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ÉCLAIRE

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Theme: Environment

D12.2 - Documentation of the DO3SE_C model

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1. Executive Summary

This deliverable provides details of a new module that has been developed for use within the DO₃SE modelling scheme that enables the estimation of both total ozone deposition and stomatal ozone uptake assuming a coupling between stomatal conductance (g_{sto}) and net photosynthesis (A_{net}). This allows stomatal ozone uptake to be closely related to three processes that are considered primarily responsible for limiting A_{net} : (i) Rubisco activity (A_c), (ii) the regeneration of ribulose-1,5-bisphosphate (RuBP) which is limited by the rate of electron transport (A_j), and (iii) an inadequate rate of transport of photosynthetic products (most commonly triose phosphate utilization). The rate of A_{net} will determine the demand for CO₂ which in turn is considered to feedback onto the CO₂ supply which is determined by g_{sto} . Theory suggests that g_{sto} will vary to ensure that an optimum supply of CO₂ is provided which at the same time limits H₂O vapour loss from the plant.

This theory is brought into the DO₃SE model by incorporating the formulations of Farquhar et al. (1980), which allow the estimate of A_{net} according to biochemical processes; the core 'Farquhar' model is updated with new and additional formulations that are described in the scientific literature and have shown improvements in the estimation of A_{net} for a range of conditions and species. The coupling between A_{net} and g_{sto} is achieved using the methods first developed by Ball et al. (1987) who discovered an empirical linear relationship, which relates g_{sto} to a combination of A_{net} and environmental parameters, such as leaf surface relative humidity (D_h) and CO₂ concentration (C_a). Again, this core method has been updated to ensure that the most recent developments that improve simulations of g_{sto} in relation to A_{net} are included (i.e. use of (i) CO₂ concentration at the leaf surface, (ii) methods that account for the CO₂ compensation point and (iii) vapour pressure deficit rather than D_h).

The new module also incorporates new methods to estimate leaf temperature (T_{leaf}), which is necessary to determine the rate of leaf biochemical processes as well as the leaf to air differences in atmospheric water status. Care has also been taken to ensure that the methods to estimate the transfer of gases across the leaf boundary layer (CO₂, H₂O vapour and O₃) are modelled consistently.

The resulting A_{net} - g_{sto} module has been incorporated into the DO₃SE model framework (essentially substituting the previous g_{sto} module, which used a multiplicative model to estimate g_{sto} based on Jarvis, 1976). The model has been used in preliminary trial simulations with ECLAIRE experimental data collected in C3, WP10 and WP11 and provides values within an expected range.

Objectives:

To develop a model describing the combined effects of O₃, other atmospheric pollutants and climate on plant CO₂ uptake, net ecosystem exchange (NEE) and C sequestration in soil and vegetation, suitable for linking to existing plant-soil biogeochemistry models.

2. Activities:

- Literature review to identify most appropriate algorithms for incorporation into new $A_{net-g_{sto}}$ module that is fundamentally based on Farquhar et al. (1980) and Ball et al. (1987).
- Identifying the mechanisms by which these algorithms can be incorporated into the existing DO₃SE model framework.
- Preliminary testing of the new model with ECLAIRE experimental data collected in C3, WPs 10 & 11.

3. Results:

- Identification of the algorithms that will together form the new $A_{net-g_{sto}}$ module
- Coding of the new algorithms into the existing DO₃SE model (substituting the existing multiplicative algorithms)
- The new model seems fit-for-purpose to estimate A_{net} , g_{sto} and hence stomatal O₃ flux.

4. Milestones achieved:

MS 55: Application of DOSE_C to develop dose-response relationships

5. Deviations and reasons:

None

6. Publications:

None

7. Meetings:

None

8. List of Documents/Annexes:

Documentation of the DO3SE_C model

1. Coupled photosynthesis-stomatal conductance model ($A_{net-g_{sto}}$)

The objective of the coupled photosynthesis-stomatal conductance model ($A_{net-g_{sto}}$) model is to quantify leaf or canopy scale g_{sto} with the help of easily accessible environmental parameters such as air temperature (T_{air}), ambient CO₂ concentration (c_a) and irradiance (PAR). The $A_{net-g_{sto}}$ model consists of a combination of two separate models, whose main components are outlined below and include i. the empirical $A_{net-g_{sto}}$ model that estimates g_{sto} (Leuning, 1990) and ii. the mechanistic and biochemical Farquhar model (Farquhar et al., 1980) that estimates net carbon assimilation or net photosynthesis (A_{net}).

