as a base for the parameter values that are listed in Table 7. The micrometeorological variables included temperature, irradiance, and [CO_2]. They were measured and calculated with the IRGA equipment (Table 1).

After parameterisation the model was tested with measurements on four vertical leaf levels at the beginning of grain filling. Data from an earlier experiment described by Tuba *et al.* (1994) were used for model validation. C_i dependence of seven [CO_2] was measured at the beginning of flowering of winter wheat cv. Martonvásári 16, which had been grown from germination either at AC or EC. Temperature was set to 20 °C and irradiance to 800 μmol m^{-2} s^{-1}.

Determination coefficients (r^2) were calculated to analyse the comparison and relationship between observed and simulated P_N.

Results

Photosynthetic pigment contents, P_N, and leaf area: Chl *a/b* ratio, Chl *a*, and carotenoid *x*+*c* contents in the flag leaves of plants grown at EC were significantly higher than in the flag leaves of control plants (Table 2). There were no differences between the values measured at the beginning of flowering and values measured at the beginning of grain filling. The radiation use efficiency was continuously and uniformly greater at EC during the whole vegetative period. These results refer to the relationship between the changes in photochemical activity and P_N under long term EC treatment: the higher pigment content led to higher radiation use efficiency with significantly higher P_N and leaf area (Table 2).

At the beginning of grain filling, P_N and leaf area of plants grown in EC were larger at all leaf levels (Table 3). Furthermore, P_N decreased as leaf level neared the bottom level. A first quick estimate of these data suggests that P_N of the whole plant was significantly higher in plants grown from germination at EC than in AC plants.

Table 1. Environmental conditions during measurement of net photosynthetic rate in flag leaves of winter wheat cv. Emma at the beginning of flowering. These values were used for model parameterisation.

	Grown at AC							EC						
C_i [μmol mol^{-1}]	37	81	171	255	410	450	750	35	86	166	224	351	549	598
Leaf temperature [°C]	22	19	19	21	21	19	20	20	19	20	20	22	21	22
PAR [μmol m^{-2} s^{-1}]	1012	1076	916	999	1048	1104	981	986	1040	928	1020	1115	995	1110

Table 2. Photosynthetic pigment contents and ratios, net photosynthetic rate (P_N), and leaf area of winter wheat cv. Emma grown from germination at AC or at EC. Measurements were made on the flag leaves at the beginning of flowering and of grain filling using 5 to 7 replicates. Gas exchange measurements were made either at 350 μmol mol^{-1} or at 700 μmol mol^{-1} [CO_2], respectively. F and t probability tests were used to determine significant differences between treatments. Significant difference at the level of * 5 % or ** 1 %. No replication was available at the beginning of grain filling for leaf area. f.m. = fresh mass.

		AC	EC	
Beginning of flowering	Chl *a* [g kg^{-1}(f.m.)]	7.81±0.64	9.77±0.57	**
	Chl *b* [g kg^{-1}(f.m.)]	2.66±0.16	2.77±0.19	
	Chl *a/b*	2.94±0.17	3.53±0.09	**
	Carotenoids (*x*+*c*) [g kg^{-1}(f.m.)]	1.45±0.20	2.19±0.11	**
	Leaf area [cm^2 plant^{-1}]	30.80±4.35	19.90±5.28	**
	P_N [μmol(CO_2) m^{-2} s^{-1}]	9.50±1.20	13.50±2.80	**
Beginning of grain filling	Chl *a* [g kg^{-1}(f.m.)]	7.58±0.57	9.20±0.57	*
	Chl *b* [g kg^{-1}(f.m.)]	2.66±0.21	2.81±0.31	
	Chl *a/b*	2.85±0.14	3.28±0.17	**
	Carotenoids (*x*+*c*) [g kg^{-1}(f.m.)]	1.35±0.13	1.97±0.30	**
	Leaf area [cm^2 plant^{-1}]	16.5	25.6	
	P_N [μmol(CO_2) m^{-2} s^{-1}]	18.9±1.1	48.3±19.8	**

Table 3. Leaf area and net photosynthetic rate (P_N) of winter wheat cv. Emma at the beginning of grain filling at four different leaf levels. *1* denotes the top leaf level and *4* the bottom leaf level. The measured photosynthetically active radiation (PAR) is also shown. No replication is available for leaf area measurements. Significant differences at the level of * 5 % or ** 1 %.

