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LEAFC3-N: Modeling Effects of Drought Stress on Photosynthesis, Stomatal Conductance and Transpiration

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Highlights: LEAFC3-N combines photosynthesis, stomatal conductance, transpiration, leaf energy balance, and leaf nitrogen content. The response to drought is simulated accounting for the effect of leaf water potential on stomatal conductance and of a finite mesophyll conductance on intracellular CO_2 concentration.

Keywords: Photosynthesis, drought stress, water potential, model.

INTRODUCTION

A previous version of LEAFC3-N (Braune et al., 2009) accounts for drought stress based on effects of leaf water potential (Ψ_l) on stomatal conductance (g_{sv}), carboxylation, and electron transport. Mesophyll conductance (g_m) was assumed infinite. However, a finite g_m may significantly affect photosynthesis under drought (Niinemets et al., 2009). Here we re-analyse these patterns by including a finite g_m into LEAFC3-N.

MODEL DESCRIPTION

LEAFC3-N (Müller et al., 2005) extends the LEAFC3 model (Nikolov et al., 1995) of the coupled processes of photosynthesis, stomatal action, transpiration, and leaf energy balance by relating the characteristics V_m, J_m, T_p, φ_a, m, θ, and R_d in the equations below to leaf nitrogen content per leaf area, N_a. For the N_a–dependencies currently used see Braune et al. (2009). Below we list only main model equations related to this study. For further explanation see the references above, and for a complete description of the model and for improvements recently introduced (accounting for different stomata frequencies at each leaf side, dynamic model of plant water transport, advanced solution algorithms, user interface and simulation tools, model extension for a finite g_m) consult documentation and code which are available by request.

$$A_n = A_g\,(1-\Gamma^*/C_c) - R_d, \qquad (1)$$

if $C_c > (1{+}3\alpha_p)\Gamma^*$:

$$\beta A_g^2 - (A_{g,e} + A_{g,p})\,A_g + A_{g,e}\,A_{g,p} = 0, \qquad 0 \le \beta \le 1, \qquad (2)$$

$$\alpha A_{g,e}^2 - (A_{g,c} + A_{g,j})\,A_{g,e} + A_{g,c}\,A_{g,j} = 0, \qquad 0 \le \alpha \le 1, \qquad (3)$$

elseif $C_c \le (1{+}3\alpha_p)\Gamma^*$:

$$\alpha A_g^2 - (A_{g,c} + A_{g,j})\,A_g + A_{g,c}\,A_{g,j} = 0, \qquad 0 \le \alpha \le 1. \qquad (4)$$

$$A_{g,c} = \frac{V_m\,C_c}{C_c + K_c(1+O/K_o)}, \qquad A_{g,j} = \frac{J\,C_c}{\mu_1\,C_c + \mu_2\,\Gamma^*}, \qquad A_{g,p} = \frac{3T_p\,C_c}{C_c - (1+3\alpha_p)\,\Gamma^*}, \qquad (5),(6),(7)$$

$$J = \left[(J_m + \varphi_a\,Q_a) - \sqrt{(J_m + \varphi_a\,Q_a)^2 - 4\theta\varphi_a\,Q_a\,J_m}\,\right]/2\theta, \qquad (8)$$

A_n: net photosynthesis rate; A_g: CO_2 exchange rate defined as the minimum of $A_{g,c}$, $A_{g,j}$, and $A_{g,p}$; $A_{g,c}$, $A_{g,j}$, and $A_{g,p}$: see eqs. (5), (6), (7); C_c: intracellular CO_2 concentration; f_Ψ: function defining a sigmoid response to Ψ_{leaf} (eq.(13)); K_c and K_o: Michaelis-Menten parameters of Rubisco for carboxylation and oxygenation of RuBP, respectively; J: electron transport rate; J_m: light saturated J; O: concentration of O_2; Q_a: absorbed photosynthetic photon flux density; R_d: mitochondrial respiration rate at given incident photosynthetic photon flux density (‘day respiration’); T_p: potential rate of triose phosphate utilisation; V_m: maximum carboxylation rate; α: coefficient defining the smoothness of the transition between $A_{g,c}$ and $A_{g,j}$; α_p: fraction of glycolate carbon not returned to chloroplast; β: coefficient defining the smoothness of the transition between $A_{g,p}$ and $A_{g,e}$; Γ^*: CO_2 compensation point in the absence of R_d; φ_a: quantum yield of electron transport based on Q_a; μ_1 and μ_2: coefficients quantifying the electron requirement for the formation of $NADPH^+$ and ATP in terms of mol electrons per mol CO_2 fixed; θ: curvature coefficient.

$$C_\mathrm{c} = C_\mathrm{a} - A_\mathrm{n} / g_\mathrm{t}, \tag{9}$$

C_c, C_a: concentration of CO_2 at the reaction site in the chloroplast, in the ambient air; g_t: total conductance for CO_2 transport.

$$g_\mathrm{t} = \frac{M_\mathrm{bv}\, g_\mathrm{bv}\, g_\mathrm{sv}\, g_\mathrm{m}}{M_\mathrm{bv}\, g_\mathrm{bv}\, g_\mathrm{sv} + 1.6\, M_\mathrm{bv}\, g_\mathrm{bv}\, g_\mathrm{m} + 1.37\, g_\mathrm{sv}\, g_\mathrm{m}}, \tag{10}$$

g_bv and g_sv: two-sided leaf boundary layer and leaf stomatal conductance, respectively, M_bv: function accounting for the effective portion of g_bv arranged in series with g_sv depending on the ratio of the numbers of stomata on each leaf side.

