



# The Use of the Ratio between the Photosynthesis Parameters $P_{ml}$ and $V_{cmax}$ for Scaling up Photosynthesis of $C_3$ Plants from Leaves to Canopies: A Critical Examination of Different Modelling Approaches

GEORG WOHLFAHRT\*<sup>†‡</sup>, MICHAEL BAHN\* AND ALEXANDER CERNUSCA\*

\**Institut für Botanik, Universität Innsbruck, Sternwartestr. 15, 6020 Innsbruck, Austria and*

*†Centro di Ecologia Alpina, Viote del Monte Bondone, 38040 Trento, Italy*

(Received on 14 January 1999, Accepted in revised form on 9 June 1999)

Recent models of photosynthesis have adopted the close correlation between the main photosynthetic component processes, the maximum rate of carboxylation and the potential rate of RuBP (ribulose-1,5-bisphosphate) regeneration, at a reference temperature of 20°C. When using the ratio between these two processes in models of photosynthesis, assumptions though have to be made about the temperature response of the potential rate of RuBP regeneration, which varies with growth conditions and among species. In order to assess the effects of deviations from the real temperature response of the potential rate of RuBP regeneration on photosynthesis, a sensitivity analysis, scaling up photosynthesis from the leaf to the canopy level, is applied in the present paper. No changes are predicted to occur for sunlit leaves, which receive both direct and diffuse radiation, as long as incident radiation does not cause carboxylation to shift from RuBP saturation to RuBP limitation, which, depending on incident radiation and canopy structure, might occur deeper down in the canopy. Carboxylation of shaded leaves, which receive solely diffuse radiation, is generally limited by the regeneration of RuBP, and is thus prone to be affected by changes in the temperature response of the potential rate of RuBP regeneration. Due to the saturation type response of the RuBP-limited rate of carboxylation to temperature at light intensities below saturation, the impact of deviations from the real temperature response is negligible at high leaf temperatures, but may become significant when leaf temperatures are low and photosynthetically active radiation incident on shaded leaves is comparably high, as in the upper canopy layers. The largest effects on whole canopy photosynthesis will therefore occur under cool conditions and a completely overcast sky, when all leaves receive diffuse radiation only.

© 1999 Academic Press

## 1. Introduction

Among the papers published during the last years, there is one which, especially in the plant gas exchange modelling community, has received special attention, since it seems to imply a promising approach which could greatly simplify the

parameterization of models of  $C_3$  photosynthetic carbon assimilation. In this article, Wullschleger (1993) presents data of the two component processes of photosynthesis, the maximum rate of carboxylation ( $V_{cmax}$ ) and the potential rate of electron transport ( $J_{max}$ ), of 109 different species, calculated from previously published  $A/C_i$ -curves. Despite multifold differences in the absolute values of  $V_{cmax}$  and the potential rate of

<sup>‡</sup> Author to whom correspondence should be addressed.  
E-mail: [georg.wohlfahrt@uibk.ac.at](mailto:georg.wohlfahrt@uibk.ac.at)

RuBP regeneration [ $P_{ml}$ , introduced by Harley & Tenhunen (1991) and used throughout this paper instead of  $J_{max}$  to which it is related by  $J_{max}/4$ ], when plotting them against each other, they surprisingly gather together around a single straight line, indicating a close correlation between these two processes. Later, Leuning (1997) further improved this correlation, accounting for the temperature dependency of these two processes, by scaling the results obtained by Wullschlegel (1993) to a common temperature of 20°C.

It was this relationship which attracted the modellers attention (Leuning *et al.*, 1995; De Pury & Farquhar, 1997; Baldocchi & Meyers, 1998), "because it reduces by one the number of parameters to be specified" (Leuning, 1997), since once  $V_{cmax}$  has been determined,  $P_{ml}$  may be calculated easily just by multiplication. Unfortunately, this is true only at the reference temperature, to which the relationship between  $P_{ml}$  and  $V_{cmax}$  is confined, since the two processes usually have different temperature responses (Farquhar *et al.*, 1980; Harley & Tenhunen, 1991; Kirschbaum & Farquhar, 1984; Wohlfahrt *et al.*, 1998, 1999). Thus, in order to compute  $P_{ml}$  at any leaf temperature besides the reference temperature, further information on its temperature response is needed. Lacking own measurements on the species under study, the missing parameters have to be retrieved from literature. Though even in the lucky case that a set of parameters for the studied species is found, it still remains unclear whether they are really appropriate, since the temperature response of  $P_{ml}$  not only differs among species (Nolan & Smillie, 1976; Armond *et al.*, 1978), but also varies with growth conditions, especially temperature (Björkman *et al.*, 1980; Sayed *et al.*, 1989). Recognizing this as a potential source of errors, it is thus instructive to investigate the effects that deviations in the temperature response of  $P_{ml}$  may have on photosynthesis. Especially when scaling up from leaves to canopies, where alterations of leaf photosynthetic performance are supposed to have strong impacts on canopy assimilation (Reynolds *et al.*, 1996), impacts which though may not be foreseen easily.

The aim of the present paper is thus to explore the sensitivity of photosynthesis of  $C_3$  plants to changes in the temperature response of

$P_{ml}$  and to evaluate the accuracy of the predictions, of such a simplified leaf model parameterization. An up-scaling exercise is carried out to track the effects of alterations in the temperature response of  $P_{ml}$ , from the level of biochemistry, over leaf scale photosynthesis to whole canopy assimilation.

For this purpose, a strain of soybean (*Glycine max*) was selected as a study object because of the large amount of published information on this species (Baldocchi, 1993; Baldocchi & Meyers, 1998; Harley & Tenhunen, 1991; Harley *et al.*, 1985). In a sensitivity analysis, three scenarios are tested and the results compared with those obtained when using the actual parameters of soybean, which will be referred to as "the reference" in the following. In *Scenario I*, a constant ratio between  $P_{ml}$  and  $V_{cmax}$  at any leaf temperature is assumed. This amounts to assuming that the temperature response of  $P_{ml}$  is proportional to that of  $V_{cmax}$ . *Scenario I* thus represents a real simplification, since  $P_{ml}$  may be determined by the means of a single parameter, the ratio between  $P_{ml}$  and  $V_{cmax}$ . *Scenarios II* and *III* are characterized by a shift in the temperature optimum of  $P_{ml}$ , 3°C to lower and higher temperature, respectively, compared with the reference. These two scenarios aim at simulating the effects of a potential acclimation of electron transport to low (resp. high) temperatures.

Since soybean is a plant species adapted to comparably warm environments, the question arises whether the results obtained for the temperature response of soybean may be regarded as general, insofar as they are valid also for plant species adapted to cold environments, e.g. for plant species from arctic or alpine regions. To address this question, the simulations at the leaf level were repeated using a parameter set obtained by Wohlfahrt *et al.* (1999) for several forbs from mountain grasslands in the Eastern Alps. Thereby the present paper contributes to the EU-TERI-project ECOMONT (Cernusca *et al.*, 1996), which *inter alia* aims at scaling up photosynthesis from the leaf to the landscape level in mountain ecosystems (Cernusca *et al.*, 1998; Tenhunen, 1999), since it implicitly contains indications of how to simplify the model of photosynthesis, and thus reduce experimental effort, without losing the basic system behaviour. Especially at larger

scales, this represents one of the key problems of current up-scaling schemes (Jarvis, 1995).

## 2. Materials and Methods

### 2.1. MODELS

In the present study, a one-dimensional, multi-layer canopy gas exchange model is used to compute the fluxes of CO<sub>2</sub> (and H<sub>2</sub>O, which are, however, out of the scope of the present paper). The model consists of coupled micrometeorological and eco-physiological modules. The micrometeorological modules compute radiative transfer, the attenuation of wind speed within the canopy and leaf temperatures. For simplicity, and to ease interpretation of the results, profiles of CO<sub>2</sub>, H<sub>2</sub>O and air temperature were assumed constant within the canopy. The environmental variables computed in the micrometeorological modules represent the driving forces for the leaf gas exchange model, which calculates net photosynthesis, stomatal conductance and transpiration. Since leaf energy losses depend upon leaf temperature, but in turn determine leaf temperature via the energy balance, iterative procedures are used to find equilibrium states. A part of the following model theory is kept short on purpose, either because the corresponding equations are well known (leaf energy balance) and/or because the model itself is not the topic of interest (radiative transfer), but rather a tool to realize the aims of the present paper, and the reader is therefore referred to the respective references for detailed information. For abbreviations and symbols refer to the appendix.

#### 2.1.1. Leaf gas exchange

Following the theory developed by Farquhar and co-workers (Farquhar, 1979; Farquhar *et al.*, 1980; Farquhar & Von Caemmerer, 1982), later modified by Harley & Tenhunen (1991), CO<sub>2</sub> assimilation is either entirely limited by the kinetic properties of RUBISCO and the respective partial pressures of the competing gases CO<sub>2</sub> and O<sub>2</sub> at the sites of carboxylation ( $W_C$ ) or by electron transport ( $W_J$ ), which limits the rate at which RuBP is regenerated. Limitations of RuBP regeneration arising from the availability of inorganic phosphate ( $P_i$ ) for photophosphorylation

( $W_P$ ; Sharkey, 1985), are not considered in the present approach. Net photosynthesis  $A$  may then be expressed as

$$A = \left(1 - \frac{0.5O}{\tau Ci}\right) \min\{W_C, W_J\} - R_{day}, \quad (1)$$

where  $O$  and  $Ci$  are the partial pressures of O<sub>2</sub> and CO<sub>2</sub> in the intercellular space, respectively.  $\tau$  is the specificity factor for RUBISCO (Jordan & Ogren, 1984),  $R_{day}$  is the rate of CO<sub>2</sub> evolution from processes other than photorespiration and  $\min\{\}$  denotes "the minimum of".  $R_{day}$  is assumed to be a proportion of the dark respiration rate,  $R_{dark}$ , depending on the incident photosynthetic photon flux density (PPFD) according to Falge *et al.* (1996).

The carboxylation rate, limited solely by the amount, activation state and kinetic properties of RUBISCO and the respective partial pressures of the competing gases CO<sub>2</sub> and O<sub>2</sub> at the sites of carboxylation is assumed to obey competitive Michaelis–Menten kinetics and is given by

$$W_C = \frac{V_{cmax} Ci}{Ci + K_C(1 + O/K_O)}, \quad (2)$$

where  $V_{cmax}$  is the maximum rate of carboxylation and  $K_C$  and  $K_O$  are the Michaelis–Menten constants for carboxylation and oxygenation, respectively.

The rate of carboxylation limited solely by the rate of RuBP regeneration due to electron transport,  $W_J$ , is given by

$$W_J = \frac{P_m}{1 + O/\tau Ci}, \quad (3)$$

where  $P_m$  is the CO<sub>2</sub> saturated rate of photosynthesis at any given irradiance and temperature. This expression of  $W_J$  is equivalent to that used by Farquhar & Von Caemmerer (1982), if their parameter  $J$  is equal to  $4P_m$  [for a detailed discussion of  $P_m$  see Harley & Tenhunen (1991)].

$P_m$  is expressed as a light dependency using the equation by Tenhunen *et al.* (1976), which was derived from Smith (1937),

$$P_m = \frac{\alpha PPF D}{(1 + \alpha^2 PPF D^2 / P_{ml}^2)^{0.5}}, \quad (4)$$

where  $\alpha$  is the initial slope of the curve relating CO<sub>2</sub>-saturated net photosynthesis to irradiance (on an incident light basis) and  $P_{ml}$  is the potential rate of RuBP regeneration.

