

Modeling carbon nutrition and photosynthesis taking into account plant stomatal resistance

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Abstract. A differential-algebraic system of equations of carbon dioxide transport and photosynthesis in vegetation is formulated for mathematical analysis of the influence on productivity and water regime of plant populations. A simple semi-empirical algebraic approximation of the true photosynthesis function is constructed for the quasi-stationary solution of the system, including the influence of stomatal regulation, leaf index, absorbed photosynthetically active radiation, and temperature.

1 Model of carbon nutrition and photosynthesis of a plant population

Consider the following model of carbon nutrition and photosynthesis of vegetation cover:

$$J_{ca} = -k_a \frac{\partial}{\partial x} c_a, \quad \frac{\partial}{\partial t} c_a = -\frac{\partial}{\partial x} J_{ca} + f_{cl}, \quad 0 \leq x \leq H_l; \quad (1)$$

$$f_{cl} = D_c S_l (c_l - c_a) p_l, \quad D_c^{-1} = (D_q + r_{cut}^{-1})^{-1} + r_{mes}; \quad (2)$$

$$J_{ca} = D_a (c_a - c_a^0), \quad x = H_l; \quad (3)$$

$$J_{ca} = 0, \quad x = 0; \quad (4)$$

$$\frac{\varepsilon \Phi \sigma(T_l)}{\Phi_0} = \frac{1}{\alpha I \Phi} + \frac{r_c}{c_l}, \quad \Phi_0 - R = -\frac{1}{S_l} \int_0^{H_l} f_{cl} dx, \quad 0 \leq x \leq H_l; \quad (5)$$

The following notations are used here:

- H_l - vegetation height
- H_a - concentration measurement height c_a^0
- J_{ca} - vertical carbon flux CO_2 in the interleaf air at a height x
- c_l - carbon concentration CO_2 in chloroplasts at height x
- c_a - carbon concentration CO_2 in the interleaf air at a height x
- c_a^0 - carbon concentration CO_2 at measurement height H_a over vegetation
- $-f_{cl} \Delta x$ - diffusive flux of carbon CO_2 from the air into the leaves of the square $S_l p_l \Delta x$
- D_c - conductivity coefficient of the path to the photosynthetic center for the molecule CO_2 , $D_c^{-1} = (D_q + r_{cut}^{-1})^{-1} + r_{mes}$
- D_q - stomatal conductance

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- r_{cut} - leaf cuticle resistance
 r_{mes} - leaf mesophyll resistance
 Φ_0 - carbon flux of true photosynthesis of a unit leaf surface per unit time, [3]
 I_ϕ - photosynthetic active radiation (PAR), absorbed by a single leaf surface
 R - plant respiration per unit of leaf surface area
 $\sigma(T_l)$ - coefficient of photochemical efficiency of radiation I_ϕ , leaf temperature dependent T_l
 r_c - carboxylation resistance

In the model (1)-(5) functions $c_a^0(t)$, $I_\phi(t)$, $S_l(t)$, $D_q(\psi_l)$, $p_l(x, t)$, $D_a(t)$, $\sigma(T_l)$, $T_l(t)$ - are considered to be formally specified. In particular, they can be defined by a complex model. Functions $c_l(x, t)$, $c_a(x, t)$, $J_{ca}(x, t)$ are the quantities sought. The other quantities are considered as constants.

2 Explanation of the carbon nutrition and photosynthesis model

In order to construct and identify dynamic models of a plant population, it is desirable to include the constituent models in a relatively simple form, In particular, this applies to models of carbon nutrition and photosynthesis.

Indeed, a plant population is a complex object. A population is the product of evolution. It has functioned and is functioning under many uncertainties that it "fights" for survival through a variety of adaptations, with no way to avoid them. Plant population models thus turn out to be essentially semi-empirical, requiring consideration of adaptations to environmental conditions and mathematical methods for estimating their parameters. Overloading such models with factors that have no reliable data to estimate is known to make the model unstable with respect to data variation and reduce its quality. Determination of significant consistent independent factors and variables, as well as the forms of their relationship makes it necessary to carry out mathematical studies of models.

The description of plant population growth and development by the dynamics of plant organ biomasses implies the description of resources consumed by plants by dependencies on biomasses and environmental conditions, [1-12]. To describe carbon consumption CO_2 and production of photosynthetic assimilates use leaf index S_l - is the area of all leaves growing on a unit area of soil surface. Since a plant leaf is a thin lamina of approximately constant thickness, the assumption that index S_l proportional to leaf biomass seems to be justified. This assumption allows us to link the dynamics of plant biomass with photosynthesis, which produces this dynamics.