The stomatal part g_sv of g_t is calculated by a modified Ball et al. (1987) model:

$$\begin{aligned} g_\mathrm{sv} &= m\, f_\Psi\, (A_\mathrm{n} + R_\mathrm{d})\, h_\mathrm{b} / C_\mathrm{b} + g_\mathrm{sv0}, && \textit{if } C_\mathrm{b} \geq 200\ \mu\mathrm{mol\,mol^{-1}} \\ g_\mathrm{sv} &= g_\mathrm{sv}(C_\mathrm{b} = 200\ \mu\mathrm{mol\,mol^{-1}}) && \textit{else}, \end{aligned} \tag{11}$$

$$m = k_{0,\mathrm{m}}\, N_\mathrm{a}^{\,k_{1,\mathrm{m}}}, \tag{12}$$

$$f_\Psi = 1 / \left[1 + (\Psi_\mathrm{l} / \Psi_\mathrm{c})^{k_\Psi} \right], \qquad 0 \leq f_\Psi \leq 1, \tag{13}$$

g_sv0: minimum g_sv; m: coefficient (dimensionless) that defines the combined sensitivity of g_s to A_n, h_b, and C_b; h_b, C_b: relative humidity (decimal fraction) and CO_2 concentration (µmol mol^{-1}) of the air at the leaf surface within the leaf boundary layer, respectively; f_Ψ defines a sigmoid response to Ψ_l; Ψ_c: critical leaf water potential [Pa]; k_Ψ: curvature parameter [dimensionless].

The mesophyll part g_m of g_t is calculated according to Yin et al. (2009):

$$g_\mathrm{m} = g_\mathrm{m0} + \delta\, (A_\mathrm{n} + R_\mathrm{d}) / (C_\mathrm{c} - \Gamma^*), \qquad \textit{if } C_\mathrm{c} > \Gamma^*, \tag{14}$$

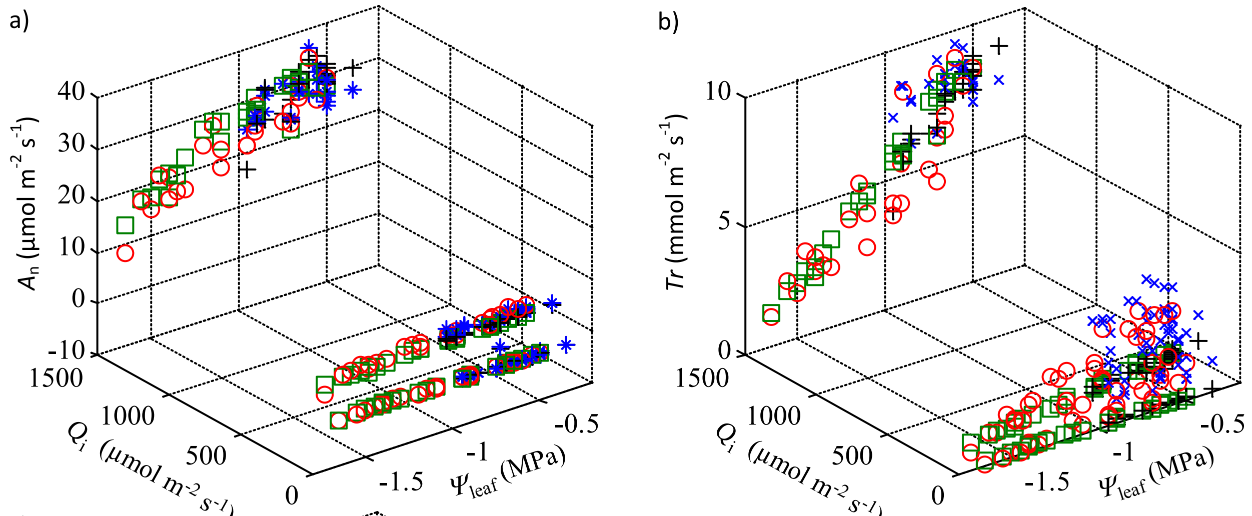
g_m0: minimum g_m; δ: proportionality factor that defines the combined sensitivity of g_m to $A_\mathrm{n} + R_\mathrm{d}$ and C_c.