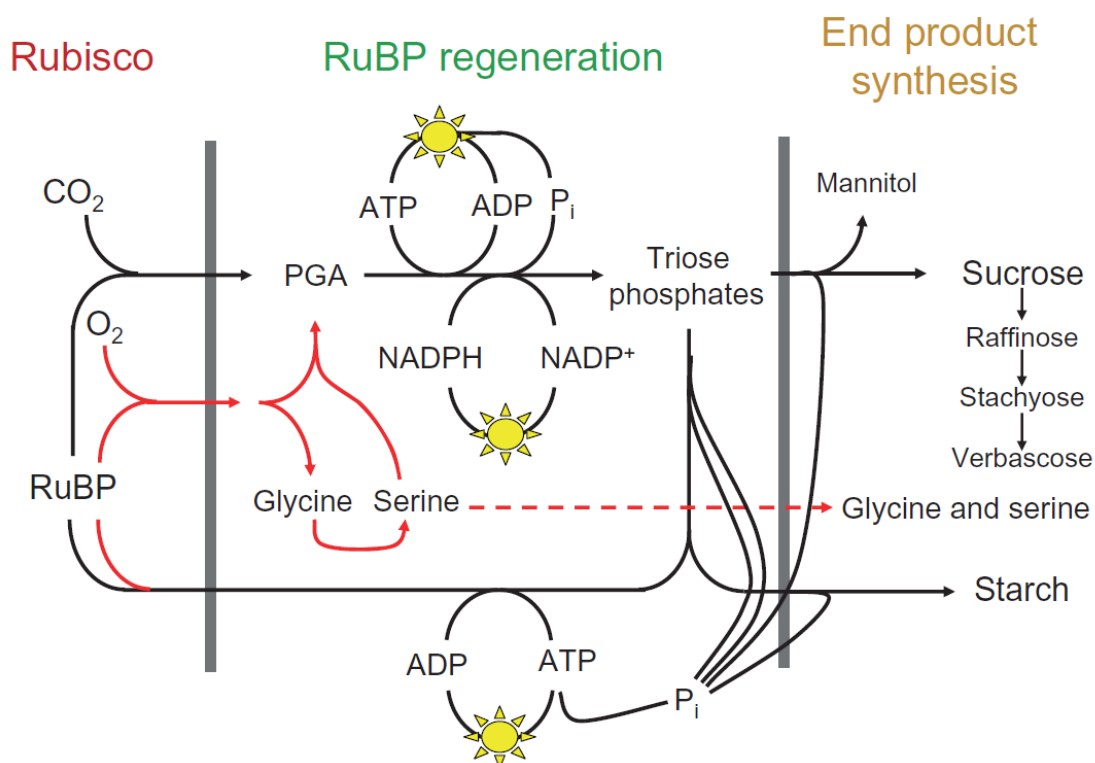
One of the first coupled $A_{net-g_{sto}}$ models was that published by (Leuning, 1990), though some other authors are often cited as the originating sources of the model (e.g. Collatz et al., 1991 and Harley et al., 1992). The models they apparently developed independently are essentially equivalent. The order of description of the $A_{net-g_{sto}}$ modelling here follows the order in which they have to be computed.