$V_{cmax}$  and  $P_{ml}$  depend upon temperature and, given their optimum response to temperature (Harley & Tenhunen, 1991; Leuning, 1997), each described using an equation based on absolute reaction theory by Johnson *et al.* (1942) and Sharpe & DeMichele (1977), normalized to a reference temperature (293.16 K) as in Leuning (1997)

$$X = \frac{X(T_{ref}) \exp[(\Delta H_a / RT_{ref})(1 - T_{ref}/T_K)]}{1 + \exp[(\Delta S T_K - \Delta H_d) / RT_K]}, \quad (5)$$

where  $X$  stands for either  $V_{cmax}$  or  $P_{ml}$ , and  $X(T_{ref})$  for the potential value that this parameter would have at the reference temperature of 293.16 K, in the absence of any deactivation due to high temperature [Schoolfield *et al.*, 1981; this parameter was misinterpreted by Leuning *et al.* (1995), who took it as the actual rate at the reference temperature).  $\Delta H_a$  is the energy of activation,  $\Delta H_d$  is the energy of deactivation,  $\Delta S$  is an entropy term,  $T_K$  is the leaf temperature and  $R$  is the gas constant.

The temperature optimum ( $T_{opt}$ ) of  $V_{cmax}$  and  $P_{ml}$  is described by the following expression, which was derived by differentiation of eqn (5) with respect to  $T_K$ :

$$T_{opt} = \frac{-\Delta H_d}{R \ln(-\Delta H_a / (\Delta H_a - \Delta H_d)) - \Delta S}. \quad (6)$$

$R_{dark}$ ,  $K_C$ ,  $K_O$  increase with temperature, whereas  $\tau$  is a declining function of temperature (see Harley & Tenhunen, 1991) and their temperature dependencies are each given by

$$X = X(T_{ref}) \exp\left[\frac{\Delta H_a}{RT_{ref}} \left(1 - \frac{T_{ref}}{T_K}\right)\right] \quad (7)$$

which is the same as eqn (5), with the denominator set to unity.  $X$  can be substituted for either  $R_{dark}$ ,  $K_C$ ,  $K_O$  or  $\tau$ .  $X(T_{ref})$ , in this case, is the actual rate at the reference temperature.

To be able to predict gas exchange at the leaf level, the photosynthesis model has to be combined with a model predicting stomatal conductance (Harley & Tenhunen, 1991). For this purpose, the empirical model by Ball *et al.* (1987), modified according to Falge *et al.* (1996), was chosen

$$g_s = g_{min} + G_{fac}(A + I_{fac}R_{dark}) \times 10^2 \frac{hs}{C_s}, \quad (8)$$

where  $g_s$  is the stomatal conductance,  $g_{min}$  is the minimum or residual stomatal conductance and  $hs$  and  $C_s$  are, respectively, the relative humidity (as a decimal fraction) and the CO<sub>2</sub> partial pressure at the leaf surface. The factor  $10^2$  corrects for the differences in the units of  $g_s$  and  $g_{min}$  and  $(A + I_{fac}R_{dark})C_s^{-1}$ .  $G_{fac}$  is an empirical coefficient representing the composite sensitivity of stomata to these factors. Stomatal opening in response to *PPFD* is controlled via  $(A + I_{fac}R_{dark})$ , which gives an estimation of gross photosynthetic rate and is considered to be related to energy requirements for maintaining guard cell turgor, where  $I_{fac}$  represents the extent to which dark respiration is inhibited in light (Falge *et al.*, 1996). Effects of non-uniform stomatal closure ("patchiness") on stomatal conductance are not considered in this model. Leaf boundary layer conductance was modelled using the equations from Nobel (1991), and the parameters  $hs$  and  $C_s$  were calculated according to Falge (1997).

Leaf internal CO<sub>2</sub> partial pressure is calculated from net photosynthesis and stomatal conductance according to Fick's law

$$C_i = C_s - \frac{A \times 1.6 \times 100}{g_s}, \quad (9)$$

where 1.6 accounts for the difference in diffusivity between CO<sub>2</sub> and H<sub>2</sub>O, and the factor 100 corrects for the difference in the units of  $C_s$  and  $A/g_s$ . Due to the fact that net photosynthesis and stomatal conductance are not independent, the model must solve for the internal CO<sub>2</sub> partial pressure in an iterative fashion (Harley & Tenhunen, 1991; Harley & Baldocchi, 1995).

### 2.1.2. Radiative transfer

Radiative transfer was modelled adopting the basic equations by Goudriaan (1977). The canopy is divided into sufficiently small [leaf area index ( $LAI$ ) =  $0.1 \text{ m}^2 \text{ m}^{-2}$ ] layers with negligible self-shading, in which leaves are assumed to be distributed symmetrically with respect to the azimuth. The model accounts for multiple scattering of radiation, assuming leaf reflection and transmission to be of equal magnitude and considers nine leaf angle classes ( $\lambda$ ). Because of the nonlinear response of photosynthesis to PPFD, the radiation incident on shaded and sunlit leaves must be considered separately. Shaded leaves receive diffuse light only [ $Q_{shade}$ , eqn (10)], while sunlit leaves receive both diffuse and direct radiation [ $Q_{sun}$ , eqn (11)]:

$$Q_{shade}(j) = \left\{ \sum_{\beta'=1}^9 \left[ \frac{\sum_{\lambda=1}^9 O(\beta', \lambda) F(\lambda)}{\sin \beta'} \right. \right. \\ \left. \left. \times (Q_{down}(j-1, \beta') + Q_{up}(j+1, \beta')) \right] \right\} \\ - Q_{dir}(j-1) \\ \times \frac{\sum_{\lambda=1}^9 O(\beta, \lambda) F(\lambda)}{\sin \beta}, \quad (10)$$

$$Q_{sun}(j) = Q_{shade}(j) + Q_{dir}(0) \frac{\sum_{\lambda=1}^9 O(\beta, \lambda) F(\lambda)}{\sin \beta}, \quad (11)$$

where  $j$  is the index of the canopy layer reckoned from top downwards,  $\beta$  stands for the inclination of the sun, and  $\beta'$  for the nine sky angle classes considered for the treatment of the diffuse radiation.  $Q_{down}$  and  $Q_{up}$  are the downward and upward moving total (diffuse and direct) radiation fluxes, respectively,  $O(\beta, \lambda)$  and  $O(\beta', \lambda)$  represent the projection of leaves into the direction of  $\beta$  and  $\beta'$ , respectively (De Wit, 1965; Goudriaan, 1988), and  $F(\lambda)$  stands for the leaf angle distribution. The (downward) flux of direct radiation ( $Q_{dir}$ ) has to be subtracted from the total radiation to give the light intensity incident on shaded leaves,

which is thus composed of sky diffuse and scattered beam radiation (Spitters, 1986).  $Q_{dir}(0)$  stands for the direct radiation measured on a horizontal plane above the canopy. The results of eqns (10) and (11) may be used directly to calculate assimilation, since PPFD in the leaf model [eqn (4)] refers to an incident light basis. In order to calculate absorbed short- and long-wave radiation, as it is required for the energy balance [eqn (12)],  $Q_{shade}$  and  $Q_{sun}$  need to be multiplied by an absorption coefficient, which is calculated as  $1 - \sigma$ , where  $\sigma$  is a leaf scattering coefficient. Radiative transfer is modelled separately for the wavebands of photosynthetically active radiation (PPFD), near-infrared (NIR) and long-wave radiation. In order to stimulate the thermal radiation emitted by the soil and the leaves, eqns (10) and (11) have to be extended to account for these additional radiation fluxes, which depend upon soil and leaf temperature, respectively, according to the Stefan-Boltzmann law (Campbell & Norman, 1998).

Solar geometry, determining the position of the sun in the sky, was calculated using the equations given in Campbell & Norman (1998). The total solar radiation was estimated following Goudriaan & Van Laar (1994). The partitioning of solar radiation into direct and diffuse, PPFD and NIR components was accomplished using the approach described in Weiss & Norman (1985). Sky long-wave radiation was estimated using the equations by Brutsaert (1984) and Monteith & Unsworth (1990).

### 2.1.3. Energy balance

Leaf temperatures were estimated solving their energy balance (Campbell & Norman, 1998)

$$Q_{abs} = Q_{loss} + \lambda E + H \quad (12)$$

in an iterative fashion, where  $Q_{abs}$  is the absorbed short- and long-wave radiation,  $Q_{loss}$  the emitted long-wave radiation,  $\lambda E$  and  $H$  represent the latent and sensible heat loss, respectively. An exponential decrease of wind speed ( $U_{(j)}$ ) within the canopy was assumed, adopting the corresponding equation from Leuning *et al.* (1995):

$$U_{(j)} = U_{(0)} \exp(-k_U LAI_{cum}(j)), \quad (13)$$

where  $U_{(0)}$  is the wind speed above the canopy,  $k_U$  is an extinction coefficient for wind speed and  $LAI_{cum(j)}$  is the cumulative  $LAI$  (from top downwards).

## 2.2. COMPARISON WITH OTHER MODELS OF CANOPY GAS EXCHANGE

As mentioned already in Leuning *et al.* (1995), “there is now significant convergence in the structure of multilayer models and the algorithms used by various authors”. The mechanistic photosynthesis model by Farquhar and others (Farquhar *et al.*, 1980; Farquhar & Von Caemmerer, 1982; Harley & Tenhunen, 1991) has become standard by now, whereas different approaches are followed to model stomatal conductance, which still awaits a mechanistic model description. The majority of modellers (Baldocchi & Harley, 1995; Baldocchi & Meyers, 1998; Falge *et al.*, 1996, 1997; Leuning *et al.*, 1995; Su *et al.*, 1996; Tenhunen *et al.*, 1994) uses equations derived from the one presented by Ball *et al.* (1987), which “appears to explain 70–80% of the variation in most data sets” (Berry *et al.* 1998; Nikolov *et al.*, 1995), although model parameters need to be adjusted as the soil dries out beyond some threshold level (Baldocchi, 1997; Sala & Tenhunen, 1996). There is also *consensus* concerning the division of the canopy into sunlit and shaded leaf area, which avoids the overestimation of canopy assimilation, when mean irradiance is used (De Pury & Farquhar, 1997; Spitters, 1986). Goudriaan (1977, 1988) has further simplified the theory of radiative transfer as presented above, although at the expense of flexibility, since the simplified model does not allow the leaf angle distribution to be a function of canopy height (Goudriaan & Van Laar, 1994). A frequently used modelling approach (Baldocchi & Harley, 1995; Baldocchi & Meyers, 1998), very similar to the one presented here, has been described by Norman (1979). More elaborate models of radiative transfer consider specular reflection (Myneni *et al.*, 1989; Royer *et al.*, 1999), penumbral effects (Oker-Blom, 1984) and even account for the three-dimensional nature of canopy architecture (Cescatti, 1997a, b; Falge *et al.*, 1997; Wang & Jarvis, 1990). The equations for the leaf energy balance are generally accepted, the various ap-

proaches differing only with regard to the solution method [see Paw U (1987) for a comparison]. Contrary to the previous points, which may be considered common features of current multilayer models, only a few models exist, which simulate the profiles of air temperature,  $CO_2$  and  $H_2O$  partial pressure over and within canopies (Baldocchi, 1992; Finnigan, 1985; Goudriaan, 1977; Meyers & Paw U, 1987; Raupach, 1988). Most canopy models arbitrarily assume, as in the present case, that the profiles of  $CO_2$ ,  $H_2O$  and air temperature are constant within the canopy (Leuning *et al.*, 1995; Falge *et al.*, 1997; Tappeiner & Cernusca, 1991, 1998; Tenhunen *et al.*, 1994), which has been shown to yield only small errors in the estimation of canopy assimilation (Baldocchi, 1992).