Next, we solve the problem of formally describing the inclusion of a leaf index S_l and stomatal resistance D_q into a model of carbon nutrition and photosynthesis of plant population. The emphasis is on obtaining, if possible, the simplest models available for further mathematical and statistical analysis.

Let us represent the vegetation cover uniformly over the soil area by a distributed layer of leaves with a surface area of $S_l(t)p_l(x, t)\Delta S\Delta x$ to the extent of $\Delta S\Delta x$ on top of x , where S_l - leaf index, and $p_l(x, t)$ defines density of leaf area distribution by height x .

Consider an upwardly elongated column of interleaf air with base ΔS and height H_a . Let's also consider the volume Ω of air enclosed between two horizontal sections of the air column at altitude x and $x + \Delta x$, $0 \leq x < x + \Delta x < H_l$. The contents $c_a\Omega$ of carbon CO_2 with volume concentration $c_a(x, t)$ to the extent of Ω replenished by the difference $[J_{ca}(x, t) - J_{ca}(x + \Delta x, t)]\Delta S$ carbon fluxes CO_2 at the lower and upper sections of the column, respectively. Let the leaves in the volume Ω flow $-f_{cl}\Delta S\Delta x$, where $\Delta S\Delta x$ - volume size Ω .

Thus,

$$\frac{\partial}{\partial t} [c_a \Omega] = -[J_{ca}(x + \Delta x, t) - J_{ca}(x, t)] \Delta S + f_{cl} \Delta S \Delta x, \text{ or}$$

$$\Delta S \Delta x \frac{\partial}{\partial t} c_a = -\frac{\partial}{\partial x} J_{ca}(x, t) \Delta x \Delta S + f_{cl} \Delta S \Delta x.$$

By cutting back on $\Delta S \Delta x$ we obtain (1). Dependence $J_{ca} = -k_a \frac{\partial}{\partial x} c_a$ standardly defines a stream J_{ca} of convective diffusion proportional to the concentration gradient c_a carbon in CO_2 . Flows J_{ca} in equations (3) - (4), where $D_a(t)$ depends on time, for example, on wind speed, seem to be formally justified if height H_a measurements c_a^0 substantially greater than the height of the cover H_l

Flow $-f_{cl} \Delta S \Delta x = D_c(c_a - c_l) S_l \Delta S p_l \Delta x$ - is the carbon diffusion flux CO_2 into the leaves of the square $S_l \Delta S p_l \Delta x$, where $p_l \Delta x$ - consumption rate CO_2 leaves in volume Ω . The diffusion flux is proportional to the difference $(c_a - c_l)$ concentrations in the path of molecules CO_2 from the interleaf air to the chloroplasts of the leaves. Along the way, the molecules overcome resistance D_c^{-1} , which, according to $D_c^{-1} = (D_q + r_{cut}^{-1})^{-1} + r_{mes}$ in (2), is defined for molecules CO_2 resistance D_q^{-1} of stomatal slits on the lower surface of leaves, resistance r_{mes} mesophyll tissue on the path of molecules from the stomata to the photosynthetic centers of leaves, as well as resistance r_{cut} cuticle - an almost impenetrable waxy protective layer on the surface of leaves.

Model (5) for flow dependence Φ_0 of assimilate carbon of true photosynthesis of unit leaf surface from absorbed photosynthetically active radiation PAR, concentration c_l and temperatures T_l is a well-known application of the Michaelis-Menten equation [3,4].

According to [1,2,4], the water regime of a population affects its productivity through its mouth resistance $D_q^{-1}(\psi_l)$, depending on water potential ψ_l leaves, which in turn depends on environmental variables such as soil water potential, air moisture deficit, etc.