2. Biochemical Farquhar model for net photosynthesis (A_{net})

The underlying assumption to Farquhar's 1980 model is that, according to prevailing environmental conditions, either rubisco activity (A_c) or the regeneration of ribulose-1,5-bisphosphate (RuBP), which is limited by the rate of electron transport (A_j), limits photosynthesis. Subsequent to Farquhar's 1980 paper, Harley et al. (1992) identified a third limitation resulting from inadequate rate of transport of photosynthetic products (most commonly this is due to triose phosphate utilization) (A_p). This limit has now become standard in many models of A_{net} (e.g. Sellers et al., 1996; Cox et al., 1999) and is included here. Taking these influences on photosynthesis into account, A_{net} is calculated by determination of the smaller of these theoretical CO_2 assimilation rates, less the rate of dark respiration (R_d) (Farquhar et al., 1980) as in eq. 1 and as described in Figure 1.

$$A_{net} = \min(A_c, A_j, A_p) - R_d \quad 1$$

Figure 1 Scheme showing some of the processes that affect photosynthetic rate. For each of the three panels, any process in that panel will cause the photosynthetic rate to vary with $[\text{CO}_2]$ in the same way. From Sharkey et al. (2007).



Within the literature there are small variations in the precise methods to estimate A_c , A_j and A_p . One important application of our $A_{net-g_{sto}}$ model is that it is to be made with empirical data collected at sites across Europe. This provides the opportunity to use empirical data to parameterise the key components of the model. However, methods to perform this parameterisation should be consistent with these methods used to estimate A_{net} . Therefore our model will follow the eqs. recently described by Sharkey et al. (2007), since these are expected to represent both the most recent formulations as well as those that are consistent with the derivation of key parameters, described in more detail in section 3. The

potential rate of assimilation limited only by Rubisco activity (A_c) is calculated according to Sharkey et al. (2007) as in eq 2.

$$A_c = V_{cmax} \left[\frac{c_i - \Gamma^*}{c_i + K_c \left(1 + \frac{O_i}{K_o}\right)} \right] \quad 2$$

Where V_{cmax} is the maximum rate of Rubisco activity, c_i and O_i are intercellular concentrations of CO_2 and O_2 respectively, K_c and K_o are the Michaelis-Menten coefficients of Rubisco for CO_2 activity (in $\mu\text{mol mol}^{-1}$) and O_2 (in mmol mol^{-1}), respectively, and Γ^* is the CO_2 compensation point in the absence of mitochondrial (dark) respiration.

The potential rate of assimilation when RuBP regeneration is limiting is given in eq. 3.

$$A_j = J \frac{c_c - \Gamma^*}{a \cdot c_c + b \cdot \Gamma^*} \quad 3$$

Where J is the electron transport rate and the parameters a and b denote the electron requirements for the formation of NADPH and ATP, respectively. The exact values differ slightly throughout the literature but are all close to $a = 4$ and $b = 8$ assuming four electrons per carboxylation and oxygenation (Sharkey et al., 2007). J is related to incident photosynthetically active photon flux density (Q) where the light response of a plants photosystem first follows a linear rise with an increase in radiation Q until it reaches an area of saturation where the electron transport rate J approaches its maximum value (J_{max}). Mathematically this is represented by the quadric relationship shown in eq. 4 after Leuning (1990).

$$J = \frac{(J_{max} + \alpha Q) - \sqrt{(J_{max} + \alpha Q)^2 - 4\alpha Q \emptyset J_{max}}}{2 \cdot \emptyset} \quad 4$$

Where α is the quantum yield of electron transport, which determines the slope of the linear rise in the low irradiance regime, and \emptyset is the curvature of the light response curve normally acquired by experimental fitting. The value of α was fixed at $0.3 \text{ mol electrons mol}^{-1} \text{ photon}$, based on an average C3 photosynthetic quantum yield of 0.093 and a leaf absorptance of 0.8 (cf. Medlyn et al., 2002). The value of \emptyset was taken to be 0.90 (Medlyn et al., 2002). These parameter values have only a slight effect on the estimated value of J_{max} .

Finally, the potential rate of assimilation when the utilization of triose phosphate is limiting assimilation (A_p) (i.e. when the chloroplast reactions have a higher capacity than the capacity of the leaf to use the products of the chloroplasts) is estimated rather simply by eq. 5 after Collatz et al. (1991).

$$A_p = 0.5 \cdot V_{cmax} \quad 5$$

The key parameters of the model J_{max} and V_{cmax} , as well as the parameters K_c , K_o and Γ^* , all vary with temperature (Medlyn et al., 2002). J_{max} and V_{cmax} also vary between species, whilst K_c , K_o and Γ^* are considered intrinsic properties of the Rubisco enzyme and therefore can be assumed constant between species (Harley et al., 1986). Due to the temperature effects on the Rubisco enzyme, which catalyses the corresponding process, Γ^* is temperature dependent as well.