## 2.3. MODEL PARAMETERIZATION

The extinction coefficient for wind speed ( $k_U$ ) was assumed to be 0.5, according to Leuning *et al.* (1995). Leaf scattering coefficients were taken as 0.2, 0.8 and 0.04 for the PPFD, NIR and long-wave waveband, respectively (Goudriaan & Van Laar, 1994) and soil reflection coefficients as 0.1, 0.25 and 0.02, respectively (Goudriaan, 1977). Parameters of the leaf model were derived from literature as indicated in Tables 1 and 2. The parameter  $P_{ml}(T_{ref})$  of the reference data in Table 2 has been adapted from the one presented in Harley & Tenhunen (1991) to give a ratio of 0.668 between  $P_{ml}$  and  $V_{cmax}$  at 20°C leaf temperature (see below).  $R_{dark}(T_{ref})$  in Table 1 has been calculated assuming a ratio of 0.015 between  $R_{dark}$  and  $V_{cmax}$  (Collatz *et al.*, 1991).

## 2.4. SITE AND STAND CHARACTERISTICS

Site, as well as stand-specific data used for the simulations have been entirely adopted from Baldocchi & Meyers (1998). The soybean canopy thus is 1 m tall and has an  $LAI$  of  $4.75 \text{ m}^2 \text{ m}^{-2}$ . The leaf angle distribution is spherical, leaves having a characteristic leaf dimension of 0.1 m and being distributed randomly within the canopy.

## 3. Results and Discussion

### 3.1. THE RATIO BETWEEN $P_{ml}$ AND $V_{cmax}$ RE-EXAMINED

When Leuning (1997) scaled the data by Wullschleger (1993), collected at leaf temperatures

TABLE 1

Parameters of the combined stomatal conductance/photosynthesis model for soybean (*Glycine max*), except for those describing the temperature dependency of  $P_{ml}$  (see Table 2). For abbreviations and symbols refer to the appendix

Parameter	Units	Value	Reference
$K_C(T_{ref})$	Pa	19.42	Badger & Collatz (1977)
$\Delta H_a(K_C)$	J mol <sup>-1</sup>	65 000	Badger & Collatz (1977)
$K_O(T_{ref})$	Pa	12 554.2	Badger & Collatz (1977)
$\Delta H_a(K_O)$	J mol <sup>-1</sup>	36 000	Badger & Collatz (1977)
$\tau(T_{ref})$	—	2 838.1	Jordan & Ogren (1984)
$\Delta H_a(\tau)$	J mol <sup>-1</sup>	- 28 990	Jordan & Ogren (1984)
$V_{cmax}(T_{ref})$	$\mu\text{mol m}^{-2} \text{s}^{-1}$	55.04	Harley & Tenhunen (1991)
$\Delta H_a(V_{cmax})$	J mol <sup>-1</sup>	74 600	Harley & Tenhunen (1991)
$\Delta H_d(V_{cmax})$	J mol <sup>-1</sup>	200 000	Harley & Tenhunen (1991)
$\Delta S(V_{cmax})$	J K <sup>-1</sup> mol <sup>-1</sup>	635	Harley & Tenhunen (1991)
$R_{dark}(T_{ref})$	$\mu\text{mol m}^{-2} \text{s}^{-1}$	0.82	Calculated according to Collatz <i>et al.</i> (1991)
$\Delta H_a(R_{dark})$	J mol <sup>-1</sup>	53 000	Baldocchi & Meyers (1998)
$\alpha$	mol CO <sub>2</sub> mol photons <sup>-1</sup>	0.055	Baldocchi & Meyers (1998)
$G_{fac}$	—	10	Baldocchi & Meyers (1998)
$G_{min}$	mmol m <sup>-2</sup> s <sup>-1</sup>	10	Baldocchi & Meyers (1998)

TABLE 2

Parameters describing the temperature dependency of  $P_{ml}$  according to eqn (5). Data from the column denoted "Reference" are those by Harley & Tenhunen (1991) for soybean (*Glycine max*). The three scenarios refer to  $P_{ml}$  being taken proportional to  $V_{cmax}$  at any leaf temperature (Scenario I), and the temperature optimum of  $P_{ml}$  being shifted 3°C to lower (Scenario II), respectively higher temperatures (Scenario III), compared with the actual data of soybean. For abbreviations and symbols refer to the appendix

Parameter	Units	Values			
		Reference	Scenario I	Scenario II	Scenario III
$P_{ml}(T_{ref})$	$\mu\text{mol m}^{-2} \text{s}^{-1}$	36.77	36.74	43.38	37.47
$\Delta H_a(P_{ml})$	J mol <sup>-1</sup>	62 600	74 600	136 985	62 554
$\Delta H_d(P_{ml})$	J mol <sup>-1</sup>	200 000	200 000	166 518	135 400
$\Delta S(P_{ml})$	J K <sup>-1</sup> mol <sup>-1</sup>	637.0	635.0	554.1	430.3

between 13 and 35°C, to a common temperature of 20°C [Fig. 1(a)], he was doing alright from a theoretical point of view, accounting for the strong temperature dependency of both  $P_{ml}$  and  $V_{cmax}$ . Practically though, applying one set of parameters to the whole variety of species amounts to assuming that the temperature response of  $P_{ml}$  and  $V_{cmax}$  is the same for all C<sub>3</sub> species. This is unlikely to be true, due to the fact that at least the temperature response of  $P_{ml}$  differs among species (Armond *et al.*, 1978;

Hikosaka, 1997; Nolan & Smillie, 1976) and moreover, also varies with growth conditions, especially temperature (Björkman *et al.*, 1980; Hikosaka, 1997; Sayed *et al.*, 1989). Leuning (1997) indeed showed that the shape of the temperature response of  $P_{ml}$  and  $V_{cmax}$  strongly influences the slope of the relationship between the two parameters, which varied between 2.16 and 2.68 in the examples he gave, and without doubt, other parameter sets, leading to even more differing results, may be found in the literature. There

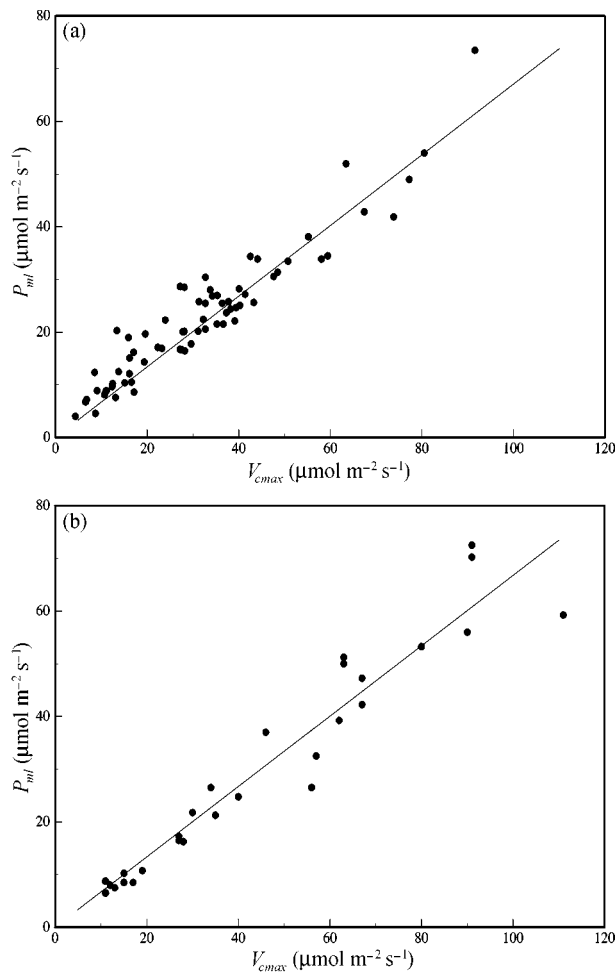


FIG. 1. Relationship between the maximum rate of carboxylation ( $V_{cmax}$ ) and the potential rate of RuBP regeneration ( $P_{m1}$ ) at a reference temperature of 20°C. (a) Data from Wullschleger (1993) scaled to the reference temperature as presented in Leuning (1997). (b) Data from Wullschleger (1993) actually measured at a leaf temperature of 20°C. Lines represent linear regressions forced through the origin [slope = 0.671,  $R^2 = 0.87$  and slope = 0.668,  $R^2 = 0.92$  in (a) and (b) respectively]. Values expressed in terms of  $J_{max}$  in Wullschleger (1993) have been transformed to  $P_{m1}$ , assuming that four electrons are sufficient to regenerate one molecule of RuBP (Harley & Tenhunen, 1991).

is no way to scale all the species compiled by Wullschleger (1993) to a common temperature, since only a minority of the publications re-examined contains information on the species-specific temperature response of  $P_{m1}$  and  $V_{cmax}$ . Fortunately though, the original data of Wullschleger (1993) contain 28 species, shown in Fig. 1(b), whose parameters have actually been determined at a leaf temperature of 20°C. The slopes of the data as compiled by Leuning (1997),

using the parameter set by Harley *et al.* (1992), and of those 28 species, are virtually the same (0.671 and 0.668, respectively, or if using  $J_{max}$  instead of  $P_{m1}$ : 2.68 and 2.67, respectively). Whether this is true due to a coincidence or whether this proves that the parameters by Harley *et al.* (1992) are the universal ones, which apply for all C<sub>3</sub> species, is a speculation. The fact is that the slope of the relationship between  $P_{m1}$  (resp.  $J_{max}$ ) and  $V_{cmax}$  as established by Leuning (1997), using the parameters by Harley *et al.* (1992), seems to hold, although Wohlfahrt *et al.* (1999) recently presented a data set of 30 species from semi-natural mountain grasslands, which are characterized by a significantly smaller slope.

### 3.2. THE TEMPERATURE RESPONSE OF $P_{m1}$

The shape of the temperature response of  $P_{m1}$  is determined by three parameters  $\Delta H_a$ ,  $\Delta H_d$  and  $\Delta S$ , as it can be seen from eqn (6), whereas the parameter  $P_{m1}(T_{ref})$  acts solely as a factor determining the absolute values of  $P_{m1}$  [eqn (5)] and thus represents an ideal tool for scaling  $P_{m1}$  (Leuning *et al.*, 1995; Wohlfahrt *et al.*, 1998). At low temperatures  $P_{m1}$  rises exponentially, since deactivation due to high temperature, mediated by the value of the denominator of eqn (5), is close to unity. As the temperature rises, the denominator of eqn (5) becomes increasingly greater than unity and causes the slope of the temperature response to decrease until activation, mediated by the exponential term in the numerator of eqn (5), and deactivation are in balance and the temperature optimum is reached. At even higher temperatures deactivation predominates and  $P_{m1}$  decreases (Schoolfield *et al.*, 1981; Sharpe & DeMichele, 1977).

