Modeling Temperature Effects on Crop Photosynthesis at High Radiation in a Solar Greenhouse

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Abstract
        The climate inside a solar greenhouse (a high-tech greenhouse essentially heated by solar energy and provided with facilities for seasonal energy storage) is more dependent on outside conditions than in ordinary greenhouses. To optimise ventilation, one has to take into account that optimum temperature for canopy photosynthesis rises with increasing concentration of atmospheric CO_2. To predict canopy photosynthesis and to relate dry weight production to temperature control, a reliable model is needed. Models of canopy photosynthesis have not yet been validated at the extreme climate situations that may be expected in a solar greenhouse in summer (high irradiation, temperature and humidity). Three versions of increasing complexity of leaf photosynthesis simulation models, $M1$, $M2$, and $M2^+$ were evaluated in a canopy photosynthesis model under such conditions. The reference (SUCROS related) model, $M1$, has been extensively validated for a tomato crop under normal greenhouse conditions. $M2$ is an extension of $M1$ with a more biochemical description of the underlying processes. $M2^+$ is an extension of $M2$, including a sub-model of stomatal resistance. In a crop model, the three sub-models were compared under fixed conditions and with observed climate data. There were substantial differences between the three models, especially at high temperatures and high radiation, irrespective of the CO_2 level. The biochemical model, $M2$, performed somewhat differently than $M1$. But, the strongest discrepancies were observed with model $M2^+$ due to the much higher predicted stomatal resistance compared to the values adopted in $M1$ and $M2$. The results demonstrate that it is necessary to investigate the performance of greenhouse crop models under a wider range of conditions when they are to be applied in a solar greenhouse.

INTRODUCTION

        Nowadays, there is sufficient technological basis to design greenhouse systems that are able to utilise solar energy for heating, in combination with, e.g., wind energy for generation of electricity, improved greenhouse insulation, climatisation, and heat storage systems (Bailey, 1985; Bredenbeck, 1989; Bot, 1992). The Dutch Solar Greenhouse (DSG) is an approach to reduce fossil energy use in Dutch greenhouse horticulture (Bot, 2001). Advanced climate control in a DSG should contribute to the reduction of the required heating, heat exchange, and energy storage capacities, whilst maintaining yield and product quality (Körner and Challa, 2001).

        From a technical point of view, it is beneficial in a DSG to accept larger temperature fluctuations than in regular greenhouses. Therefore, air temperature should increase with radiation more than in traditional climate regimes. Maintaining a high CO_2 level in the greenhouse air (as long as ventilation can be avoided) is favourable for photosynthesis, because it suppresses photorespiration (Berry and Björkmann, 1980). In a DSG, therefore, it may be anticipated that at high radiation there will be either a high CO_2 concentration that can be maintained at little or no ventilation or atmospheric CO_2 with ample ventilation.

        In this optimisation, a reliable crop photosynthesis model is needed to predict

production as a function of greenhouse climate. However, present tomato crop growth models as described by Heuvelink (1996) and Van Keulen and Dayan (1993) are designed for and have been validated under normal, moderate greenhouse conditions.

The SUCROS based crop photosynthesis model that is incorporated in TOMSIM (Heuvelink, 1996) uses the leaf photosynthesis module, *M1*, where stomatal resistance is a constant and the behaviour of several biochemical key processes has been summarised in a simplified description. This model was successfully validated by Heuvelink (1996) under normal temperature and relative humidity conditions, but we wondered how this simplified version would perform under the more extreme conditions of a DSG.

To answer this question, the performance of a complete greenhouse crop photosynthesis model as described by Gijzen (1992) was investigated at high radiation, temperature, and humidity conditions. The performance of this model with the reference leaf photosynthesis model, *M1*, was compared with the results of alternative leaf photosynthesis-modules, *M2* and *M2*$^+$. In *M2*, the simplified description of the underlying biochemical key processes was replaced by a more process-based description. *M2*$^+$ is the same as *M2*, but it also includes a model of the stomatal resistance, r_s, according to Stanghellini (1987) instead of using a fixed r_s.