The original model of Farquhar et al. (1980) used a purely empirical polynomial from Brooks & Farquhar (1985), which approximated the temperature dependence of these different parameters. Since then many studies have investigated these temperature dependencies more thoroughly; here we follow the rational of Medlyn et al. (2002) who advised using the temperature relationships provided by

Bernacchi et al. (2001) who used an Arrhenius equation to describe the processes and based these functions on measurements made *in vivo* without disturbance of the leaf. The rate of dark respiration R_d , Γ^* and the Michaelis-Menten constants for CO_2 and O_2 (K_c and K_o) are computed using the standard formulations described in eq 6 and 7.

$$P(T) = P_{T,Ref} \cdot \exp\left(\frac{\Delta H \cdot (T - T_{ref})}{T_{ref} \cdot R \cdot T}\right) \quad 6$$

$$P(T) = P_{T,Ref} \cdot \exp\left(\frac{\Delta H_a \cdot (T - T_{ref})}{T_{ref} \cdot R \cdot T}\right) \cdot \frac{1 + \exp\left(\frac{T_{ref} \Delta S - \Delta H_d}{T_{ref} \cdot R}\right)}{1 + \exp\left(\frac{T \Delta S - \Delta H_d}{T \cdot R}\right)} \quad 7$$

where P denotes the different quantities, ΔH is the activation energy, ΔH_d is the deactivation energy and ΔS is entropy for the processes; values for each process follow those given in Bernacchi et al. (2001). In general this formula describes a normal Arrhenius equation modified to incorporate an inhibition term at high temperatures.

The parameters ΔH_a and ΔH_d (energy for activation or deactivation of the process) describe the shape of the response function. Their values are species dependent and have to be fitted to experimental laboratory datasets. Medlyn et al. (2002) give a review of experimental values, Leuning (2002) assesses uncertainties incorporated by using mean values and Wohlfahrt et al. (1999) quantifies the mistakes caused by a wrong parameterisation. The value of the two quantities at $T = 25^\circ\text{C}$, $P_{T,ref}$, can be more easily determined *via* gas exchange measurements. Wullschleger (1993) reviewed several experimental datasets and reports a wide set of values for different species.

In summary, the Farquhar model mathematically quantifies a detailed mechanistic understanding of the biochemical processes in the chloroplasts which govern photosynthesis. It allows for the estimation and calculation of the CO_2 assimilation rate as a function of leaf temperature, irradiance and internal CO_2 concentration.

3. Coupled photosynthesis-stomatal conductance (A_{net} - g_{sto}) model.

Based on earlier observations of the constant ratio of g_{sto} to net CO₂ assimilation rate (A_{net}), Ball et al. (1987) discovered an empirical linear relationship, which relates g_{sto} to a combination of A_{net} and environmental parameters, such as leaf surface relative humidity (D_h) and CO₂ concentration (C_a) as shown in Figure 2.