EXPERIMENTAL DESIGN

Spring barley (*Hordeum vulgare* L., cv. 'Scarlett') was grown in a climate chamber in pots containing sandy loam soil at different treatments of water supply (W1, W2). Wc1 was maintained at optimum soil water content, which corresponds to 60 % of soil water capacity (W_c) or a water content of 23.1 vol. %. Wc2 was dried to 35 % of W_c (or 13.5 vol. %) and then kept on this level. The drought stress period of nine days was started when the visible part of leaf number four of the main tiller had reached a length of 10 cm. Further growth conditions were: incident photon flux density Q_i = 310 µmol m^{-2} s^{-1}, $C_\mathrm{a} \approx$ 360 µmol mol^{-1}, and ambient air humidity $h_\mathrm{a} \approx$ 60 %. On leaves of rank four, the following characteristics required for analyzing the data with the LEAFC3-N model were measured: area, contents of chlorophyll and total nitrogen (N), water potential (Ψ_l), light and CO_2 response curves of net photosynthesis rate. After gas exchange measurements, the leaf blades were quickly covered by plastic sheaths made of thin foil and then cut off at the proximal emersion point at the measurement chamber. The water potential of these leaf parts was then measured using a scholander pressure bomb.

RESULTS AND DISCUSSION

In the present simulation study, the basic parameterization of LEAFC3-N was adopted from Braune et al. (2009). However, the parameters K_c, K_o, V_m, and J_m (respectively the slopes s_v and s_j of the linear relations of V_m and J_m to N_a) were revised as required in case of introducing a finite g_m. Considering corresponding results of Bernacci et al. (2002) and Yin et al. (2009), we re-analyzed the diurnal time course measurements of A_n, Tr, and g_sv given by Braune et al. (2009). The revised parameters introduced on this basis were K_c = 272 µmol mol^{-1}, K_o = 166 mmol mol^{-1} (Bernacci et al., 2002), s_v = 91.62 µmol CO_2 (g N)$^{-1}$, and s_j = 158.6 µmol e$^-$ (g N)$^{-1}$. Further, we derived from that parameterization study with respect to the N_a–dependency of m (eq. (12)): $k_{0,\mathrm{m}}$ = 20.58 m^2 g^{-1} and $k_{1,\mathrm{m}}$ = -0.45, with respect to f_Ψ (eq. (13)): Ψ_c = -1.7 MPa and k_Ψ = 3, and with respect to g_m (eq. (14)): δ = 1.1 and g_m0 = 0.1 mol m^{-2} s^{-1}. Based on this parameterization, the diurnal time courses of A_n, Tr, and g_sv, including the midday depression, could be reproduced well by the new model version that was extended by introducing a finite g_m (eqs. (10) and (14)). No additional effects of Ψ_l on V_m and J_m were assumed as in Braune et al. (2009). This result here was confirmed based on data obtained by the special experimental design described above. With the same parameter values as before, except setting Ψ_c = -1.2 MPa, A_n, Tr, and g_sv simulated for a range of incident photon flux density (Q_i) and Ψ_l agreed quite well with the corresponding measurements (Fig.1, Table 1).



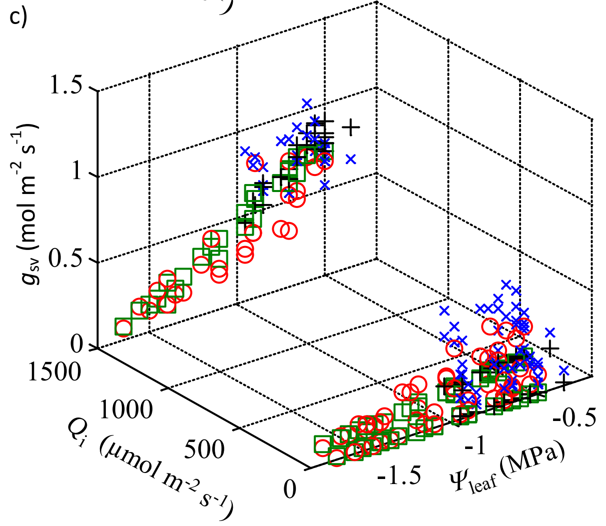


Fig. 1. Simulation results for a) A_n, b) Tr, and c) g_{sv} for a range of Ψ_{leaf} and Q_i; measurements W1 (x), W2 (○) and simulations W1 (+), W2 (□).

Table 1. Linear regression of simulated vs. measured values: **r²**= coefficient of determination **a₁**= slope of regression **a₀**= absolute term of regression

	W	r^2	a_1	a_0
A_n	1	0.97	1.04	-0.390
Tr		0.89	1.09	-1.822
g_{sv}		0.79	1.03	-0.151
A_n	2	0.96	1.09	-0.295
Tr		0.82	1.06	-0.397
g_{sv}		0.78	1.05	-0.023

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