		Leaf area [cm^2]		P_N [μmol(CO_2) m^{-2} s^{-1}]			PAR [μmol m^{-2} s^{-1}]
[CO_2] [μmol mol^{-1}]		375	700	375		700	
Leaf level	*1*	3.1	6.2	19.0±1.1	**	48.3±20	1200-1300
	2	4.9	7.4	9.9±0.7		13.7±5.2	1200-1300
	3	4.7	6.9	1.3±1.5	*	11.2±0.3	500
	4	3.8	5.1	1.5±1.7	*	10.2±0.2	500

Model parameterisation: The parameterisation of the FACASHA model was performed on winter wheat cv. Emma, using P_N measurements on flag leaves at seven different air CO_2 concentrations, at the beginning of flowering for plants grown at AC or at EC. The measured small temperature fluctuations (Table 1) were calculated during model parameterisation. Parameter values of Harley *et al.* (1992)—a model parameterised for cotton grown either at AC or at EC—were used as a base. Parameter values $c(K_c)$, $c(V_{cmax})$, and $c(T)$, which were used to describe the temperature dependence of Michaelis constant of C_i for carboxylation (K_c), the maximum rate of carboxylation (V_{cmax}), and rate of phosphate release in triose phosphate utilisation (T), had to be altered. Table 4 lists experimental parameter values and compares them to those of Harley *et al.* (1992). The determination coefficients between observed and simulated net photosynthetic rates were $r^2 = 0.916$ for plants grown at AC and $r^2 = 0.980$ for plants grown at EC. Simulation results of the parameterised model are shown in Fig. 1*A*. Simulation results were not affected by irradiation because of radiation saturated conditions. Both measured and simulated P_N were very sensitive to small temperature fluctuations (Fig. 1*A*), which means very good approximation. In both treatments P_N was limited by the rate of phosphate release in triose phosphate utilisation at higher [CO_2]. The CO_2 saturation concentration and the saturated P_N were smaller for AC plants than for the EC ones.

Testing the model: The model was tested using two sets of data. The first data set was taken from the present experiment. P_N was measured at the beginning of grain filling on four vertical leaf levels of winter wheat. For lower leaf levels, K_c, K_o, and V_{cmax} had to be multiplied by constants listed in Table 5. The values of these constants depended on the vertical leaf levels. In all cases, there was high correlation between observed and simulated P_N values. Fig. 2 indicates the outcome of the comparison test results where $r^2 = 0.960$ for plants grown and measured at AC, $r^2 = 0.940$ for plants grown at EC and measured at AC, $r^2 = 0.980$ for plants grown at AC and measured at EC, $r^2 = 0.865$ for plants grown and measured at EC. Rate of phosphate release in triose phosphate utilisation limitation of P_N occurred at the top leaf level and radiation limitation occurred at the bottom level in both treatments.

For a realistic validation of the model a second data set from an earlier experiment (Tuba *et al.* 1994) was used (Fig. 1*B*). The data set included C_i concentration and P_N at the beginning of flowering of winter wheat cv. Martonvásári 16, air temperature (20 °C), and irradiance (800 μmol m^{-2} s^{-1}). Parameter values described above in "Model parameterisation" were used. Determination coefficients between observed and simulated P_N were significantly greater than zero, where $r^2 = 0.940$ for plants grown at AC and $r^2 = 0.980$ for plants grown at EC.