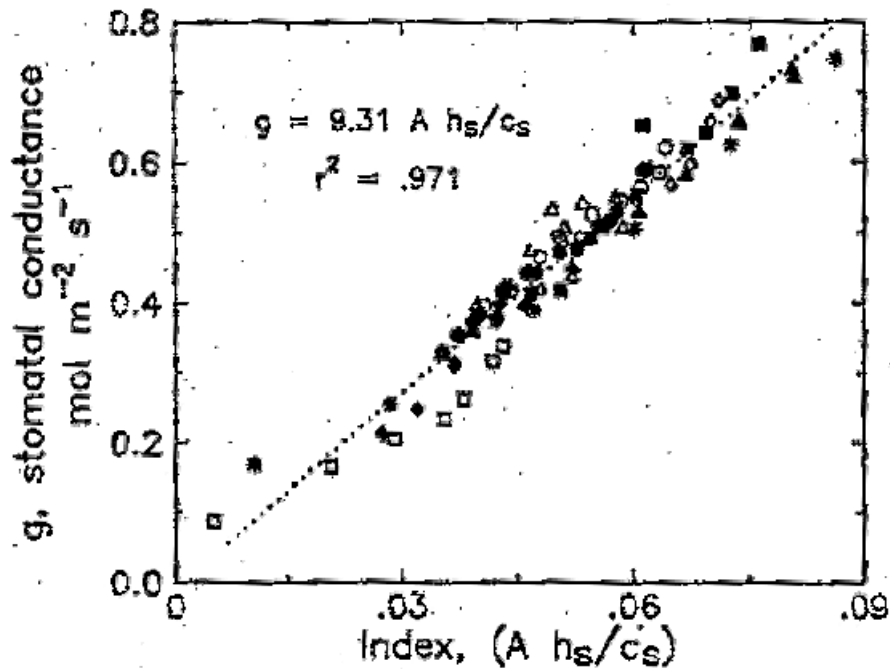


Figure 2. The original BWB model. Stomatal conductance plotted against the BWB Index. From Ball et al. (1987).

Leuning (1990 and 1995) modified the original Ball et al. (1987) relationship so that the function used leaf surface CO₂ concentration (C_s) less the CO₂ compensation point (Γ). They argued that the use of C_s rather than C_a (the CO₂ concentration outside the leaf boundary layer) eliminates complications arising from the transfer of CO₂ through the leaf boundary layer. The introduction of the Γ term allows the correct simulation of stomatal behaviour at low CO₂ concentrations which will tend towards zero as A_{net} becomes minimal close to the Γ . The use of humidity deficit (D_s) rather than relative humidity (D_h) accounts for the fact that stomates respond to humidity deficit rather than surface relative humidity. This response is actually mediated through leaf transpiration (Et_{leaf}), but the close link between Et_{leaf} and D_s means that the use of D_s is appropriate for simulations. Leuning (1995) found that a hyperbolic function for D_s provided an improved humidity response by accounting for the response of D_s to leaf temperature. The resulting formulation they propose is given in eq.8.

$$g_{sto} = g_0 + m \cdot \frac{A_{net}}{[(C_s - \Gamma)(1 + D_s/D_0)]} \quad 8$$

The parameter g_0 is interpreted as the minimal g_{sto} (Leuning, 1990) and is equivalent to the intercept of the regression which is sometimes greater, but often close, to zero. The parameter m is the so called composite sensitivity of g_{sto} to assimilation rate and humidity/CO₂ concentration and can be obtained

via a linear regression of g_{sto} against experimental data from steady state gas exchange measurements. The value of m is surprisingly consistent amongst many different species, and ranges between 5 and 15 (Kosugi et al., 2003) (if all quantities are in units consistent with Ball et al. (1987), m is dimensionless).

Despite the empirical and non-mechanistic nature of this model, it allows for the mathematical quantification of the key environmental feedbacks on stomatal behaviour: (1) Rising irradiance causes stomata to open (incorporated through the positive influence of radiation on A_{net}) until reaching the light compensation point; (2) Rising CO_2 causes stomata to close (incorporated through the negative influence of limited RuBP regeneration); (3) To minimize water loss, stomata close when the transpiration rate rises (incorporated through the response to leaf surface humidity deficit).

However, caution has to be exercised concerning interpretation of the model. It allows for no mechanistic explanation or causal interpretation of the feedbacks between the different parameters (see Aphalo & Jarvis (1993) for a discussion) and is, strictly speaking, only a statistical correlation.

4. Micrometeorological CO_2 supply model

It becomes clear that to calculate g_{sto} , the value of A_{net} is needed and for the calculation of A_{net} it is necessary to know g_{sto} . Baldocchi (1994) found an analytical solution for parts of the problem, and Su et al. (1996) and Nikolov et al. (1995) developed solutions for other sets of coupled equations. Still the vast majority of published models had to use numerical loops to iteratively guess values for different parameters that satisfy the different equations as the available analytic solutions are limited to certain sets of given environmental quantities and model formulations. An additional cross dependency is added to the model when T_{leaf} values have to be computed from T_{air} , as transpiration is a main driving force for leaf surface temperature control. Therefore g_{sto} is needed to calculate T_{leaf} , which can only be calculated when A_{net} is known and for this, again, T_{leaf} is needed (see Nikolov et al. (1995) for a solution).