The actual temperature response of  $P_{m1}$  for soybean, as well as those of the three scenarios, respectively their deviation from the reference, are shown in Fig. 2(a) and (b). The parameters of the four curves have been chosen in such a way that they intersect at the same value at 20°C, which corresponds to 0.668  $V_{cmax}$  (see the previous section). In Scenario I it is assumed that this ratio is maintained at any temperature. There is little evidence that  $P_{m1}$  behaves in such a way; in fact in many studies, using gas exchange



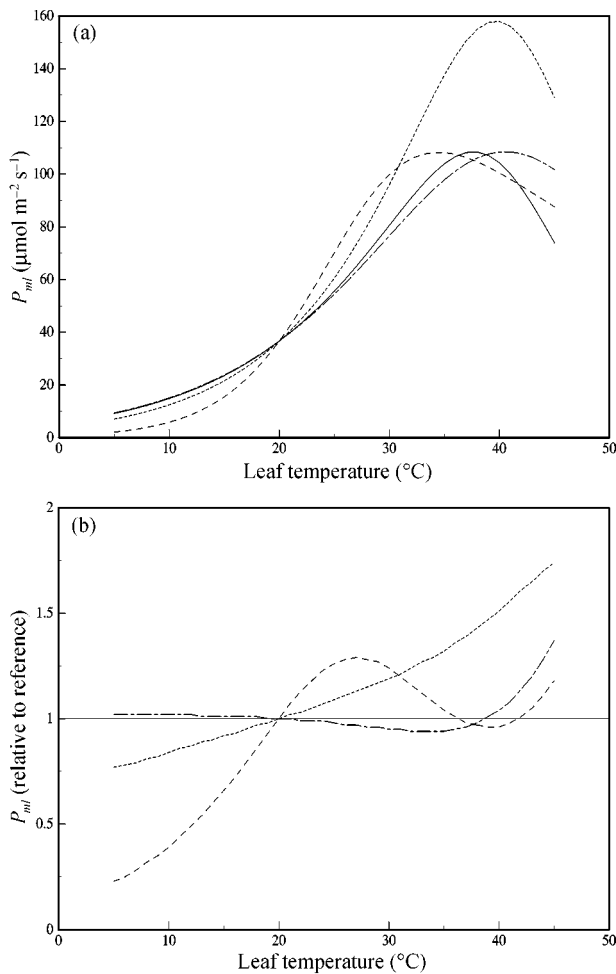


FIG. 2. Temperature response of the potential rate of RuBP regeneration ( $P_{ml}$ ). "Reference" represents the data of soybean (*Glycine max*) from Harley & Tenhunen (1991) (—). The three scenarios refer to  $P_{ml}$  being taken proportional to  $V_{cmax}$  at any leaf temperature [Scenario I (· · · ·)], and the temperature optimum of  $P_{ml}$  being shifted 3 $^{\circ}\text{C}$  to lower [Scenario II (- - -)], respectively higher temperatures [Scenario III (- · - ·)], compared to the actual temperature response of soybean.

techniques, the temperature optimum of  $P_{ml}$  is reported to be reached at lower temperatures compared with  $V_{cmax}$  (Harley & Baldocchi, 1995; Harley & Tenhunen, 1991; Harley *et al.*, 1992; Niinemets & Tenhunen, 1997; Wohlfahrt *et al.*, 1999). Although Hikosaka (1997) presents a data set for *Eucalyptus pauciflora*, re-calculated from Kirschbaum & Farquhar (1984), where the temperature response of  $P_{ml}$  is very similar to that of  $V_{cmax}$ . On a speculative note, this might be regarded as an evolutive adaptation, since assimilation is limited by the regeneration of RuBP, and thus  $P_{ml}$ , *inter alia* under low levels of PPFD

(Farquhar *et al.*, 1980; Woodrow & Berry, 1988), which in natural environments are often accompanied by low temperatures due to a reduced heat load. Despite all this Scenario I represents a real simplification in the sense of Leuning (1997), since  $P_{ml}$  may be determined by the means of a single parameter, the ratio between  $P_{ml}$  and  $V_{cmax}$ . Scenario I is characterized by a maximum which is almost 50% higher than the reference [Fig. 2(a)]. This causes the slope to be increasingly steeper than the reference as temperatures deviate from 20 $^{\circ}\text{C}$ , causing an underestimation at temperatures below 20 $^{\circ}\text{C}$  and an overestimation at higher temperatures [Fig. 2(b)]. Scenarios II and III aim at simulating the effects of an acclimation of electron transport to low (resp. high) temperatures, being characterized by shift in the temperature optimum. Many studies (Armond *et al.*, 1978; Björkman *et al.*, 1980; Sayed *et al.*, 1989) have reported such adaptations according to the prevailing environmental conditions, especially temperature, even over time-scale of days (Quinn, 1988). Below 20 $^{\circ}\text{C}$  and up to approximately 27 $^{\circ}\text{C}$ , Scenario II, which is characterized by a 3 $^{\circ}\text{C}$  shift in the temperature optimum to lower temperatures [Fig. 2(a)], exhibits the largest deviations from the reference, but tends to reapproximate the reference at temperatures above 27 $^{\circ}\text{C}$  [Fig. 2(b)]. In Scenario III, the temperature optimum has been shifted 3 $^{\circ}\text{C}$  to higher temperatures [Fig. 2(a)]. This causes only minor deviations from the reference within the range of 5–38 $^{\circ}\text{C}$ . Only at temperatures exceeding 38 $^{\circ}\text{C}$ , does Scenario III tend to overestimate the reference [Fig. 2(b)].

### 3.3. IMPLICATIONS FOR LEAF PHOTOSYNTHETIC RATES

Following the theory developed by Farquhar *et al.* (1980) and others, photosynthesis is either saturated with respect to RuBP, where carboxylation is limited by the respective partial pressures of  $\text{CO}_2$  and  $\text{O}_2$  at the sites of carboxylation and the kinetic properties of RUBISCO ( $W_C$ ), or limited by the rate at which RuBP is regenerated in the integrated Calvin cycle ( $W_J$ ). The latter is usually limited by electron transport and thus depends on the availability of photosynthetically active radiation and the intrinsic

properties of the thylakoid membrane, which in turn depend upon temperature. Alterations of the temperature response of  $P_{ml}$  thus do affect net photosynthesis only if they either cause carboxylation to shift from RuBP saturation to RuBP limitation by reducing  $W_J$  below  $W_C$  and vice versa or, in the case carboxylation is limited by RuBP regeneration ( $W_J < W_C$ ), by modifying the extent of this limitation.

This is illustrated in Figs 3 and 4, which show the temperature dependency of net photosynthesis,  $W_C$  and  $W_J$  at saturating ( $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and non-saturating PPFD ( $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), respectively. At saturating PPFD (Fig. 3), changes in the temperature response of  $P_{ml}$  do not affect photosynthesis, except for Scenario II, despite changes in the temperature response of  $W_J$ , because assimilation in these cases is always limited by RUBISCO activity ( $W_C$ ). In Scenario II the considerably decreased values of  $P_{ml}$  at lower temperatures (Fig. 2), cause carboxylation rate to shift from RuBP saturation to RuBP limitation at temperatures below  $15^\circ\text{C}$  [Fig. 3(d)], which results in the observed lower photosynthetic rates at temperatures below  $15^\circ\text{C}$  [Fig. 3(c)]. Similar effects on the temperature

response of net photosynthesis, arising from transitions between RuBP saturation and RuBP limitation, have also been reported for *Eucalyptus pauciflora* and *Larrea divaricata* by Hikosaka (1997).

At low, non-saturating PPFD (Fig. 4) the situation is different, since assimilation is almost entirely limited by RuBP regeneration. Therefore, any alteration in  $P_{ml}$ , given that it is transformed into a change of  $W_J$ , will affect the assimilation rate, either by modifying the extent to which  $W_J$  limits carboxylation or in the case  $W_J$  increases above  $W_C$ , by causing carboxylation to shift from RuBP limitation to RuBP saturation. Surprisingly, such alterations in  $W_J$  are detectable, if at all, only at low temperatures [Fig. 4(b), (d) and (f)]. The reason for this can be seen from the temperature dependency of  $P_m$  as illustrated in Fig. 5. The light response of  $P_m$  [which is equal to  $J$  as used in Farquhar *et al.* (1980) by  $J/4$ ] follows a rectangular hyperbola (Farquhar *et al.*, 1980), increasing linearly with PPFD until saturation is reached, as described by eqn (4). In eqn (4) only  $P_{ml}$ , the rate obtained at saturating PPFD, varies with temperature, leading to small differences in  $P_m$  at low and large

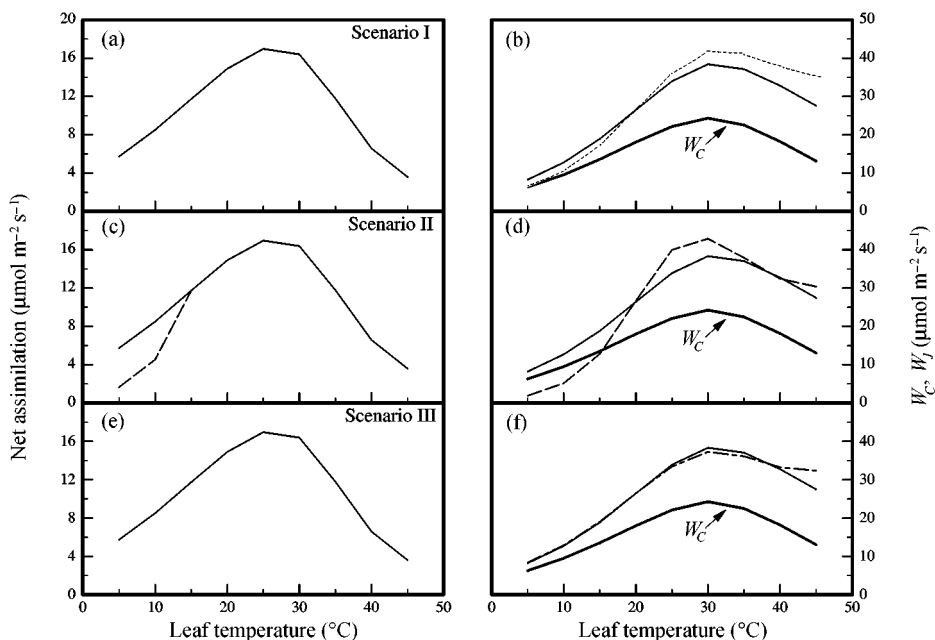


FIG. 3. Temperature response of net photosynthesis [(a), (c), (e)] and the RuBP-saturated ( $W_C$ ) and RuBP-limited ( $W_J$ ) rates of carboxylation [(b), (d), (f)] at a photosynthetic photon flux density (PPFD) of  $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$  and ambient  $\text{CO}_2$  partial pressure (35 Pa). Scenario I, II and III are compared with the reference in the top, middle and bottom panels, respectively. Symbols are the same as in Fig. 2, except for the solid bold lines, which represent  $W_C$ .