Steady state comparisons were made for a range of temperatures, CO_2 concentrations, and radiation levels. In addition, canopy gross photosynthesis was simulated dynamically under climate conditions obtained from two identical, mechanically cooled, closed greenhouse compartments with a tomato crop used for measuring canopy photosynthesis (data not presented in this study).

MATERIAL AND METHODS

Climate Data

In two identical semi-closed greenhouses at Wageningen University, The Netherlands, CO_2 concentration was maintained at 350 and 750 μmol mol^{-1} between 22 August and 29 September 2000 for two successive days in turns to avoid photosynthetic acclimation of the tomato plants to elevated CO_2. Day temperature was 20, 24, 28, 32, and 36 ºC. CO_2 concentration inside the greenhouses was measured every 275 s by an infrared gas analyser (URAS 3G, Hartmann and Braun, Frankfurt, Germany). Pure CO_2 was injected proportionally to the difference of measured and target CO_2 concentration through a thermal mass flow controller (5850E, Brooks, Hatfield, PA, USA) with 150 g CO_2 h^{-1} maximum flow rate. The system was controlled by commercial control software (HP VEE 5.0, Hewlett Packard, Englewood, CO, USA). Air temperature and relative humidity (*RH*) were measured at three positions inside each greenhouse and controlled by a commercial computer system (VitaCo, Hoogendoorn, 's Gravenzande, The Netherlands). *RH* increased with greenhouse temperature and was between 80% at 20 ºC and 88-98% at 36 ºC, corresponding to 0.46 and 0.70 kPa or 0.06 kPa vapour pressure deficit (*VPD*). Leaf temperature was measured every 5 s, averaged over 5 minutes and stored on a data logger (DT 600, Esis, Roseville, NSW, Australia) by 10 evenly distributed type-K thermocouples (Ø 0.025 mm) in each greenhouse. Thermocouples were attached to the bottom of sunlit leaves with tension and glue (Tarnopolsky and Seginer, 1999). Photosynthetic photon flux density (*PPFD*) was measured above the canopy at a height of 2.15 m with a 100 cm line quantum sensor (LI-191SA, LI-COR, Lincoln, NE, USA).

Model

Leaf photosynthesis is described by a two parameter (maximum gross photosynthesis, $P_{g,max}$, and leaf photochemical efficiency, α_L), negative exponential light-response curve (Thornley, 1976). From this, canopy photosynthesis was derived based upon the calculated sunlit and shaded leaf area index (*LAI*) (Goudriaan, 1977) and integrated over canopy height with three point Gaussian integration according Goudriaan and Van Laar (1994). As explained before three leaf photosynthesis models (*M1*, *M2*, and

$M2^+$) were compared. In *M1*, descriptive formulae are used to calculate the initial slope, α, and light-saturation value, $P_{g,max}$, according to Farquhar et al. (1980) and simplified according to Gijzen (1994). In *M2*, the original biochemical-based equations derived by Farquhar et al. (1980) were used (Table 1). Instead of a constant stomatal resistance used in *M1* and *M2*, stomatal resistance in $M2^+$ is modeled as a function of leaf temperature, ambient CO_2, short-wave radiation absorption by the canopy, *LAI*, and *VPD* according to Stanghellini (1987).

Canopy Light Response Curves

Light response curves were fitted to the results of simulated canopy gross photosynthesis obtained with climatic data from the greenhouse experiments. To this end, maximum canopy gross photosynthesis ($P_{gc,max}$) and canopy photochemical efficiency (α_c) in the negative-exponential equation (eq. 1) as used by Heuvelink (1996) were estimated by non-linear least squares iteration using the PROC NLIN procedure of SAS 6.12 (SAS, 1994).

$$P_{gc} = P_{gc,max} \cdot (1 - e^{\frac{-\alpha_c \cdot PPFD}{P_{gc,max}}}) \tag{1}$$

