forests

Supplementary Material

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_j	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_v	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_{CMAX}-T_L curve
H_{dv}	Parameter of V_{CMAX}-T_L curve
$J_{MAX,25}$	Maximum electron transport rate at 25 °C
l_t	Effective leaf thickness
N	Number of canopy layers

NIR	Near-Infrared Radiation
Pamb	Air pressure
PAR	Photosynthetically Active Radiation
R_d	Dark respiration rate
RH	Relative Humidity
R_n^*	Isothermal net radiation
S_{CV}	Schmidt number
S_{vv}	parameter of V_{CMAX}-T_L curve
SW	Short wave radiation
LW	Long wave radiation
τ	Thermal time constant
ΔT_{90}	Thermal breadth of photosynthesis
T_A	Air temperature
T_{CRIT}	Critical temperature
T_L	Leaf temperature
$T_{L,max}$	Maximum leaf temperature within the warmest 3-days period
T_{max}	Maximum temperature
U	Mean wind speed
U*	Friction velocity
$V_{CMAX,25}$	Maximum carboxylation rate at 25 °C
α_{NIR}	NIR albedo
α_{PAR}	PAR albedo
β	Parameter that accounts for the sensitivity of g_1 to water availability
ε	Leaf emissivity
λ	Latent heat of vaporization
ϱ	Density of air
σ	Stefan Boltzman constant
Ψ_s	Soil water potential
ψ_{SiL}	Predawn leaf water potential

2. APES MODEL

2.1. General description

The APES [1] 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

$$\frac{\partial C T_L}{\partial t} = (1-\alpha)SW + \varepsilon(LWin - \sigma T_L^4) - c_p g_b (T_L - T_A) - \lambda g_{v,eff} D_L - \Sigma f_m \quad \text{(eq. 1)}$$

where C is leaf heat capacity, c_p heat capacity of air in constant pressure, α albedo, ε leaf emissivity, σ Stefan-Boltzman constant, λ latent heat of vaporization, D_L (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 (Σf_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:

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

where $R_n^* = (1-\alpha)SW - \varepsilon(LW_{in} - \sigma T_A^4)$ is the isothermal net radiation and $g_r = 4/c_p \varepsilon \sigma T_A^3$ (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:

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

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

T_L 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):

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

where R_d is the dark respiration rate. In the absence of water stress, the maximum electron transport rate $J_{MAX,25}$ and $r_{d,25}$ 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 Ψ_{siL}. In severe water stress, $V_{CMAX,25}$ and $J_{MAX,25}$ decrease non-linearly as a response to Ψ_{siL} following Kellomaki and Wang [6].

Following [4] g_s is:

$$g_s = g_{cut} + 1.6\left(1 + \frac{g_1}{\sqrt{D_L}}\right)\frac{A_{net}}{C_s} \quad \text{(eq. 5)}$$

where A_{net} is the net CO_2 exchange (μmolm^{-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_L, 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_2O, 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 (α) and emissivity (ε), 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, $V_{CMAX,25}$; 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 β [4, 9]; the effective leaf thickness, l_t; and the albedo to PAR and NIR, α_{PAR} and α_{NIR}.

The characteristic leaf dimension l_t (m) is central for controlling g_b. It is here computed assuming leaves flat as flat plates [10] exposed to parallel free (subscript fr) and forced (subscript fo) convection; in this case $g_b = 2 * g_{b\_fo} + 1.5 * g_{b\_fr}$ [11]

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

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

where ρ 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 Grashoff numbers respectively and U is wind speed. The first term accounts for forced and the latter for free convection.