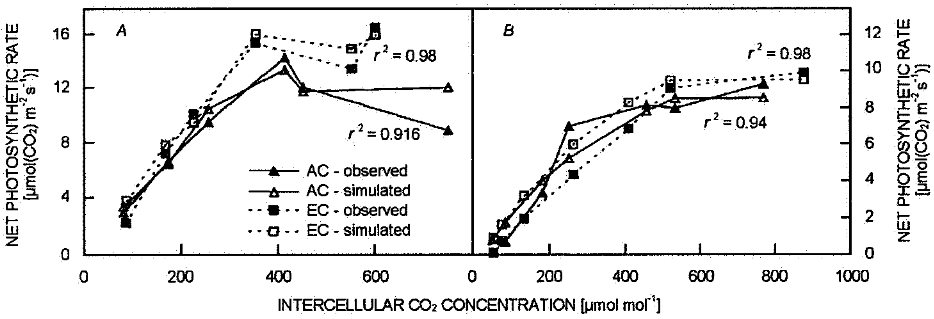

Fig. 1. Measured and simulated net photosynthetic rate of flag leaves of winter wheat cv. Emma (*A*) or Martonvásári 16 (*B*, values from Tuba *et al.* 1994) grown from germination at ambient, AC (control), or enhanced, EC CO_2 concentration. r^2 denotes determination coefficient between observed and simulated values.

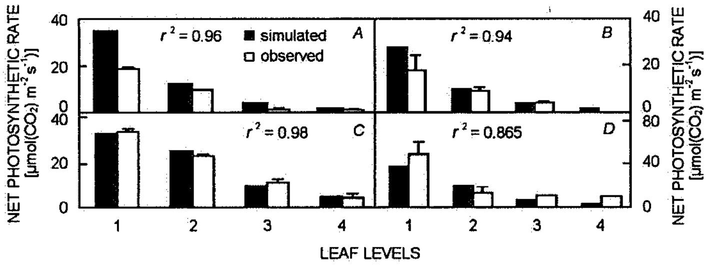

Fig. 2. Measured and simulated net photosynthetic rate of winter wheat cv. Emma grown from germination at ambient, AC (control) (*A*, *C*), or enhanced, EC CO_2 concentration (*B*, *D*) and measured at CA (*A*, *B*) or EC (*C*, *D*). r^2 denotes determination coefficient between observed and simulated values.

Table 4. Altered temperature dependence values of K_c, V_{cmax}, and T in FACASHA model, compared to Harley *et al.* (1992). (See also Table 7.)

Parameter	Harley *et al.* (1992)	Present study	Harley *et al.* (1992)	Present study
	[CO_2] [μmol mol^{-1}]			
	350		650-700	
$c(K_c)$	35.79	36.1	35.79	36.35
$c(V_{cmax})$	51.07	51	49.46	49.65
$c(T)$	23.59	23.29	23.59	23.39

Applications: The model can be used to calculate the temperature dependent variables V_{cmax}, J_{max}, and T for comparison with values from the literature: Table 6 compares calculated V_{cmax}, J_{max}, and T values with average values of 109 C_3 species and with seven different winter wheat cultivars (Wullschleger 1993). At T = 20 or 25 °C calculated values of V_{cmax}, J_{max}, and T from the current study approach the averages of 109 species and the averages of seven different winter wheat cultivars. The last two columns of Table 6 show, how quickly the

Table 5. Multiplication constants of temperature dependent parameters (K_c, K_o, and V_{cmax}) of the FACASHA model.

Leaf level	K_c	K_o	V_{cmax}
1	1.0	1.0	1.00
2	1.0	1.0	0.35
3	1.5	0.3	0.35
4	3.0	0.3	0.35

temperature dependent parameter values increase with increase in temperature.

A second application of the model is in drawing up P_N/C_i curves at different temperatures for Hungarian winter wheat cultivars grown at AC and EC. The high sensitivity of P_N to temperatures between 20 and 40 °C is seen (Fig. 3). At different temperatures, saturated P_N occurs at different C_i. The quick decline of P_N can be obtained when temperature reaches 40 °C.

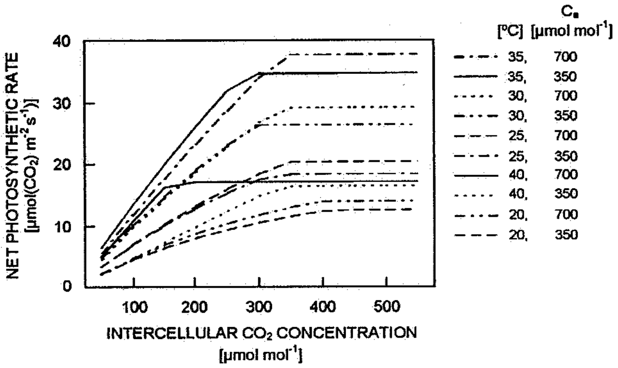

Fig. 3. Simulated temperature and intercellular CO_2 concentration dependence of net photosynthetic rate of flag leaves of winter wheat grown from germination at ambient (350) or enhanced (700) CO_2 concentration

Table 6. Average parameter values of V_{cmax}, J_{max}, and T for 109 species and seven different winter wheat cultivars (Wullschleger 1993), and calculated parameter values from the present study of wheat grown from germination at AC or EC.