RESULTS

Simulation of P_{gc} with Steady State Climate Conditions

The P_{gc} with *M1* and *M2* responded only slightly to temperature between 20 and 34 °C (Fig. 1) but with $M2^+$, there was a strong response in this range. P_{gc}, however, exhibited an optimal temperature response in all three sub-models. *M1* had a 6-degree long plateau optimum between 26 and 32 ºC for all radiation intensities tested (Fig. 2), *M2* and $M2^+$ responded in an optimal point. At higher ambient CO_2 concentration, the P_{gc} response to temperature was steeper in all three sub-models and the optimum temperature for P_{gc} increased only slightly with increasing CO_2. However, the response pattern of P_{gc} to temperature was clearly different between *M1* and *M2*. With *M1*, there were discontinuities that were not observed with the biochemically-based *M2*. When stomatal behaviour was incorporated in the model ($M2^+$), the stomatal resistance was higher and this had pronounced consequences for the temperature response of P_{gc}. Maximum P_{gc} was observed at lower temperatures and there was a much stronger decrease with increasing temperature than in the other modules considered. For all CO_2 radiation levels tested, P_{gc} was lower with $M2^+$ than with *M1* and *M2*.

Simulation of P_{gc} with Observed Climate Conditions

Simulations with *M1* and $M2^+$ using observed climatic data and fitted light response curves (parameters in Table 2) are illustrated in Fig. 2. In all cases fitted P_{gc} was higher with *M1* than with $M2^+$. This difference increased with radiation and temperature. At higher temperatures the response of P_{gc} to radiation with $M2^+$ was more linear than with *M1*. $P_{gc,max}$ increased with temperature up to 32 °C with *M1* at both CO_2 levels. With $M2^+$, on the other hand, $P_{gc,max}$ decreased over the range from 24 to 36 °C at 350 µmol mol^{-1} CO_2 and from 28 to 36 °C at 750 µmol mol^{-1} CO_2. The overall level of P_{gc} was higher at elevated CO_2 in both models, where the relative difference between the two was the same as at ambient CO_2 concentration. The photochemical efficiency was slightly higher for almost all situations tested.

DISCUSSION

The performance of the three models differed considerably in the situations tested. In particular, the incorporation of r_s to the model resulted in a different response to increasing temperature and CO_2. Stomatal resistance, with the model used in this study, appeared to have a major impact on canopy gross photosynthesis and its response to temperature. In $M2^+$, the increase of P_{gc} with ambient CO_2 and temperature was less than

expected from literature (e.g. Cannell and Thornley, 1998). In their case, this was a combined effect of quantum yield, which corresponds to α_c in our model, and light saturated photosynthesis, which is similar to $P_{gc,max}$. They did not include r_s in their model, but adopted a fixed quotient of 0.7 between ambient and intercellular CO_2 concentration.

With *M2* and fixed r_s, the response of P_{gc} to temperature and CO_2 was not as pronounced as reported by Long (1991). Our results, however, are in agreement with Cannell and Thornley (1998), who also reported that canopy gross photosynthesis shows less CO_2 – temperature interaction than leaf photosynthesis. This probably is due to low light levels inside the canopy (i.e. light limited photosynthesis).

The DSG is planned to be equipped with an energy efficient dehumidification unit (Bot, 2001), which will affect temperature and vapour pressure. Due to relatively low ventilation rates and relaxed climate control in the DSG (Körner and Challa, 2001), *VPD*, a factor that affects r_s according to the model of Stanghellini (1988) used in $M2^+$, is likely to vary as well. As we have seen, variations in r_s may strongly influence the canopy photosynthesis rate and, therefore, have to be taken into account in crop photosynthesis models.

Based on the comparison of the performance of the three model versions in the present study, it can be concluded that although *M1* performs well under standard conditions, it may not be able to adequately predict extreme situations encountered in the DSG. Both incorporation of more detailed biochemical processes and behaviour of stomata would be needed for model-based climate control. Experiments on canopy photosynthesis are needed to verify whether the crop photosynthesis model improvements observed by simulations can also be measured in the crop.

