Role of plant traits on CO2 assimilation and thermal damage avoidance under warmer and drier climates in boreal forests

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1. List of symbols (in alphabetical order)

- $A_L$: Light-limited assimilation rate
- $A_{net}$: Net assimilation rate
- $A_{net,cum}$: Cumulated net assimilation over the growing season
- $A_{net,max}$: Maximum net assimilation over the growing season
- $A_r$: Rubisco-limited assimilation rate
- $c$: Leaf heat capacity
- $c_p$: Heat capacity of air in constant pressure
- $D_L$: Leaf-air vapor pressure difference
- $D_V$: Molecular diffusivity of water vapor in air
- $e_s$: Saturation vapor pressure
- $e_a$: Ambient vapor pressure
- $g_1$: Species-specific stomatal model slope
- $g_b$: Boundary layer conductance
- $g_{cut}$: Cuticular conductance
- $g_{eff}$: Effective conductance
- $g_r$: Radiative conductance
- $G_r$: Grashoff number
- $g_s$: Stomatal conductance
- $H_{av}$: Parameter of $V_{C_{MAK}}-T_l$ curve
- $H_{dv}$: Parameter of $V_{C_{MAK}}-T_l$ curve
- $J_{M_{25}}$: Maximum electron transport rate at 25 °C
- $l_t$: Effective leaf thickness
- $N$: Number of canopy layers
2. APES MODEL

2.1. General description

The APES model is a process-based 1-dimensional multilayer, multi-species forest canopy-soil model, designed especially to describe the interplay between microclimate and vertical structure and functional diversity of boreal forests. The model solves the coupled energy, water and carbon fluxes in the soil-vegetation-atmosphere system using physical and physiological theory.

In APES, leaf temperature ($T_l$) is determined through leaf energy balance, given as
where $C$ is leaf heat capacity, $c_p$ heat capacity of air in constant pressure, $\alpha$ albedo, $\varepsilon$ leaf emissivity, $\sigma$ Stefan-Boltzman constant, $\lambda$ latent heat of vaporization, $D_i$ (mol mol$^{-1}$) non-dimensional vapor pressure difference between leaf and the bulk air outside leaf boundary layer. In the absence of intercepted water on the leaf surface, the net radiation, determined as balance of absorbed SW and net LW radiation (1st and 2nd term in rhs) is consumed mainly in sensible heat exchange, and in latent heat exchange via transpiration. Assuming negligible leaf heat storage change (lhs) and energy consumed in metabolic processes ($\Sigma f_m$) with respect to the other terms of eq. 1, and linearizing the long-wave radiation balance 2, the leaf temperature can be written as:

$$T_L = T_A + \frac{R_n^* - \lambda g_{v,eff} D_L}{c_p (g_b + g_f)}$$ (eq. 2)

where $R_n^* = (1 - \alpha)SW - \varepsilon (LW in - \sigma T_A^4)$ is the isothermal net radiation and $g_f = 4/c_p \varepsilon \sigma T_A^3$ (mol m$^{-2}$ s$^{-1}$) the radiative conductance. The bulk conductance $g_{v,eff}$ (mol m$^{-2}$ s$^{-1}$) represents conductance to water vapor transport through stomata and leaf boundary layer:

$$g_{v,eff} = \frac{g_s g_{b,v}}{g_s + g_{b,v}}$$ (eq. 3)

where $g_s$ is the stomatal and $g_{b,v}$ the boundary layer conductance for water vapor.

$T_i$ is solved separately for sunlit and shaded leaves at each canopy layer (here 100 layers) by equation 2 and 3 coupled with the quantification of the net CO$_2$ assimilation rate ($A_{net}$) based on the Farquhar model 3 and using the stomatal conductance model proposed by 4.

Finally, $A_{net}$ is computed as a minimum of rubisco-limited ($A_v$) and light-limited ($A_j$) rate (equation 4):

$$A_{net} = \min(A_v, A_j) - R_d$$ (eq. 4)

where $R_d$ is the dark respiration rate. In the absence of water stress, the maximum electron transport rate $J_{MAX,25}$ and $R_{L25}$ at reference temperature 25°C are described linearly proportional to maximum carboxylation rate $V_{CMAX,25}$. The temperature responses of all Farquhar- parameters are as in Medlyn, et al. 5. The $V_{CMAX,25}$ varies vertically as response to leaf nitrogen gradient, and is affected by the phenologic state of vegetation as well as the predawn leaf water potential $\Psi_{siL}$. In severe water stress, $V_{CMAX,25}$ and $J_{MAX,25}$ decrease non-linearly as a response to $\Psi_{siL}$ following Kellomaki and Wang 6.

Following 4 $g_s$ is:

$$g_s = g_{cut} + 1.6 \left(1 + \frac{g_1}{P_L}\right) \frac{A_{net}}{c_s}$$ (eq. 5)

where $A_{net}$ is the net CO$_2$ exchange (umol m$^{-2}$ s$^{-1}$), C$_s$ the CO$_2$ mixing ratio (ppm) at leaf surface and $g_{cut}$, the residual (cuticular) conductance (mol m$^{-2}$ s$^{-1}$), and $g_1$ (kPa$^{0.5}$) are parameters related to plant hydraulic traits 4.

To facilitate solution of $T_i$, the photosynthetic active (PAR) and near-infrared (NIR) radiation, and the long-wave balance are computed for each canopy layer 7-8 and the ambient CO$_2$, H$_2$O, T$_A$ and wind (U) profiles computed using 1st-order closure schemes. These microclimatic properties and the leaf-level exchange rates are iteratively solved until convergence. The above-ground and soil processes are coupled through water and heat fluxes and feedbacks between soil and vegetation (rainfall interception, root uptake, feedbacks to leaf physiologic parameters).