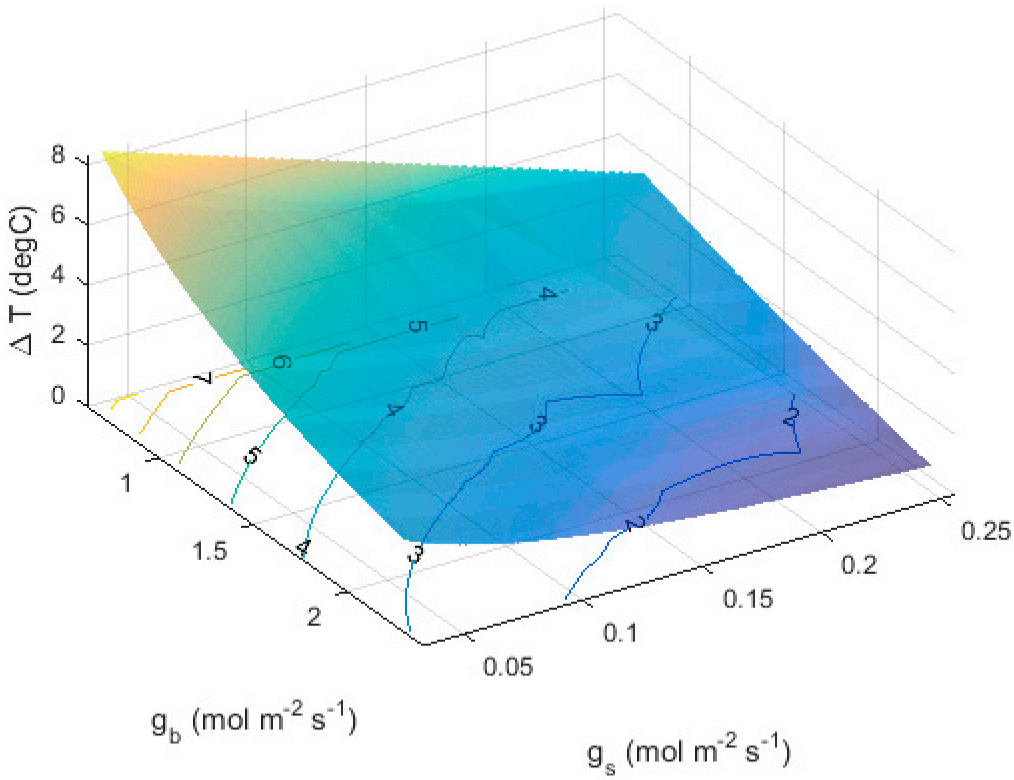

Fig. S1. Response of leaf-to-air temperature difference $\Delta T = T_L - T_A$ to stomatal conductance g_s and boundary conductance $g_{b,v}$. Following conditions were used to simulate the leaf temperature: PAR= 1000 μmolm^{-2}s^{-1}, Rn* = 325 Wm^{-2}, T_A= 25 °C, RH=40%, U=0.5ms^{-1}. The variations in g_b were created by varying leaf effective thickness from 0.01 to 0.20 m and those in g_s by varying $V_{CMAX,25}$ in range 30 – 80 μmolm^{-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. V_{CMAX} and Temperature

Several alternative functions have been proposed to model the temperature dependences of V_{cmax} 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:

$$f(T_N) = k_{25} * \exp\left(\frac{H_{av}}{R * T_N} * \left(1 - \frac{T_N}{T_k}\right)\right) * \frac{1 + \exp(\frac{S_{vv} * T_N - H_{dv})}{R * T_N}}{1 + \exp(\frac{S_{vv} * T_k - H_{dv})}{R * T_k}} \quad \text{(eq. 8)}$$

The parameters can be interpreted as follows: k_{25} is the value of V_{CMAX} 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 V_{CMAX} dependence to T_L by varying $V_{CMAX,25}$ from 10 to 80 μmolm^{-2}s^{-1}.

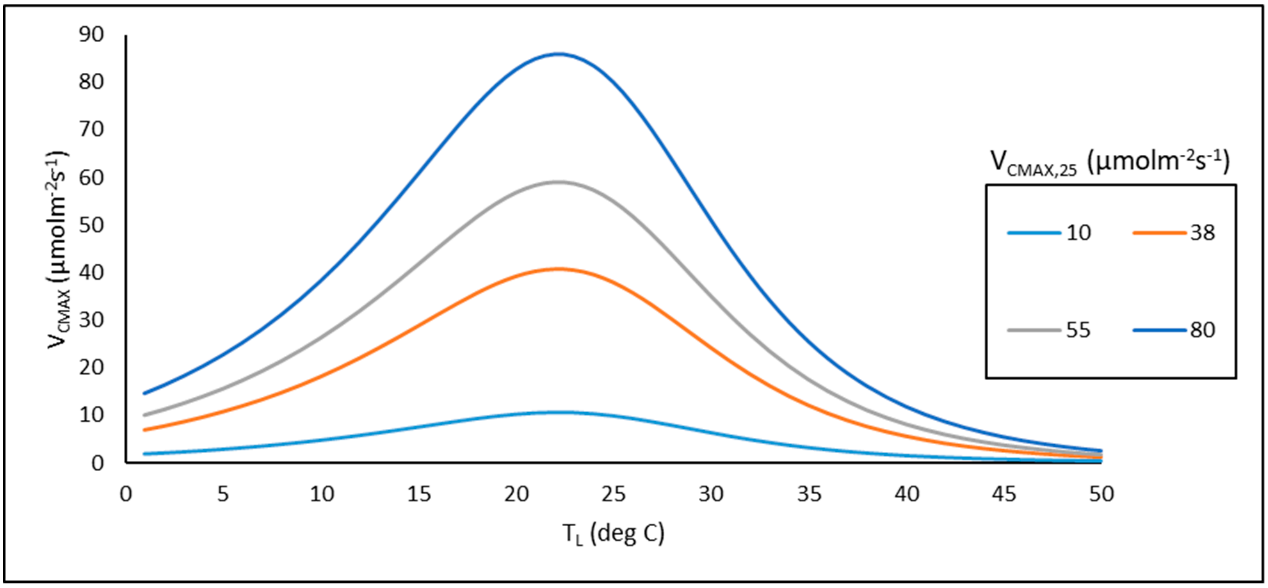

Fig. S2. Response of V_{CMAX} as a function of leaf temperature following equation 7 with the parameters as: H_{av}= 69.83e^3 Jmol^{-1}, H_{dv}= 200e^3 Jmol^{-1}, and S_{vv}= 672 Jmol^{-1}K^{-1}. The reference temperature is 298.15 K and the gas constant R is 8.31. $V_{CMAX,25}$ varies within the range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

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