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 CO₂ 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 (Ψl) on stomatal conductance (gsv), carboxylation, and electron transport. Mesophyll conductance (gm) was assumed infinite. However, a finite gm may significantly affect photosynthesis under drought (Niinemets et al., 2009). Here we re-analyse these patterns by including a finite gm 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 Vm, Jm, Ta, ϵa, m, θ, and Rd in the equations below to leaf nitrogen content per leaf area, Na. For the Na-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 gm) consult documentation and code which are available by request.

\[ A_n = A_g (1 - \Gamma^* / C_c) - R_d , \] (1)

\[ \text{if } C_c > (1 + 3 \alpha_p) \Gamma^* : \]
\[ \beta A_g^j - (A_g^c + A_g^j) A_g^c + A_g^c A_g p = 0, \quad 0 \leq \beta \leq 1, \] (2)
\[ \alpha A_g^j - (A_g^c + A_g^j) A_g^c + A_g^c A_g i = 0, \quad 0 \leq \alpha \leq 1, \] (3)

\[ \text{elseif } C_c \leq (1 + 3 \alpha_p) \Gamma^* : \]
\[ \alpha A_g^j - (A_g^c + A_g^j) A_g^c + A_g^c A_g i = 0, \quad 0 \leq \alpha \leq 1. \] (4)

\[ A_g^c = \frac{V_m C_c}{C_c + K_c (1 + O / K_o)}, \quad A_g^j = \frac{J_a^c C_o}{\mu_1 C_c + \mu_2 \Gamma^*}, \quad A_g p = \frac{3 T_p C_c}{C_c - (1 + 3 \alpha_p) \Gamma^*}, \] (5), (6), (7)

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

A_n: net photosynthesis rate; A_g: CO₂ exchange rate defined as the minimum of A_g,c, A_g,i, and A_g,p; see eqs. (5), (6), (7); C_c: intracellular CO₂ concentration; f_a: function defining a sigmoid response to Ψ_l (eq.13); K_c: Michaelis-Menten parameters of Rubisco for carboxylation and oxygenation of RuBP, respectively; J: electron transport rate; J_e,c: light saturated J; O: concentration of O₂; 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,i; α_p: fraction of glycolate carbon not returned to chloroplast; β: coefficient defining the smoothness of the transition between A_g,c and A_g,i; γ: CO₂ compensation point in the absence of Rd; ϵ_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 CO₂ fixed; θ: curvature coefficient.
\[ C_c = C_a - A_n / g_t, \]  
(9)

\[ g_t = \frac{M_m g_{sv} g_m}{M_b g_{sv} + 1.6 M_b g_{sv} + 1.37 g_{sv} g_m}, \]  
(10)

g_{sv} and \( g_m \): two-sided leaf boundary layer and leaf stomatal conductance, respectively, \( M_b \): function accounting for the effective portion of \( g_m \) 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:

\[ g_{sv} = \begin{cases} m f_p (A_n + R_d) h_b / C_b + g_{sv0}, & \text{if } C_b \geq 200 \, \mu\text{mol mol}^{-1} \\ g_{sv} (C_b = 200 \, \mu\text{mol mol}^{-1}) & \text{else}, \end{cases} \]  
(11)

\[ m = k_{n,m} N_{h,m}, \]  
(12)

\[ f_p = \left[ 1 + \left( \Psi' / \Psi'' \right)^{k_p} \right], \]  
(13)

\( g_{sv0} \): coefficient (dimensionless) that defines the combined sensitivity of \( g_t \) to \( A_n \), \( h_b \), and \( C_b \); \( C_c \): relative humidity (decimal fraction) and \( \text{CO}_2 \) concentration (\( \mu\text{mol mol}^{-1} \)) of the air at the leaf surface within the leaf boundary layer, respectively; \( f_p \): defines a sigmoid response to \( \Psi'' \); \( \Psi' \): critical leaf water potential \([\text{Pa}]\); \( k_p \): curvature parameter \([\text{dimensionless}]\).

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

\[ g_m = g_{m0} + \delta (A_n + R_d) / (C_c - \Gamma^*), \]  
(14)

\( g_{m0} \): minimum \( g_m \); \( \delta \): proportionality factor that defines the combined sensitivity of \( g_m \) to \( A_n + R_d \) and \( C_c \).

**EXPERIMENTAL DESIGN**

Spring barley (\emph{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 \( Q_i = 310 \, \mu\text{mol m}^{-2} \text{s}^{-1} \), \( C_c \approx 360 \, \mu\text{mol mol}^{-1} \), and ambient air humidity \( h_b \sim 60 \% \). 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 \((\Psi_c)\), light and \( \text{CO}_2 \) 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 \( K_v, K_m, V_m, \) and \( J_m \) (respectively the slopes \( s_v \), and \( s_j \) of the linear relations of \( V_m \) and \( J_m \) to \( N_3 \) 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 \( K_v = 272 \, \mu\text{mol mol}^{-1}, K_m = 166 \, \mu\text{mol mol}^{-1} \) (Bernacci et al., 2002), \( s_v = 91.62 \, \mu\text{mol CO}_2 \, \text{(g N)}^{-1} \), and \( s_j = 158.6 \, \mu\text{mol CO}_2 \, \text{g}^{-1} \). Further, we derived from that parameterization study with respect to the \( N_3 \)-dependency of \( m \) (eq. (12)): \( k_{n,m} = 20.58 \, \text{m}^2 \, \text{g}^{-1} \) and \( k_{l,m} = -0.45 \), with respect to \( f_p \) (eq. (13)): \( \Psi'' = -1.7 \, \text{MPa} \) and \( k_p = 3 \), and with respect to \( g_m \) (eq. (14)): \( \delta = 1.1 \) and \( g_{m0} = 0.1 \, \text{mol m}^{-2} \text{s}^{-1} \). 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 \( \Psi' \) 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 \( \Psi'' = -1.2 \, \text{MPa}, A_n, Tr, \) and \( g_{sv} \) simulated for a range of incident photon flux density \((Q_i)\) and \( \Psi_t \) agreed quite well with the corresponding measurements (Fig.1, Table 1).
Table 1. Linear regression of simulated vs. measured values:

- \( r^2 \): coefficient of determination
- \( a_1 \): slope of regression
- \( a_0 \): absolute term of regression

<table>
<thead>
<tr>
<th>Variable</th>
<th>W</th>
<th>( r^2 )</th>
<th>( a_1 )</th>
<th>( a_0 )</th>
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</thead>
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<tr>
<td>( A_n )</td>
<td>1</td>
<td>0.97</td>
<td>1.04</td>
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<td>( T_R )</td>
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<td>1.09</td>
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<tr>
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<td>1.03</td>
<td>-0.151</td>
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<tr>
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<td>1.09</td>
<td>-0.295</td>
</tr>
<tr>
<td>( T_R )</td>
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<td>1.06</td>
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<tr>
<td>( g_{sv} )</td>
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<td>1.05</td>
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</tr>
</tbody>
</table>

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LITERATURE CITED