2.2. Leaf energy balance, temperature and traits

Figure S1 illustrates how leaf-air temperature difference responds to variation in stomatal and boundary layer conductances given certain ambient conditions. Investigating eq. 1 and 2 reveals the optical properties albedo ($\alpha$) and emissivity ($\varepsilon$), the physical traits affecting boundary-layer conductance, and the physiological properties that regulate stomatal conductance are the primary factors determining $T_l$ for given ambient microclimatic conditions. Consequently, the analysis of $T_l$.
in boreal forests needs to focus on the primary plant traits regulating the $g_b$, $g_s$, and absorption of solar radiation. Figure S1 reveals how the difference between leaf and air temperature substantially increases as stomatal or boundary layer conductance decreases. In forest ecosystems, also the interplay between leaf energy balance and canopy microclimate, canopy structure and soil-to-leaf feedbacks needs to be accounted for. That is why we focused here, as specified in the main document, in the following five traits: maximum carboxylation rate at 25 °C, $V_{\text{CMAX},25}$; the parameters of the stomatal model, stomatal model slope in well-watered conditions $g_1$ and a parameter describing the sensitivity of $g_1$ to soil water potential $\beta_{g1}$; the effective leaf thickness, $l_t$; and the albedo to PAR and NIR, $\alpha_{\text{PAR}}$ and $\alpha_{\text{NIR}}$.

The characteristic leaf dimension $l_t$ (m) is central for controlling $g_b$. It is here computed assuming leaves flat as flat plates exposed to parallel free (subscript fr) and forced (subscript fo) convection; in this case $g_b = 2 * g_{b,fo} + 1.5 * g_{b,fr}$

$$g_{b,v,fo} = 0.664 * \rho * D_v * S_{CV}^{1/3} \frac{(l_t * \frac{\nu}{\mu})^{1/2}}{l_t} \quad (\text{eq. 6})$$

$$g_{b,v,fr} = 0.54 * \rho * D_v * \frac{(G_r * S_{CV})^{1/4}}{l_t} \quad (\text{eq. 7})$$

where $\rho$ is the density of air at 20 °C, $D_v$ is the molecular diffusivity of water vapor air at 20 °C, $S_{CV}$ and $G_r$ are the Schmidt and the Grashof numbers respectively and $U$ is wind speed. The first term accounts for forced and the latter for free convection.

**Fig. S1.** Response of leaf-to-air temperature difference $\Delta T = T_l - T_a$ to stomatal conductance $g_s$ and boundary conductance $g_{b,v}$. Following conditions were used to simulate the leaf temperature: PAR=1000 μmol m$^{-2}$s$^{-1}$, $R_n$=325 W m$^{-2}$, $T_a$= 25 °C, RH=40%, $U$=0.5ms$^{-1}$. The variations in $g_s$ were created by varying leaf effective thickness from 0.01 to 0.20 m and those in $g_b$ by varying $V_{\text{CMAX},25}$ in range 30 – 80 μmol m$^{-2}$s$^{-1}$ and $g_1$ having a value either 2.3 or 5.0, roughly corresponding to variability between boreal coniferous and deciduous tree species.
3. VCMAX and Temperature

Several alternative functions have been proposed to model the temperature dependences of Vcmax and other kinetic parameters of the Farquhar model (see Medlyn, et al. 5 for a review). However, all these equations represent alternative expressions of two basic functions: the Arrhenius function and a peaked function 12, which is essentially the Arrhenius equation modified by a term that describes how conformational changes in the enzyme at higher temperatures start to negate the on-going benefits that would otherwise come from further increasing temperature 5. This formulation is used in APES and is expressed as:

\[ f(T_N) = k_{25} \exp \left( \frac{H_{av}}{R \cdot T_N} \cdot \left( 1 - \frac{T_N}{T_k} \right) \right) \cdot \frac{1 + \exp \left( S_{vv} \cdot T_N - H_{dv} \right)}{1 + \exp \left( S_{vv} \cdot T_k - H_{dv} \right)} \] (eq.8)

The parameters can be interpreted as follows: \( k_{25} \) is the value of VCMAX at temperatures 25 °C; \( T_k \) is the temperature of reference (generally 25 °C) and \( T_N \) is the temperature of interest (i.e. the leaf temperature at this moment) respectively; the \( H_{av} \) gives the rate of exponential increase of the function below the optimum; \( H_{dv} \) describes the rate of decrease of the function above the optimum. \( S_{vv} \) is known as an entropy factor but is not readily interpreted.

Here, we used \( H_{av}, H_{dv} \) and \( S_{vv} \) values as in 5. Figure S2 shows how the VCMAX dependence to \( T_L \) by varying VCMAX,25 from 10 to 80 µmolm⁻²s⁻¹.

![Figure S2](image_url)

Fig. S2. Response of VCMAX as a function of leaf temperature following equation 7 with the parameters as: \( H_{av} = 69.83 \times 10^3 \) Jmol⁻¹, \( H_{dv} = 200 \times 10^3 \) Jmol⁻¹, and \( S_{vv} = 672 \) Jmol⁻¹K⁻¹. The reference temperature is 298.15 K and the gas constant R is 8.31. VCMAX,25 varies within the range 10 – 80 µmolm⁻²s⁻¹.

References


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