	Wullschleger (1993) 20 and 25 °C Average parameters of:		Present study - irradiance of 1 000 μmol mol^{-2} s^{-1} 20 °C Parameter values for: [CO_2] [μmol mol^{-1}]		25 °C		20 °C and 25 °C Average parameter	30 °C
	109 species	7 wheat cvs.	365	700	365	700		
V_{cmax} [μmol mol^{-2} s^{-1}]	64.0	60.0	30.0	38.0	56.0	46.0	42.5	135.9
J_{max} [μmol mol^{-2} s^{-1}]	134.0	145.4	94.0	99.0	144.0	111.0	112.0	236.3
T [μmol mol^{-2} s^{-1}]	10.10	-	4.70	5.20	6.40	5.70	5.50	9.47

Discussion

The aim of our experiment was to get information on how the model of Farquhar *et al.* (1980) and Farquhar and Caemmerer (1982) modified by Sharkey (1985) and Harley and Sharkey (1991) describes P_N of Hungarian winter wheat cultivars under different environment. Results of P_N measurements yielded two important factors: first, there was a large increase in P_N as a result of EC, and second, there was increased acclimation to low irradiance in the canopy. Photosynthetic activity was significantly increased in the lower canopy layer where irradiance was very poor, particularly within the canopy of EC plants. This corroborates the conclusion of earlier investigations (Szente *et al.* 1998) that production of shadow layer influences the total production of plant stands. Our argument is further strengthened by the fact that the amount of most photosynthetic pigments increased under EC. The greater pigment content of plants grown at EC led to more photosynthetic units and better radiation use efficiency.

Our study also supports the use of the model for describing P_N of different C_3 plants under several environmental conditions. Parameterisation and validation for different plant species is essential, but our results show that the same parameterisation can be used for two different Hungarian winter wheat cultivars grown in different years. P_N measured and simulated on four different vertical leaf levels indicates how carefully P_N of the whole canopy has to be calculated, especially when studying the effects of some environmental changes. In many crop growth simulation models, P_N of a canopy has been described in very simplified form. The simulated effects of EC on plant production can be misleading: little account is taken of higher canopy densities and lower irradiance in the lower shade canopy level, and decreased P_N due to long term exposure to EC (Cure and Acock 1986, Harnos 2000). Photosynthetic pigment contents of flag leaves did not change during [CO_2] treatments at different developmental stages, which meant they had the same radiation use efficiency. This made the model parameterisation easier, and it may be one reason why the model worked well with the same parameter set for several developmental stages.

In conclusion, FACASHA model is suitable for describing P_N of different winter wheat cultivars under various environmental conditions (irradiance, temperature, CO_2). Hence FACASHA should be included in winter wheat growth simulation models.

Table 7. List of model parameters and the parameters used to describe their temperature dependencies. Source: Harley *et al.* (1992). Parameter values in italics had to be changed in this study.