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Tables

Table 1. Maximum carboxylation rate ($V_{C,\max}$), maximum electron transport rate ($J_{\max}$), CO$_2$ compensation point (Γ), and dark respiration rate (R_D) for the three leaf photosynthesis modules (*M1*, *M2*, and *M2*[+]). Leaf temperature (T_L) is variable. All other parameters are constants. Maximum carboxylation and dark respiration rates at 25 ºC are $R_{D,25}$ and $V_{C,\max,25}$ and Q$_{10}$ for dark respiration is $Q_{10,RD}$. Activation energy (E) and Michaelis-Menten constant (K) are according to their subscripts: *C*, O, *VC*, *J*, *D*, and 25 (Rubisco carboxylation and –oxygenation, $V_{C,\max}$, $J_{\max}$, dark respiration rate, and 25 °C). $V_{O,C}$. $\rho_{O_{2i}}$ is O$_2$ partial pressure, *S* and *H* are optimum curve temperature dependent electron transport rates, and R_g is the gas constant.

	M1	*M2 / M2*[+]
$V_{C,\max}$	$V_{C,\max,25} \cdot Q_{10,Vc}^{(T_L-25)/10}$	$V_{C,\max,25} \cdot e^{E_{VC} \cdot (T_L-25)/(T_L \cdot R \cdot 25)}$
$J_{\max}$	*Optimal temperature step function* (Bertin and Heuvelink, 1993)	$J_{\max,25} \cdot e^{\left(\dfrac{E_J \cdot (T_L-25)/(T_L \cdot R \cdot 25)}{1+e^{\frac{(S-H)/T_L}{R_g}}} \middle/ 1+e^{\frac{(S-H)/25}{R_g}} \right)}$
Γ	$42.7 + 1.68 \cdot (T_L - 25) + 0.012 \cdot (T_L - 25)^2$	$\dfrac{\rho_{O_{2i}} \cdot V_{O,\max} / V_{C,\max}}{2} \cdot \dfrac{K_{C,25} \cdot e^{E_C \cdot (T_L-25)/(T_L \cdot R \cdot 25)}}{K_{O,25} \cdot e^{E_O \cdot (T_L-25)/(T_L \cdot R \cdot 25)}}$
R_D	$R_{D,25} \cdot Q_{10,RD}^{(T_L-25)/10}$	$R_{D,25} \cdot e^{E_D \cdot (T_L-25)/(T_L \cdot R_g \cdot 25)}$

Table 2. Fitted values for maximum gross photosynthesis $P_{gc,max}$ (g CO_2 m^{-2} h^{-1}) and photochemical efficiency α_c (g CO_2 {µmol photons}$^{-1}$) for modules $M1$ and $M2^+$. Parameters were fitted with P_{gc} simulations for one hour consisting of 5 min input values of leaf temperature, RH and outside global radiation at 350 ± 30 and 750 ± 30 µmol mol^{-1} at 24, 28, 32 and 36 ^{o}C air temperature.