To facilitate the calculation of the internal (C_i) and surface (C_s) CO_2 from ambient CO_2 concentrations (C_a), a boundary layer model equivalent to that used for calculating the exchange of O_3 across the same physical pathway is used. C_s is calculated as a function of C_a , A_{net} and g_b ; C_i also requires an estimate of g_{sto} . These equations also follow those described in von Caemmerer & Farquhar (1981) and are as described in eq. 9 and 10.

$$c_s = c_a - A_{net} \cdot \frac{1.37}{g_b} \quad 9$$

$$c_i = c_a - A_{net} \frac{1.6 g_b + 1.37 g_{sto}}{g_b \cdot g_{sto}} \quad 10$$

The g_b and g_{sto} conductance values are for water vapour and therefore eqs. 9 and 10 use the factors 1.6 and 1.37 (which are the ratios of the diffusivity of CO_2 and water vapour in still and semi turbulent air respectively).

Finally, the leaf surface humidity deficit D_s also has to be calculated. Firstly, the leaf surface relative humidity (h_s) is calculated as described in Nikolov et al. (1995) and eq. 11.

$$h_s = \frac{g_{sto} \cdot e_i + g_b \cdot e_a}{e_s(T_{leaf}) \cdot (g_{sto} + g_b)} \quad 11$$

where e_i is the water-vapor pressure in the intercellular air space of the leaf, $e_s(T_{leaf})$ is the saturation vapor pressure at leaf temperature and e_a is the vapour pressure in the ambient air (all in Pa). This implies that the air inside the leaf boundary layer is at leaf temperature. In the case of a wet leaf, Eq. 11 does not apply because the air next to a wet surface is normally vapour-saturated and, therefore, $h_s = 1$.

D_s is then calculated using standard equations to convert relative humidity (here leaf surface relative humidity) into leaf to air vapour pressure deficits (here then leaf surface humidity deficit), which rely on temperature (here leaf temperature).

References

- Aphalo, P.J., & Jarvis, P. G. (1993). An analysis of Ball's empirical model of stomatal conductance. *Annals of Botany*, 72, 312–327.
- Baldocchi, D. (1994). An analytical solution for coupled leaf photosynthesis and stomatal conductance models. *Tree Physiology*, 14(7-8-9), 1069–1079. doi:10.1093/treephys/14.7-8-9.1069
- 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 J. Biggens (Ed.), *Progress in photosynthesis research, Vol IV*. Dordrecht: Martinus Nijhoff.
- Bernacchi, C. J., Singaas, E. L., Pimentel, C., Portis Jr, a. R., & Long, S. P. (2001). Improved temperature response functions for models of Rubisco-limited photosynthesis. *Plant, Cell and Environment*, 24(2), 253–259. doi:10.1046/j.1365-3040.2001.00668.x
- Brooks, G.D., & Farquhar, A. (1985). Effect of temperature on the CO₂/O₂ specificity of ribulose-1,5-bisphosphate carboxylase/ oxygenase and the rate of respiration in light. *Planta*, 165, 397–406.
- Collatz, G.J., Ball, J.T., Grivet, C. and Berry, J. A. (1991). Physiological and environmental regulation of stomatal conductance , photosynthesis and transpiration : a model that includes a laminar boundary layer *. *Agricultural and Forest Meteorology*, 54(1074), 107–136.
- Cox, P. M., Betts, R. a., Bunton, C. B., Essery, R. L. H., Rowntree, P. R., & Smith, J. (1999). The impact of new land surface physics on the GCM simulation of climate and climate sensitivity. *Climate Dynamics*, 15(3), 183–203. doi:10.1007/s003820050276
- Farquhar, G.D., von Caemmerer, S., Berry, J. A. (1980). A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta*, 149, 78–90.
- Harley, P. C., Thomas, R. B., Reynolds, J. F., & Strain, B. R. (1992). Modelling photosynthesis of cotton grown in elevated CO₂. *Plant, Cell and Environment*, 15(3), 271–282. doi:10.1111/j.1365-3040.1992.tb00974.x
- Harley, P.C., Tenhunen, J.D., and Lange, O. L. (1986). Use of an analytical model to study limitations on net photosynthesis in *Arbutus unedo* under field conditions. *Oecologia*, 70, 393–401.
- Kosugi, Y., Shibata, S., Kobashi, S., & Caemmerer, V. (2003). Parameterization of the CO₂ and H₂O gas exchange of several temperate deciduous broad-leaved trees at the leaf, 285–301.
- Leuning, R. (1990). MODELING STOMATAL BEHAVIOR AND PHOTOSYNTHESIS OF EUCALYPTUS-GRANDIS. *AUSTRALIAN JOURNAL OF PLANT PHYSIOLOGY*, 17(2), 159–175.
- Leuning, R. (1995). A critical appraisal of a combined stomatal-photosynthesis model for C₃ plants. *Plant, Cell and Environment*, 18(4), 339–355. doi:10.1111/j.1365-3040.1995.tb00370.x
- Leuning, R. (2002). Temperature dependence of two parameters in a photosynthesis model. *Plant, Cell and Environment*, 1205–1210.