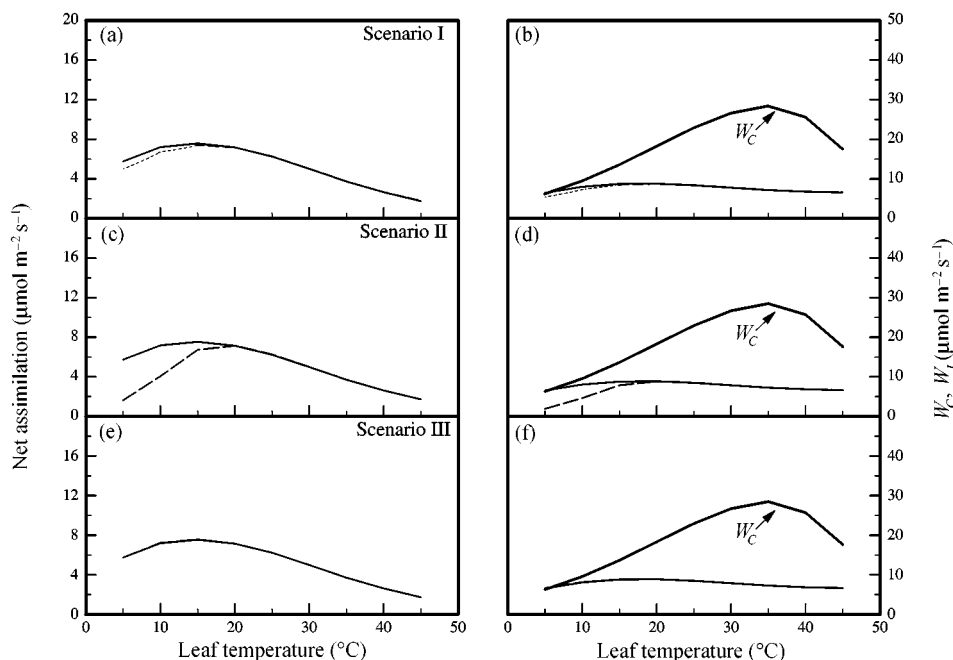


FIG. 4. Temperature response of net photosynthesis [(a), (c), (e)] and the RuBP-saturated ( $W_C$ ) and RuBP-limited ( $W_J$ ) rate of carboxylation [(b), (d), (f)] at a photosynthetic photon flux density (PPFD) of  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$  and ambient  $\text{CO}_2$  partial pressure (35 Pa). Scenarios I, II and III are compared with the reference in the top, middle and bottom panels, respectively. Symbols are the same as in Fig. 2, except for the solid bold lines, which represent  $W_C$ .

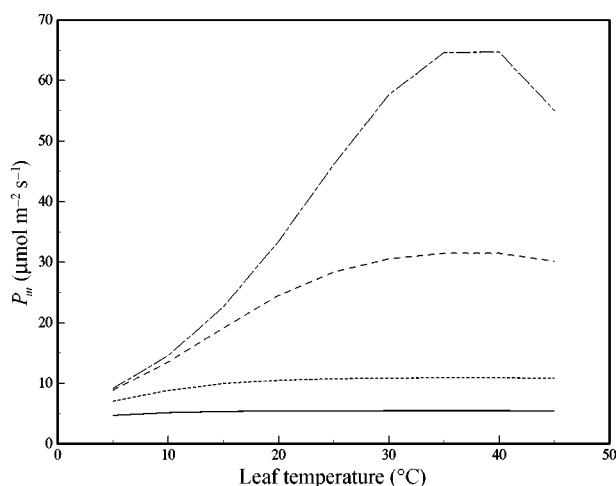


FIG. 5. Temperature response of  $P_m$ , the  $\text{CO}_2$ -saturated rate of photosynthesis at any given irradiance and temperature (Harley & Tenhunen, 1991), at four different photosynthetic photon flux densities (PPFD). 100  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (—); 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (.....); 600  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (---); 1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (-.-.).

differences at high PPFD, as temperature varies (Fig. 5). At low PPFD,  $P_m$  does not exhibit an optimum response to temperature, as it is observed for high irradiances, but rather tends to

increase linearly with temperature until a level of saturation, depending on incident radiation, is reached (Fig. 5). Differences in  $P_{mI}$  will thus only be transformed into  $P_m$  when  $P_{mI}$  is small, which is the case at low temperatures, as it is observed in Fig. 4(b), (d) and (f). Since at higher temperatures, virtually no differences between the reference and the three scenarios exist with respect to  $C_i$  (data not shown), this is clearly the reason, as is evident from eqn (3), for the lack of differences with regard to  $W_J$  at higher temperatures [Fig. 4(b), (d) and (f)].

At high leaf temperatures, especially beyond the temperature optimum of photosynthesis, effects of alterations in the temperature response of  $P_{mI}$  are furthermore expected to be small, since an increasingly larger part of the carboxylated  $\text{CO}_2$  is lost by respiration (Farquhar *et al.*, 1980; Farquhar & Von Caemmerer, 1982), which increases exponentially with temperature (Amthor, 1994; Harley & Tenhunen, 1991; Ryan *et al.*, 1994).

Since deviations in the temperature response of  $P_{mI}$  affect photosynthesis of soybean mainly at low leaf temperatures, the question arises,

whether this is true only for soybean, a plant species adapted to comparatively warmer environments, or true also for the plant species from cold environments, i.e. from arctic or alpine regions. To examine this, the same sensitivity analysis as presented above for soybean (Figs 3 and 4), was performed using a parameter set obtained by Wohlfahrt *et al.* (1999) for several forbs from mountain grasslands in the Eastern Alps. Despite being characterized by a considerably lower temperature optimum of  $P_{ml}$  as compared with soybean (30.7 vs. 37.6°C), the effects on net photosynthesis (Fig. 6) were substantially the same as for soybean, underlining the generality of the observed effects.

#### 3.4. IMPLICATIONS FOR CANOPY PHOTOSYNTHESIS

Whether, and to what extent, canopy assimilation is affected by alterations in the temperature response of  $P_{ml}$ , depends upon the environmental driving forces, as discussed in the previous section, and the percentage of leaves concerned by these, since the micro-climatic conditions within

the canopy differ between sunlit and shaded leaves and vary spatially with canopy depth.

Due to the contrasting attenuation of direct and diffuse light (Goudriaan, 1977), two extreme sky conditions, with significant consequences for the radiative transfer within the canopy, may be distinguished: a completely overcast sky, where no direct light occurs, and a clear sky, with a high (80%) percentage of direct light. To assess the effects of leaf temperature on canopy assimilation further the overcast and clear day scenarios were combined with three air temperature scenarios, of 15, 25 and 30°C, respectively (since leaf temperatures were modelled solving their energy balance, their temperatures deviate from that of the air, though not more than 2°C in any of the tested scenarios).

Figure 7 shows the profiles of PPFD for the overcast and clear-day scenario, at the time of maximum solar elevation. The clear-day scenario is characterized by a bimodal distribution of light within the canopy (Spitters, 1986). Sunlit leaves receive both direct and diffuse radiation and are thus characterized by high photon flux densities

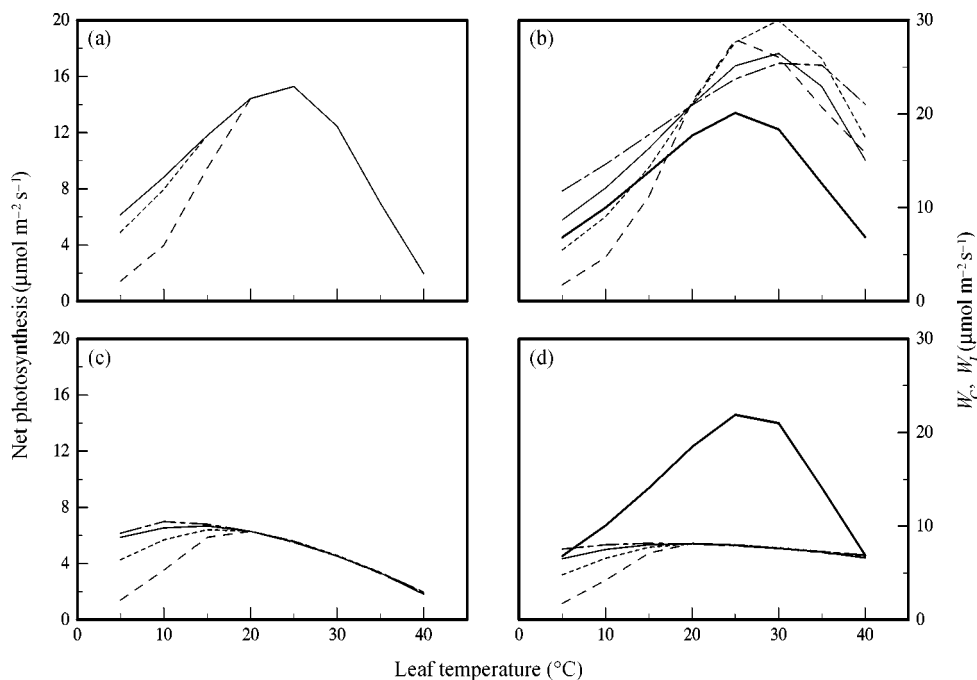


FIG. 6. Temperature response of net photosynthesis [(a), (c)] and the RuBP-saturated ( $W_c$ ) and RuBP-limited ( $W_j$ ) rate of carboxylation [(b), (d)] using the parameters given for forbs from mountain grasslands by Wohlfahrt *et al.* (1999). Simulations were carried out at a photosynthetic photon flux density (PPFD) of 1500 [(a), (b)] and 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  [(c), (d)] and an ambient  $\text{CO}_2$  partial pressure of 35 Pa. Symbols are the same as in Fig. 2, except for the solid bold lines in (b), and (d), which represent  $W_c$ .

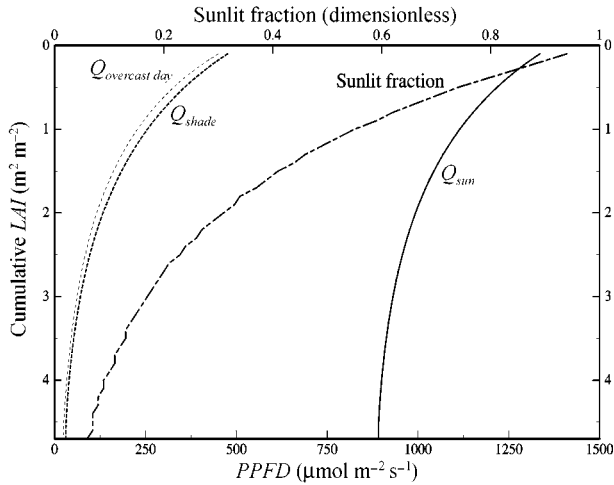


FIG. 7. Vertical profiles, as a function of the cumulative leaf area index (*LAI*), of the photosynthetic photon flux density (PPFD) incident on sunlit ( $Q_{sun}$ ) and shaded leaves ( $Q_{shade}$ ), as well as the fraction of sunlit leaves (sunlit fraction) on a typical clear day and PPFD incident on all leaves on a completely overcast day ( $Q_{overcast}$ ), for the time of maximum solar elevation on Julian Day 245.

even deep in the canopy ( $> 900 \mu\text{mol m}^2 \text{s}^{-1}$ ), whereas shaded leaves receive diffuse radiation only, which decreases to values around the light compensation point near the soil surface. The fraction of sunlit leaves decreases exponentially with canopy depth. On an overcast day all incoming radiation is diffuse, leading to a profile equal to that of diffuse radiation on a clear day. These profiles correspond well with what can be found in literature for canopies of similar *LAI* and a spherical leaf angle distribution (e.g. Leuning *et al.*, 1995), and may thus be considered typical for clear and completely overcast days.