Parameter	Unit	Temperature parameters	$[CO_2]$ [µmol mol^{-1}]		Unit
			350	650	
K_c	Pa (CO_2)	$c(K_c)$	***35.79***		-
		$\Delta H_a(K_c)$	80.47		[kJ mol^{-1}]
K_o	Pa (CO_2)	$c(K_o)$	9.59		-
		$\Delta H_a(K_o)$	14.51		[kJ mol^{-1}]
τ	-	$c(\tau)$	-3.9489		-
		$\Delta H_a(\tau)$	-28.99		[kJ mol^{-1}]
R_{day}	µmol(CO_2) m^{-2} s^{-1}	$c(R_{day})$	Estimated; $R_{day} = 0.82$		-
		$\Delta H_a(R_{day})$			[kJ mol^{-1}]
V_{cmax}	µmol(CO_2) m^{-2} s^{-1}	$c(V_{cmax})$	***51.07***	***49.46***	-
		$\Delta H_a(V_{cmax})$	116.3	112.4	[kJ mol^{-1}]
		$\Delta H_d(V_{cmax})$	202.9	201.7	[kJ mol^{-1}]
		$\Delta S(V_{cmax})$	0.65	0.65	[kJ K^{-1} mol^{-1}]
J_{max}	µmol(CO_2) m^{-2} s^{-1}	$c(J_{max})$	37.08	32.88	-
		$\Delta H_a(J_{max})$	79.5	69.1	[kJ mol^{-1}]
		$\Delta H_d(J_{max})$	201.0	201.1	[kJ mol^{-1}]
		$\Delta S(J_{max})$	0.65	0.65	[kJ K^{-1} mol^{-1}]
T	µmol(CO_2) m^{-2} s^{-1}	$c(T)$	***23.59***	***23.59***	-
		$\Delta H_a(T)$	53.1	53.1	[kJ mol^{-1}]
		$\Delta H_d(T)$	201.8	201.6	[kJ mol^{-1}]
		$\Delta S(T)$	0.65	0.65	[kJ K^{-1} mol^{-1}]
α	mol(electron) mol^{-1}(photon)	-	0.24		-

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Appendix

Symbols and units:
RuBP: ribulose-1,5-bisphosphate
RuBPCO: RuBP carboxylase/oxygenase
P_N [μmol m^{-2} s^{-1}]: net photosynthetic rate of leaf
V_c [μmol m^{-2} s^{-1}]: rate of carboxylation at RuBPCO
V_o [μmol m^{-2} s^{-1}]: rate of oxygenation at RuBPCO
τ: specifity factor for RuBPCO (Jordan and Orgen 1984)
C_i [Pa]: partial pressure of CO_2 in the intercellular space
O_i [kPa]: partial pressure of O_2 in the intercellular space ($O_i = 30$ kPa)
R_{day} [μmol m^{-2} s^{-1}]: day respiration rate (excluding photorespiration) (Brooks and Farquhar 1985)
W_c [μmol m^{-2} s^{-1}]: RuBPCO (amount, activation state and kinetic properties) limited carboxylation rate
W_j [μmol m^{-2} s^{-1}]: RuBP regeneration-limited carboxylation rate
T [μmol m^{-2} s^{-1}]: rate of phosphate release in triose phosphate utilisation (starch and sucrose production)
W_p [μmol m^{-2} s^{-1}]: T-limited carboxylation rate (Sharkey 1985, Harley and Sharkey 1991, Harley *et al.* 1992)
V_{cmax} [μmol m^{-2} s^{-1}]: maximum rate of carboxylation
K_c [μmol m^{-2} s^{-1}]: Michaelis constant of C_i for carboxylation
K_o [μmol m^{-2} s^{-1}]: Michaelis constant of O_i for oxygenation
J [μmol m^{-2} s^{-1}]: potential rate of electron transport (Smith 1937)
I [μmol m^{-2} s^{-1}]: quantum flux density absorbed by the leaf
α: efficiency of radiant energy conversion on an incident irradiance basis [mol(electron) mol^{-1}(photon)]
J_{max} [μmol m^{-2} s^{-1}]: radiation saturated rate of electron transport

To model net photosynthetic rate (P_N) of the C_3 plant winter wheat, the model presented by Farquhar *et al.* (1980) and Farquhar and Caemmerer (1982) was used. It was modified to include a potential phosphate limitation arising from the failure of triose phosphate utilisation (starch and sucrose production) to keep up with triose phosphate production in the Calvin cycle by Sharkey (1985) and Harley and Sharkey (1991).

P_N can be expressed:

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

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

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

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

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

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

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 (Farquhar and Caemmerer 1982). The radiation dependency in the model is on electron transport (Smith 1937):

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

and

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

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

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

and

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

(Johnson *et al.* 1942), where c is a scaling constant, ΔH_a is an activation energy, R is the gas constant ($R = 0.00831$ kJ K^{-1} 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. Parameter values are listed in Table 4 and Table 7.