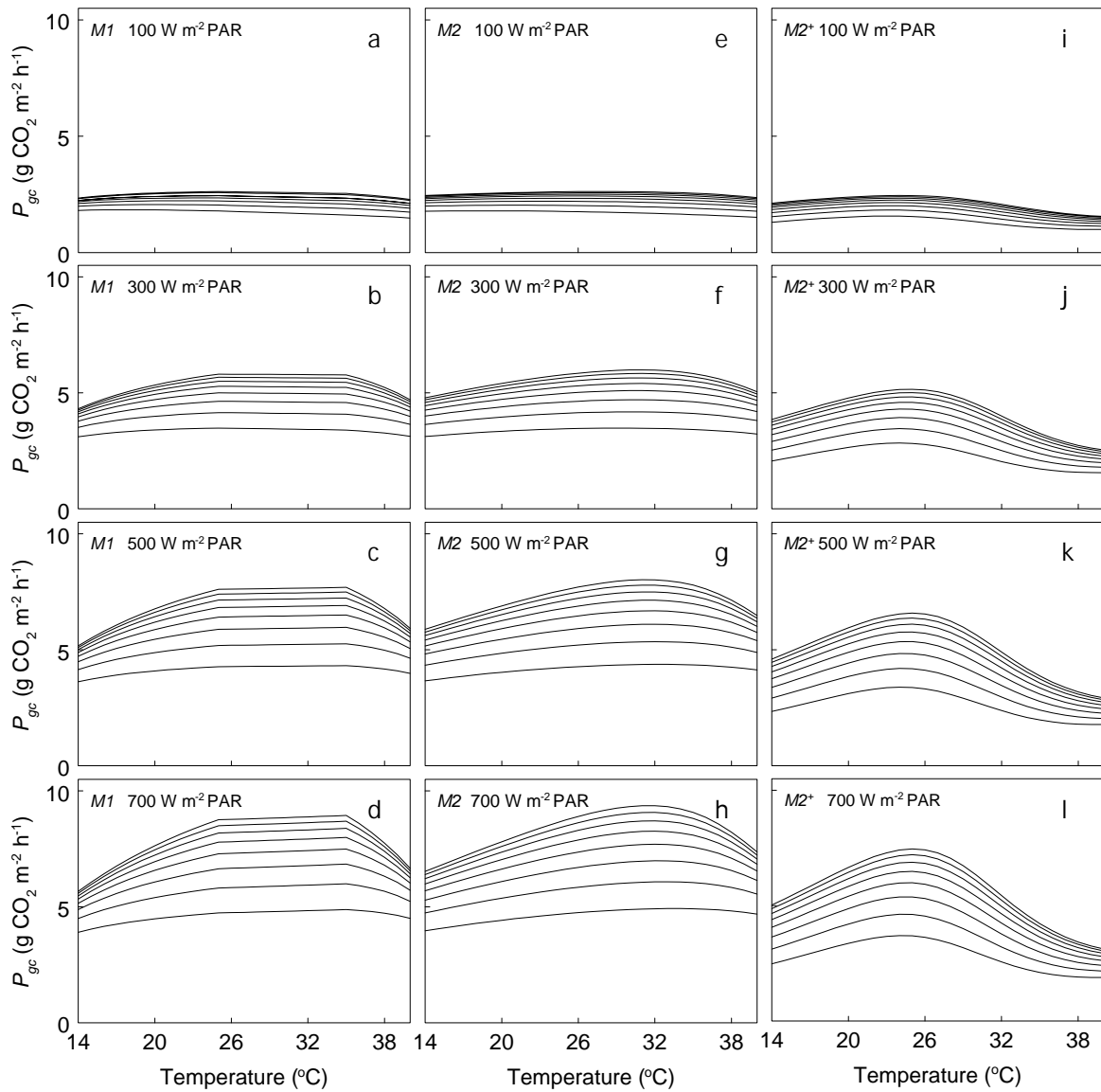| Model | Parameter | CO_2 350 µmol mol^{-1} | | | | CO_2 750 µmol mol^{-1} | | | |
| | | Temperature (°C) | | | | | | | |
		24	28	32	36	24	28	32	36
$M1$	α_c ($\bullet 10^{-6}$)	2.3	2.3	2.3	2.7	2.7	2.8	2.5	2.7
	$P_{gc,max}$	5.9	6.3	6.5	5.8	9.0	9.1	14.8	14.3
$M2^+$	α_c ($\bullet 10^{-6}$)	2.3	2.3	2.2	2.5	2.7	2.8	2.6	2.6
	$P_{gc,max}$	4.7	4.7	4.1	3.0	7.6	7.6	7.4	5.5