The effects these scenarios have on the profile of net photosynthesis are depicted in Fig. 8. As it may be expected from the previous section, alterations in  $P_{m1}$ , as simulated in the three scenarios, have no effect on the photosynthetic rate of sunlit leaves on a clear day [Fig. 8(d)–(f)]. The reason for this can be seen from Fig. 9 which is the same as Fig. 8, but shows the RuBP saturated and

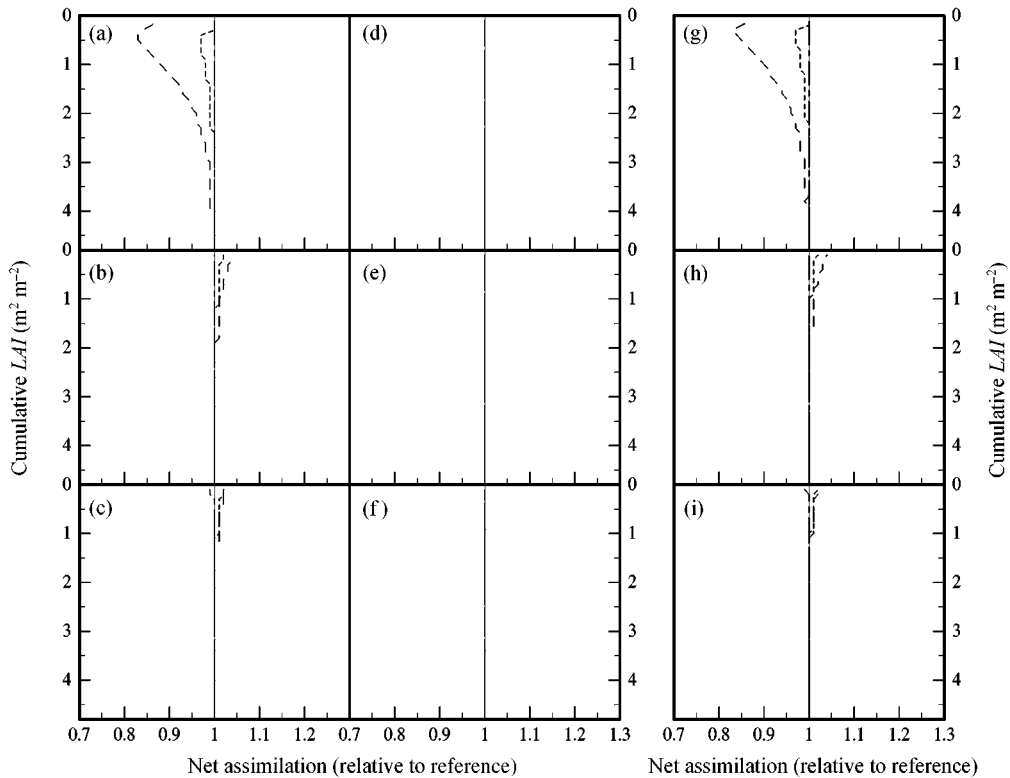


FIG. 8. Vertical profiles, as a function of the cumulative leaf area index (*LAI*), of net assimilation, expressed in relative terms of net assimilation obtained when using the reference parameters from Table 2. Simulations were carried out for the time of maximum solar elevation on Julian Day 245. (a)–(c) and (d)–(f) refer to shaded and sunlit leaves, respectively, on a clear day and (g)–(i) to all leaves on an overcast day. Air temperatures within the canopy were set to 15°C [(a), (d), (g)], 25°C [(b), (e), (h)] and 30°C [(c), (f), (i)]. Symbols are the same as in Fig. 2.

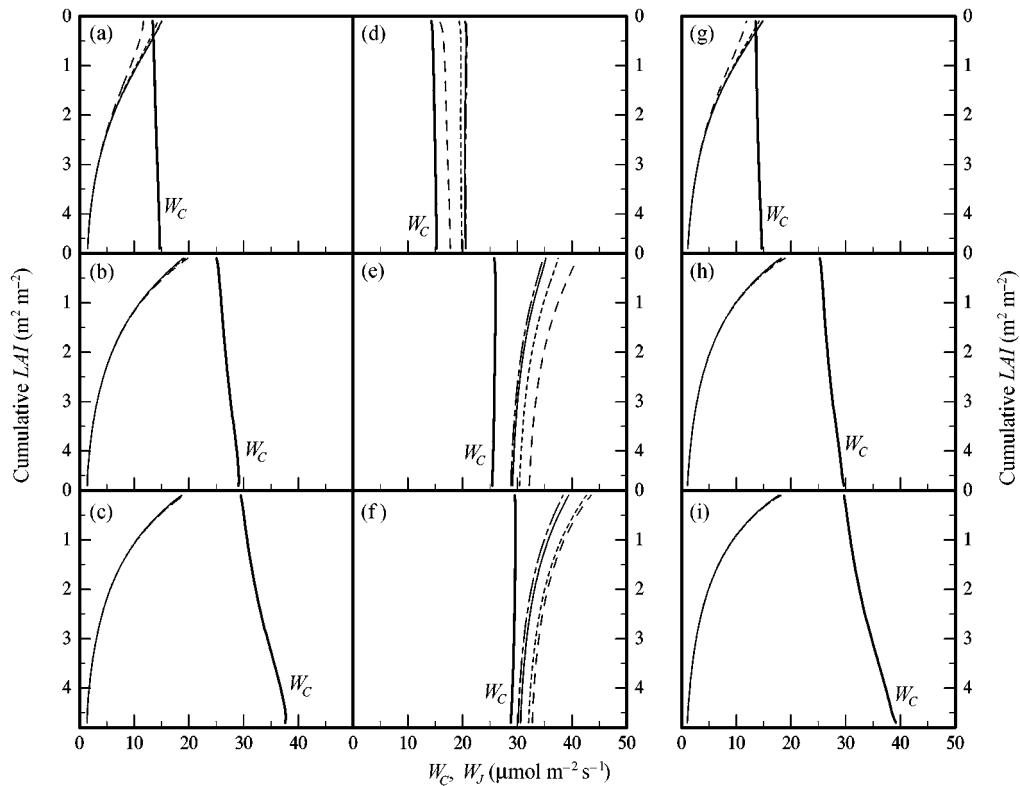


FIG. 9. Vertical profiles, as a function of the cumulative leaf area index ( $LAI$ ), of the RuBP-saturated ( $W_C$ ) and the RuBP-limited ( $W_J$ ) rate of carboxylation. Simulations were carried out for the time of maximum solar elevation on Julian Day 245. (a)–(c) and (d)–(f) refer to shaded and sunlit leaves, respectively, on a clear day and (g)–(i) to all leaves on an overcast day. Air temperatures within the canopy were set to 15°C [(a), (d), (g)], 25°C [(b), (e), (h)] and 30°C [(c), (f), (i)]. Symbols are the same as in Fig. 2, except for the solid bold lines, which represent  $W_C$ .

limited rates of carboxylation,  $W_C$  and  $W_J$ , respectively. Assimilation of sunlit leaves, over the entire canopy profile, is saturated with respect to RuBP and thus unaffected by  $W_J$ , which varies between the reference and Scenarios I–III [Fig. 9(d)–(f)] but without causing carboxylation to shift from RuBP saturation to limitation. In contrast, photosynthesis of shaded leaves, on a clear as well as an overcast day, is affected by the alterations in  $P_{ml}$ , since assimilation is limited by RuBP regeneration, except for the uppermost canopy layers. The effects on photosynthesis of shaded leaves are small for the 25 and 30°C scenarios [Fig. 8(b), (c), (h) and (i)], but in the case of the 15°C scenario a decrease in photosynthesis up to 5% for Scenario I and 20% for Scenario II [Fig. 8(a) and (g)] is observed. Here again applies, what has been discussed in the previous section: at low, non-saturating light intensities, effects of alterations in the temperature response

of  $P_{ml}$  are larger at low temperatures, since at low levels of PPFD,  $P_m$  exhibits a saturation type response to temperature and is thus more sensitive to changes in  $P_{ml}$  when  $P_{ml}$  is small, which is the case at low temperatures. No effects on  $W_J$  can be detected for Scenario III, since deviation from the reference is almost negligible at temperatures below 38°C in this case (Fig. 2). In the uppermost canopy layers, photosynthesis of shaded leaves shifts from RuBP limitation to RuBP regeneration, except for Scenario II, which remains RuBP limited [Fig. 9(a) and (g)], due to the considerably reduced values of  $P_{ml}$  at 15°C (Fig. 2). This is also the cause for the photosynthesis rate of Scenario II to re-approximate the reference in the uppermost canopy layers, as shown in Fig. 8(a) and (g). All this corresponds well with the findings of Baldocchi (1993), who reports photosynthesis of sunlit leaves of a similar soybean canopy to be saturated with respect

to RuBP and shaded leaves to be limited by RuBP regeneration throughout the canopy profile.

Summing up the contribution of sunlit and shaded leaves over the different canopy layers to whole canopy assimilation, results on a clear day in almost no changes for Scenarios I and III, and a 3% reduction for Scenario II at an air temperature of 15°C [Fig. 10(a)]. This decrease in canopy assimilation must be attributed solely to the shaded leaves, since the photosynthetic rates of sunlit leaves remain unchanged [Fig. 8(a)–(c)]. The portion of shaded leaves in the upper region of the canopy, where reductions in net photosynthesis of shaded leaves up to 20% occur

[Fig. 8(a)], although quite small (Fig. 7), causes the observed marginal reductions in canopy assimilation [Fig. 10(a)]. For the overcast day scenario [Fig. 10(b)] the above-mentioned effects have a larger proportional impact, since all leaves receive diffuse radiation only, causing canopy assimilation to decrease about 8% for Scenario II at 15°C. This holds also for canopies where even during clear days both shade and sun leaves are limited by the rate of RuBP regeneration, as has been reported by Baldocchi (1993) for a broadleaf forest.

#### 4. Conclusion

The present paper shows that a simplified leaf model parameterization, either by taking  $P_{ml}$  proportional to  $V_{cmax}$  at any leaf temperature (Scenario I), or by selecting inappropriate temperature-dependent parameters for  $P_{ml}$  from literature (Scenario II and III), may critically affect the resulting predictions of net photosynthesis at the leaf, but less at the canopy level. Deviations from the real temperature response of  $P_{ml}$  at high leaf temperatures, as simulated in Scenario I, affect leaf carbon gain much less as compared with deviations at low leaf temperatures, as simulated in Scenario II. The impact of the above-mentioned deviations on whole canopy photosynthesis increases with the proportion of leaf area limited by the rate of RuBP regeneration, i.e. generally with the fraction of shaded leaves. These findings can be generalized, insofar as they have been shown to be equally valid not only for soybean, but also for cold-adapted plant species from mountain grasslands.

This work was conducted within the framework of the EU-TERI-project ECOMONT (Project No. ENV4-CT95-0179), coordinated by Alexander Cernusca (Universität Innsbruck, Austria). Helpful comments on an earlier version of the paper were contributed by Alessandro Cescatti.

#### REFERENCES

- AMTHOR, J. S. (1994). Scaling CO<sub>2</sub>-photosynthesis relationships from the leaf to the canopy. *Photosynthesis Res* **39**, 321–350.
- ARMOND, P. A., SCHREIBER, U. & BJÖRKMAN, O. (1978). Photosynthetic acclimatisation in the desert shrub *Larrea divaricata*. II. Light harvesting efficiency and electron transport. *Plant Physiol.* **61**, 411–415.

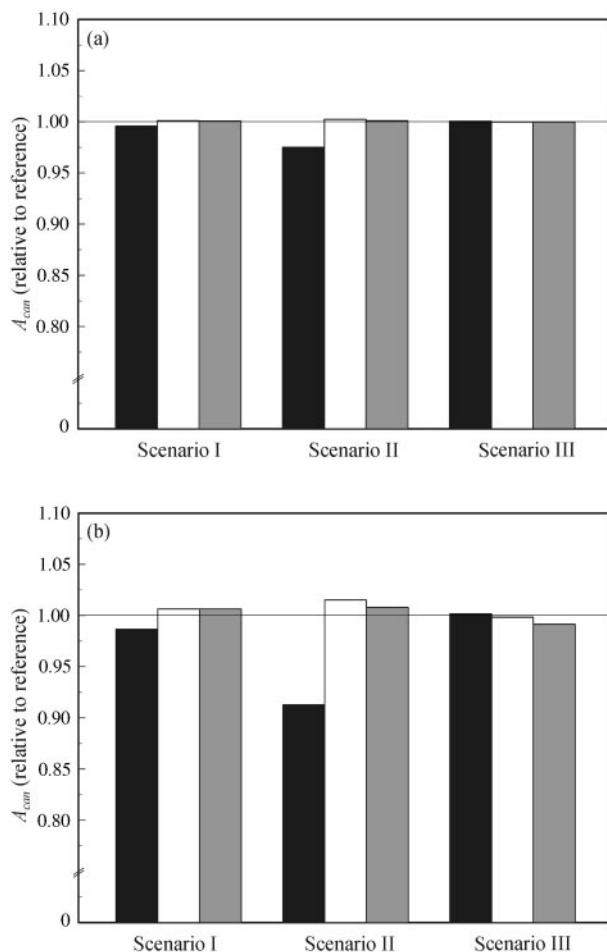


FIG. 10. Whole canopy net assimilation ( $A_{can}$ ) on a clear (a) and a completely overcast (b) day at the time of maximum solar elevation on Julian Day 245. Results are expressed in relative terms of net assimilation obtained when using the reference parameters from Table 2. (■) 15°C; (□) 25°C; (■) 30°C.