- Medlyn, B. E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P. C., Kirschbaum, M. U. F., ... Loustau, D. (2002). Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant, Cell and Environment*, 25(9), 1167–1179. doi:10.1046/j.1365-3040.2002.00891.x
- Medlyn, B. E., Duursma, R. a., Eamus, D., Ellsworth, D. S., Prentice, I. C., Barton, C. V. M., ... Wingate, L. (2011). Reconciling the optimal and empirical approaches to modelling stomatal conductance. *Global Change Biology*, 17(6), 2134–2144. doi:10.1111/j.1365-2486.2010.02375.x
- Nikolov, 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 3 plants. *Ecological Modelling*, 80, 205–235.
- Sellers, P. J., Berry, J. A., Collatz, G. J., Field, C. B., & Hall, F. G. (1992). Canopy reflectance, photosynthesis, and transpiration. III - A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sensing of Environment*, 42(3), 187–216.
- Sellers, P.J., Randall. D.A., Collatz, G.J., Berry, J.A., Field, C.B., Dazlich, D.A., Zhang, C., Collelo, G.D. and Bounoua, L. (1996). A revised land surface parameterisation (SiB2) for atmospheric GCMs. Part I. Model formulation. *Journal of Climate*, 9, 676–705.
- Sharkey, T. D., Bernacchi, C. J., Farquhar, G. D., & Singsaas, E. L. (2007). Fitting photosynthetic carbon dioxide response curves for C(3) leaves. *Plant, Cell & Environment*, 30(9), 1035–40. doi:10.1111/j.1365-3040.2007.01710.x
- 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. *Journal of Applied Meteorology*, 35, 733–748. Retrieved from [http://journals.ametsoc.org/doi/pdf/10.1175/1520-0450\(1996\)035<0733:DOACLA>2.0.CO;2](http://journals.ametsoc.org/doi/pdf/10.1175/1520-0450(1996)035<0733:DOACLA>2.0.CO;2)
- Von Caemmerer, S. & Farquhar, G. D. (1981). Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta*, 153, 376–387.
- Wang, Y., & Leuning, R. (1998). A two-leaf model for canopy conductance , photosynthesis and partitioning of available energy I : Model description and comparison with a multi-layered model. *Agricultural and Forest Meteorology*, 91, 89–111.
- Wohlfahrt, G., Bahn, M., Haubner, E., Horak, I., Michaeler, W., Rottmar, K., ... 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 and Environment*, 22(10), 1281–1296. doi:10.1046/j.1365-3040.1999.00479.x
- Wullschlegel, S. D. (1993). Biochemical Limitations to Carbon Assimilation in C 3 Plants — A Retrospective Analysis of the j Curves from 109 Species. *Journal of Experimental Botany*, 44(262), 907–920.