Fig. 1. Simulated canopy photosynthesis (P_{gc}) as function of temperature. Eight CO_2 concentrations (300-1000 μmol mol^{-1}, lines) and four photosynthetic active radiation (PAR) intensities are compared (100 (a, e, i), 300 (b, f, j), 500 (c, g, k), and 700 (d, h, l) Wm^{-2}). *M1* (a-d), *M2* (e-h), and *M2*$^+$ (i-l).
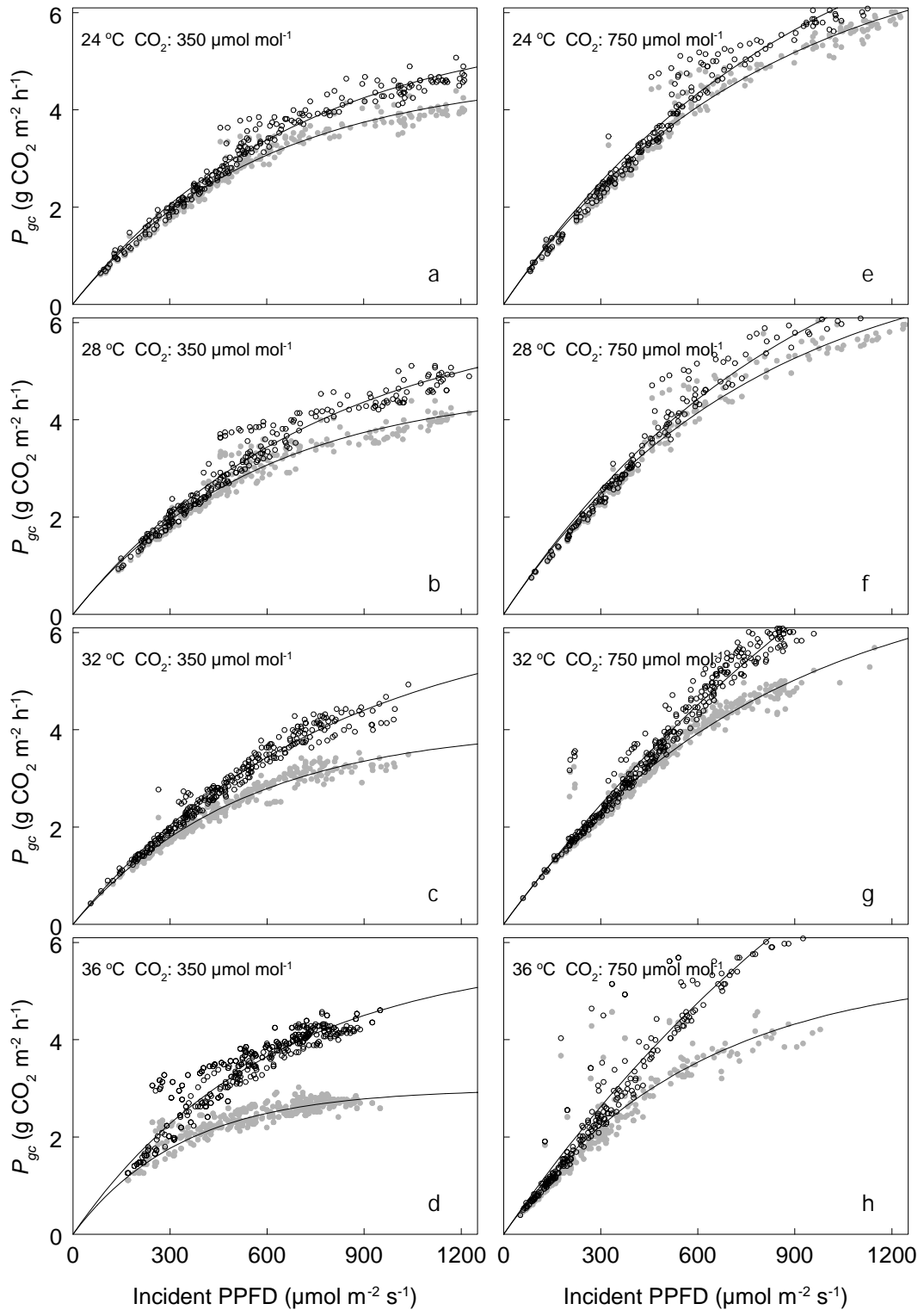
Fig. 2. Simulated P_{gc} on climate data achieved from crop assimilation experiment at 350 ± 30 μmol mol^{-1} (a-d) and 750 ± 30 μmol mol^{-1} (e-h) at 24 (a, e), 28 (b, f), 32 (c, g) and 36 (d, h) °C for *M1* (○) and *M2^{+}* (●) as function of photosynthetic photon flux density (*PPFD*). P_{gc} was simulated for a one-hour interval, consisting of 5 min input values of leaf temperature, relative humidity and outside global radiation. Negative-exponential functions (eq. 1) with $P_{gc,\mathrm{max}}$ and α_c were fitted by to the data (lines) (Table 2).