- BADGER, M. R. & COLLATZ, G. J. (1977). Studies on the kinetic mechanism of ribulose-1,5-bisphosphate carboxylase and oxygenase reactions, with particular reference to the effect of temperature on kinetic parameters. *Year Book Carnegie Institute Washington* **76**, 355–361.
- BALDOCCHI, D. D. (1992). A Lagrangian random walk model for simulating water vapor, CO<sub>2</sub> and sensible heat flux densities and scalar profiles over and within a soybean canopy. *Boundary Layer Meteorol.* **61**, 113–144.
- BALDOCCHI, D. D. (1993). Scaling water vapour and carbon dioxide exchange from leaves to canopy: rules and tools. In: *Scaling Physiological Processes: Leaf to Globe* (Ehleringer, J. R. & Field, C. B., eds), pp. 77–116. San Diego: Academic Press.
- BALDOCCHI, D. D. (1997). Measuring and modelling carbon dioxide and water vapor exchange over a temperate broad-leaved forest during the 1995 summer drought. *Plant Cell Envir.* **20**, 1108–1122.
- BALDOCCHI, D. D. & MEYERS, T. (1998). On using eco-physiological, micrometeorological and biogeochemical theory to evaluate carbon dioxide, water vapor and trace gas fluxes over vegetation: a perspective. *Agric. For. Met.* **90**, 1–25.
- BALL, J. T., WOODROW, I. E. & BERRY, J. A. (1987). A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: *Progress in Photosynthesis Research* (Biggens, J., ed.), Vol. IV, pp. 221–224. Dordrecht: Martinus Nijhoff.
- BERRY, J. A., COLLATZ, G. J., DENNING, A. S., COLELLO, G. D., FU, W., GRIVET, C., RANDALL, D. A. & SELLERS, P. J. (1998). SiB2, a model for simulation of biological processes within a climate model. In: *Scaling-up: from Cell to Landscape* (Van Gardingen, P. R., Foody, G. M. & Curran, P. J., eds), pp. 347–369. Society of Experimental Biology Seminar Series, Vol. 63, Cambridge: Cambridge University Press.
- BJÖRKMAN, O., BADGER, M. R. & ARMOND, P. A. (1980). Response and adaptation of photosynthesis to higher temperatures. In: *Adaption of Plants to Water and High Temperature Stress* (Turner, N. C. & Kramer, P. J., eds), pp. 233–249. New York: John Wiley & Sons Inc.
- BRUTSAERT, W. (1984). *Evaporation into the Atmosphere: Theory, History, and Applications*. Boston: D. Reidel Publishing.
- CAMPBELL, G. S. & NORMAN, J. M. (1998). *An Introduction to Environmental Biophysics*, 2nd edn. New York: Springer-Verlag.
- CERNUSCA, A., BAHN, M., BAYFIELD, N., CHEMINI, C., FILLAT, F., GRABER, W., ROSSET, M., SIEGWOLF, R., TAPPEINER, U. & TENHUNEN, J. (1998). (1998). ECOMONT—a combined approach of field measurements and process-based modelling for assessing effects of land-use changes in mountain landscapes. *Ecol. Modell.* **113**, 167–178.
- CERNUSCA, A., TAPPEINER, U., BAHN, M., BAYFIELD, N., CHEMINI, C., FILLAT, F., GRABER, W., ROSSET, M., SIEGWOLF, R. & TENHUNEN, J. (1996). ECOMONT—Ecological effects of land use changes on European terrestrial mountain ecosystems. *Pirineos* **147–148**, 145–172.
- CESCATTI, A. (1997a). Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. I. Model structure and algorithms. *Ecol. Model.* **101**, 263–274.
- CESCATTI, A. (1997b). Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. II. Model testing and application in a Norway spruce stand. *Ecol. Model.* **101**, 275–284.
- COLLATZ, G. J., BALL, J. T., GRIVET, C. & BERRY, J. A. (1991). Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agric. For. Met.* **54**, 107–136.
- DE PURY, D. G. G. & FARQUHAR, G. D. (1997). Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant Cell Env.* **20**, 537–557.
- DE WIT, C. T. (1965). *Photosynthesis of Leaf Canopies*. Agricultural Research Report no. 663. Wageningen: Pudoc.
- FALGE, E. M. (1997). Die Modellierung der Kronendachtranspiration von Fichtenbeständen (*Picea abies* (L.) KARST.). Ph. D. Thesis, University of Bayreuth, Germany. *Bayreuther Forum Ökologie*, **48**.
- FALGE, E., GRABER, W., SIEGWOLF, R. & TENHUNEN, J. D. (1996). A model of the gas exchange of *Picea abies* to habitat conditions. *Trees* **10**, 277–287.
- FALGE, E., RYEL, R. J., ALSHEIMER, M. & TENHUNEN, J. D. (1997). Effects of stand structure and physiology on forest gas exchange: a simulation study for Norway spruce. *Trees* **11**, 436–448.
- FARQUHAR, G. D. (1979). Models describing the kinetics of ribulose bisphosphate carboxylase–oxygenase. *Arch. Biochem. Biophys.* **193**, 456–468.
- FARQUHAR, G. D. & VON CAEMMERER, S. (1982). Modelling photosynthetic response to environmental conditions. In: *Physiological Plant Ecology, Vol. II, Encyclopedia of Plant Physiology 12B* (Lange, O. L., Nobel, P. S., Osmond, C. B. & Ziegler, H., eds), pp. 549–588. Berlin: Springer-Verlag.
- FARQUHAR, G. D., VON CAEMMERER, S. & BERRY, J. A. (1980). A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta* **149**, 78–90.
- FINNIGAN, J. J. (1985). Turbulent transport in flexible plant canopies. In: *The Forest Atmosphere Interaction* (Hutchinson, B. A. & Hicks, B. B., eds), pp. 443–480. Dordrecht: D. Reidel Publishing.
- GOUDRIAAN, J. (1977). *Crop Micrometeorology: A Simulation Study*. Simulation Monographs, Centre for Agricultural Publishing and Documentation. Wageningen: Pudoc.
- GOUDRIAAN, J. (1988). The bare bones of leaf angle distribution in radiation models for canopy photosynthesis and energy exchange. *Agric. For. Met.* **43**, 155–169.
- GOUDRIAAN, J. & VAN LAAR, H. H. (1994). *Modelling Crop Growth Processes*. Amsterdam: Kluwer.
- HARLEY, P. C. & BALDOCCHI, D. D. (1995). Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. I. Leaf model parameterization. *Plant Cell Env.* **18**, 1146–1156.
- HARLEY, P. C. & TENHUNEN, J. D. (1991). Modelling the photosynthetic response of C<sub>3</sub> leaves to environmental factors. In: *Modelling Crop Photosynthesis—from Biochemistry to Canopy* (Boote, K. J. & Loomis, R. S., eds), pp. 17–39. CSSA Special Publication no. 19. Madison, Wisconsin: American Society of Agronomy and Crop Science Society of America.
- HARLEY, P. C., THOMAS, R. B., REYNOLDS, J. F. & STRAIN, B. R. (1992). Modelling photosynthesis of cotton grown under elevated CO<sub>2</sub>. *Plant Cell Env.* **15**, 271–282.



- HARLEY, P. C., WEBER, J. A. & GATES, D. M. (1985). Interactive effects of light, leaf temperature, CO<sub>2</sub> and O<sub>2</sub> on photosynthesis in soybean. *Planta* **165**, 249–263.
- HIKOSAKA, K. (1997). Modelling optimal temperature acclimation of the photosynthetic apparatus in C<sub>3</sub> plants with respect to nitrogen use. *Ann. Bot.* **80**, 721–730.
- JARVIS, P. G. (1995). Scaling processes and problems. *Plant Cell Env.* **18**, 1079–1089.
- JOHNSON, F., EYRING, H. & WILLIAMS, R. (1942). The nature of enzyme inhibitions in bacterial luminescence: sulfanilamide, urethane, temperature and pressure. *J. Cell. Comp. Physiol.* **20**, 247–268.
- JORDAN, D. B. & OGREN, W. L. (1984). The CO<sub>2</sub>/O<sub>2</sub> specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase. Dependence on ribulose-bisphosphate concentration, pH and temperature. *Planta* **161**, 308–313.
- KIRSCHBAUM, M. U. F. & FARQUHAR, G. D. (1984). Temperature dependence of whole-leaf photosynthesis in *Eucalyptus pauciflora* Sieb. ex Spreng. *Aust. J. Plant Physiol.* **11**, 519–538.
- LEUNING, R. (1997). Scaling to a common temperature improves the correlation between the photosynthesis parameters  $J_{max}$  and  $V_{max}$ . *J. Exp. Bot.* **48**, 345–347.
- LEUNING, R., KELLIHER, F. M., DE PURY, D. G. G. & SCHULZE, E. D. (1995). Leaf nitrogen, photosynthesis, conductance and transpiration: scaling from leaves to canopies. *Plant Cell Env.* **18**, 1183–1200.
- MEYERS, T. P. & PAW U, K. T. (1987). Modelling the plant canopy micrometeorology with higher order closure principles. *Agric. For. Met.* **41**, 143–163.
- MONTEITH, J. L. & UNSWORTH, M. H. (1990). *Principles of Environmental Physics*, 2nd edn. London: Edward Arnold.
- MYNENI, R. B., ROSS, J. & ASRAR, G. (1989). A review on the theory of photon transport in leaf canopies. *Agric. For. Met.* **45**, 1–153.
- NIINEMETS, Ü. & TENHUNEN, J. D. (1997). A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade-tolerant species *Acer saccharum*. *Plant Cell Env.* **20**, 845–866.
- NIKOLOV, N. T., MASSMAN, W. J. & SCHOETTLE, A. W. (1995). Coupling biochemical and biophysical processes at the leaf level: an equilibrium photosynthesis model for leaves of C<sub>3</sub> plants. *Ecol. Model.* **80**, 205–235.
- NOBEL, P. S. (1991). *Physicochemical and Environmental Plant Physiology*. San Diego: Academic Press.
- NOLAN, W. G. & SMILLIE, R. M. (1976). Multi temperature effects on Hill reaction activity of barley chloroplasts. *Biochim. Biophys. Acta* **440**, 461–475.
- NORMAN, J. M. (1979). Modelling the complete crop canopy. In: *Modification of the Aerial Environment of Crops* (Barfield, G., ed.), pp. 249–280. St. Joseph, MI: American Society of Agricultural Engineers.
- OKER-BLOM, P. (1984). Penumbra effects of within-plants and between-plant shading on radiation distribution and leaf photosynthesis: a Monte-Carlo simulation. *Photosynthetica* **18**, 522–528.
- PAW U, K. T. (1987). Mathematical analysis of the operative temperature and energy budget. *J. Therm. Biol.* **12**, 227–233.
- QUINN, P. J. (1988). Effects of temperature on cell membranes. In: *Plants and Temperature* (Long, S. P. & Woodward, F. I., eds), pp. 237–258. Symposium of the Society of Experimental Botany, Vol. 42, Cambridge.
- RAUPACH, M. R. (1988). Canopy transport processes. In: *Flow and Transport in the Natural Environment* (Steffen, W. L. & Denmead, O. T., eds). Berlin: Springer-Verlag.
- REYNOLDS, J. F., TENHUNEN, J. D., LEADLEY, P. W., LI, H., MOORHEAD, D. L., OSTENDORF, B. & CHAPIN, F. S. III (1996). Patch and landscape models of arctic tundra: potentials and limitation. In: *Landscape Function and Disturbance in Arctic Tundra* (Reynolds, J. F. & Tenhunen, J. D., eds), pp. 293–324. Ecol. Studies, Vol. 120. Berlin: Springer-Verlag.
- ROYER, S., CERNUSCA, A., TAPPEINER, U. & ROYER, A. (1999). A model for multi-species grassland canopies. In: *Land-Use-Changes in European Mountain Ecosystems. ECOMONT—Concepts and Results* (Cernusca, A., Tappeiner, U. & Bayfield, N., eds). Blackwell-Wissenschaftsverlag, Berlin (in press).
- RYAN, M. G., LINDER, S., VOSE, J. M. & HUBBARD, R. M. (1994). Dark respiration of pines. *Ecol. Bull.* **43**, 50–63.
- SALA, A. & TENHUNEN, J. D. (1996). Simulations of canopy net photosynthesis and transpiration in *Quercus ilex* L. under the influence of seasonal drought. *Agric. For. Met.* **78**, 203–222.
- SAYED, O. H., EARNSHAW, M. J. & EMES, M. J. (1989). Photosynthetic responses of different varieties of wheat to high temperature. II. Effect of heat stress on photosynthetic electron transport. *J. Exp. Bot.* **40**, 633–638.
- SCHOOLFIELD, R. M., SHARPE, P. J. H. & MAGNUSON, C. E. (1981). Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. *J. theor. Biol.* **88**, 719–731.
- SHARKEY, T. D. (1985). Photosynthesis in intact leaves of C<sub>3</sub> plants: physics, physiology and limitations. *Bot. Rev.* **51**, 53–105.
- SHARPE, P. J. H. & DEMICHELE, D. W. (1977). Reaction kinetics of poikilotherm development. *J. theor. Biol.* **64**, 649–670.
- SMITH, E. (1937). The influence of light and carbon dioxide on photosynthesis. *J. Gen. Physiol.* **20**, 807–830.
- SPITTERS, C. J. T. (1986). Separating the diffuse and direct component of global radiation and its implication for modelling canopy photosynthesis. Part II. Calculation of canopy photosynthesis. *Agric. For. Met.* **38**, 231–242.
- SU, H. B., PAW U, K. T. & SHAW, R. H. (1996). Development of a coupled leaf and canopy model for the simulation of plant-atmosphere interaction. *J. Appl. Meteorol.* **35**, 733–748.
- TAPPEINER, U. & CERNUSCA, A. (1991). The combination of measurements and mathematical modelling for assessing canopy structure effects. In: *Facets of Modern Ecology: Basic and Applied Aspects* (Esser, G. & Overdieck, D., eds), pp. 161–193. Amsterdam: Elsevier.
- TAPPEINER, U. & CERNUSCA, A. (1998). Model simulation of spatial distribution of photosynthesis in structurally differing plant communities in the Central Caucasus. *Ecol. Model.* **113**, 201–223.
- TENHUNEN, J. D. (1999). Model hierarchies for relating vegetation structure, ecosystem physiology, and plant community distribution to landscape water use. In: *Land-use Changes in European Mountain Ecosystems. ECOMONT—Concepts and Results* (Cernusca, A., Tappeiner, U. & Bayfield, N., eds). Blackwell-Wissenschaftsverlag, Berlin (in press).
- TENHUNEN, J. D., SIEGWOLF, R. T. W. & OBERBAUER, S. F. (1994). Effects of phenology, physiology, and gradients in community composition, structure, and microclimate on tundra ecosystem CO<sub>2</sub> exchange. In: *Ecophysiology of Photosynthesis* (Schulze, E. D. & Caldwell, M. M., eds), pp. 431–460. Berlin: Springer-Verlag.

- TENHUNEN, J. D., WEBER, J. A., YOCUM, C. S. & GATES, D. M. (1976). Development of a photosynthesis model with emphasis on ecological applications. II. Analysis of a data set describing the  $P_m$  surface. *Oecologia* **26**, 101–109.
- WANG, Y. P. & JARVIS, P. G. (1990). Description and validation of an array model—MAESTRO. *Agric. For. Met.* **51**, 257–280.
- WEISS, A. & NORMAN, J. M. (1985). Partitioning of solar radiation into direct and diffuse, visible and near-infrared components. *Agric. For. Met.* **34**, 205–213.
- WOHLFAHRT, G., BAHN, M., HORAK, I., TAPPEINER, U. & CERNUSCA, A. (1998). A nitrogen sensitive model of leaf carbon dioxide and water vapour gas exchange: application to 13 key species from differently managed mountain grassland ecosystems. *Ecol. Model.* **113**, 179–199.
- WOHLFAHRT, G., BAHN, M., HAUBNER, E., HORAK, I., MICHAELER, W., ROTTMAR, K., TAPPEINER, U. & CERNUSCA, A. (1999). Interspecific variation of the biochemical limitation to photosynthesis and related leaf traits of 30 species from mountain grassland ecosystems under different land use. *Plant Cell Env.* (in press).
- WOODROW, I. E. & BERRY, J. A. (1988). Enzymatic regulation of photosynthetic  $\text{CO}_2$  fixation in  $\text{C}_3$  plants. *Ann. Rev. Plant Physiol.* **39**, 533–594.
- WULLSCHLEGER, S. D. (1993). Biochemical limitations to carbon assimilation in  $\text{C}_3$  plants—a retrospective analysis of the  $A/C_i$  curves from 109 species. *J. Exp. Bot.* **44**, 907–920.

## APPENDIX

### Symbols and Abbreviations

$A$	net photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$K_C(T_{ref})$	Michaelis–Menten constant for carboxylation at the reference temperature of 293.16 K (Pa)
$A_{can}$	whole canopy net photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$K_O$	Michaelis–Menten constant for oxygenation (Pa)
$C_i$	internal $\text{CO}_2$ partial pressure (Pa)	$K_O(T_{ref})$	Michaelis–Menten constant for oxygenation at the reference temperature of 293.16 K (Pa)
$C_s$	leaf surface $\text{CO}_2$ partial pressure (Pa)	$k_U$	extinction coefficient for wind speed (dimensionless)
$F$	fraction of leaves in leaf angle class (dimensionless)	$LAI$	total leaf area index ( $\text{m}^2 \text{m}^{-2}$ )
$G_{fac}$	stomatal sensitivity coefficient (dimensionless)	$LAI_{cum}$	cumulative leaf area index ( $\text{m}^2 \text{m}^{-2}$ )
$g_{min}$	minimum stomatal conductance ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	$NIR$	near-infrared radiation ( $\text{W m}^{-2}$ )
$g_s$	stomatal conductance ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	$O$	internal $\text{O}_2$ partial pressure (Pa)
$H$	sensible heat loss ( $\text{W m}^{-2}$ )	$O(\beta, \lambda)$	projection of leaves with inclination $\lambda$ into inclination $\beta$ (dimensionless)
$h_s$	leaf surface relative humidity (dimensionless)	$O(\beta', \lambda)$	projection of leaves with inclination $\lambda$ into inclination $\beta'$ (dimensionless)
$I_{fac}$	coefficient representing the degree to which $R_{dark}$ is inhibited in the light (dimensionless)	$P_i$	inorganic phosphate
$j$	subscript indicating canopy layer	$P_m$	$\text{CO}_2$ -saturated photosynthesis rate at any given irradiance and temperature ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$J_{max}$	maximum electron transport capacity ( $\mu\text{mol electrons m}^{-2} \text{s}^{-1}$ )	$P_{ml}$	potential rate of RuBP regeneration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$K_C$	Michaelis–Menten constant for carboxylation (Pa)	$P_{ml}(T_{ref})$	potential rate of RuBP regeneration at the reference temperature of 293.16 K in the absence of any deactivation due to high temperature ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
		$PPFD$	photosynthetic photon flux density ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
		$Q_{abs}$	absorbed short- and long-wave radiation ( $\text{W m}^{-2}$ )
		$Q_{dir}$	downward flux of direct radiation ( $\text{W m}^{-2}$ )
		$Q_{down}$	downward flux of total (direct and diffuse) radiation ( $\text{W m}^{-2}$ )
		$Q_{loss}$	leaf emitted long-wave radiation ( $\text{W m}^{-2}$ )
		$Q_{shade}$	radiation incident on shaded leaves ( $\text{W m}^{-2}$ )
		$Q_{sun}$	radiation incident on sunlit leaves ( $\text{W m}^{-2}$ )
		$Q_{up}$	upward flux of total (direct and diffuse) radiation ( $\text{W m}^{-2}$ )
		$R$	universal gas constant ( $8.31 \text{ m}^3 \text{ Pa mol}^{-1} \text{ K}^{-1}$ )
		$R_{dark}$	dark respiration rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
		$R_{dark}(T_{ref})$	dark respiration rate at the reference temperature of 293.16 K ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )

$R_{day}$	respiration rate from processes other than photorespiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )		limited by inorganic phosphate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
RUBISCO	ribulose-1,5-bisphosphate carboxylase/oxygenase	<i>Greek letters</i>	
RuBP	ribulose-1,5-bisphosphate	$\alpha$	apparent quantum yield of net photosynthesis at saturating CO <sub>2</sub> ( $\text{mol CO}_2 \text{ mol photons}^{-1}$ )
$T_K$	absolute leaf temperature (K)		
$T_{opt}$	temperature optimum ( $^{\circ}\text{C}$ )		
$T_{ref}$	reference temperature (293.16 K)	$\beta$	elevation of sun (radiant)
$U$	wind speed ( $\text{m s}^{-1}$ )	$\beta'$	elevation of nine sky angle classes (radiant)
$V_{cmax}$	maximum rate of carboxylation ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$\Delta H_a$	energy of activation ( $\text{J mol}^{-1}$ )
$V_{cmax}(T_{ref})$	maximum rate of carboxylation at the reference temperature of 293.16 K in the absence of any deactivation due to high temperature ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$\Delta H_d$	energy of deactivation ( $\text{J mol}^{-1}$ )
		$\Delta S$	entropy term ( $\text{J K}^{-1} \text{mol}^{-1}$ )
		$\lambda$	leaf angle (radiant)
$W_C$	RUBISCO-limited rate of carboxylation ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$\lambda E$	latent heat loss ( $\text{W m}^{-2}$ )
$W_J$	RuBP-limited rate of carboxylation, when RuBP regeneration is limited by electron transport ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$\sigma$	leaf scattering coefficient (dimensionless)
$W_P$	RuBP-limited rate of carboxylation, when RuBP regeneration is	$\tau$	RUBISCO specificity factor (dimensionless)
		$\tau(T_{ref})$	RUBISCO specificity factor at the reference temperature of 293.16 K (dimensionless)