3 System of equations for the photosynthesis function Φ_0

Assuming in (1) $\partial c_a / \partial t \cong 0$, and also assuming negligibly small changes of $D_c(c_l - c_a)$ on the height of vegetation cover, we obtain a system of algebraic equations with respect to the sought ones Φ_0 and c_l as functions of area S_l leaves

Under these assumptions integrating $\partial J_{ca} / \partial x = f_{cl}$ in (1), we obtain

$$-J_{ca}|_{x=H_l} + J_{ca}|_{x=0} + \int_0^{H_l} D_c S_l (c_l - c_a) p_l dx = 0, \tag{6}$$

and from (2) - (3) for a small varying value $D_c(c_l - c_a)$ we obtain a system of algebraic equations

$$-D_a(c_a - c_a^0) + D_c S_l (c_l - c_a) = 0, f_{cl} = D_c S_l (c_l - c_a) p_l,$$

from which we exclude $c_l - c_a$:

$$-D_a(c_l - c_a^0) - D_a(c_a - c_l) + D_c S_l (c_l - c_a) = 0, \text{ or}$$

$$-D_a(c_l - c_a^0) + (D_c S_l + D_a)(c_l - c_a) = 0.$$

From here

$$c_l - c_a = \frac{D_a}{D_c S_l + D_a} (c_l - c_a^0), f_{cl} = \frac{D_c S_l D_a}{D_c S_l + D_a} (c_l - c_a^0), \text{ or}$$

$$f_{cl} = -S_l \frac{c_a^0 - c_l}{r_l} p_l, \text{ where } r_l := \frac{D_c S_l + D_a}{D_c D_a} = \frac{S_l}{D_a} + \frac{1}{D_c}. \tag{7}$$

Let's substitute the last expression into (5):

$$\Phi_0 - R = -\frac{1}{S_l} \int_0^{H_l} f_{cl} dx = \frac{c_a^0 - c_l}{r_l} \frac{1}{S_l} \int_0^{H_l} S_l p_l dx = \frac{c_a^0 - c_l}{r_l}.$$

Hence, the system of algebraic equations for the photosynthesis functions is Φ_0 and concentrations c_l looks like:

$$\begin{aligned} \frac{\varepsilon_{\Phi} \sigma(T_l)}{\Phi_0} &= \frac{1}{\alpha I_{\Phi}} + \frac{r_c}{c_l}, \Phi_0 - R = \frac{C_{a0} - c_l}{r_l}; \text{ or} \\ \frac{\varepsilon_{\Phi} \sigma(T_l)}{\Phi_0} &= \frac{1}{\alpha I_{\Phi}} + \frac{r_c}{C_{a0} - r_l \Phi_0}, c_l = C_{a0} - r_l \Phi_0. \end{aligned} \tag{8}$$

where $C_{a0} = c_a^0 + r_l R$,

4 Approximation of the solution of the system for Φ_0

It is easy to see that equation (8) for Φ_0 is transformed to a quadratic equation with respect to Φ_0 . In fact.,

$$\begin{aligned} \frac{A_l}{\Phi_0} &= \frac{1}{\alpha I_{\Phi}} + \frac{r_c}{C_{a0} - r_l \Phi_0}, \text{ where } A_l = \varepsilon_{\Phi} \sigma(T_l), \text{ or} \\ A_l(C_{a0} - r_l \Phi_0) &= \Phi_0(C_{a0} - r_l \Phi_0) \frac{1}{\alpha I_{\Phi}} + r_c \Phi_0, \text{ or} \\ \alpha I_{\Phi}(A_l C_{a0} - A_l r_l \Phi_0) &= (C_{a0} \Phi_0 - r_l \Phi_0^2) + r_c \Phi_0 \alpha I_{\Phi}, \text{ or} \\ r_l \Phi_0^2 - (C_{a0} + r \alpha I_{\Phi}) \Phi_0 + A_l C_{a0} \alpha I_{\Phi} &= 0, \text{ where } r = r_c + A_l r_l. \end{aligned}$$

Let us assume the following:

$$\Phi_0 = \frac{C_{a0}}{r} X^{-1}, \nu := \alpha I_{\Phi} \frac{r}{C_{a0}}.$$

In the new notations the equation will take the form:

$$\begin{aligned} r_l \left(\frac{C_{a0}}{r}\right)^2 X^{-2} - (C_{a0} + C_{a0} \nu) \frac{c_a^0}{r} X^{-1} + A_l C_{a0} \frac{C_{a0}}{r} \nu &= 0, \\ \frac{r_l}{r} - (1 + \nu)X + A_l \nu X^2 &= 0, \\ X &= \frac{1}{2A_l \nu} \left\{ 1 + \nu + \sqrt{(1 + \nu)^2 - 4A_l \nu r_l / r} \right\}; \end{aligned}$$

It should be noted that:

$$\begin{aligned} (1 + \nu)^2 - 4A_l \nu \frac{r_l}{r} &= 1 - 2\nu + \nu^2 + 4\nu \left\{ 1 - A_l \frac{r_l}{r} \right\} = (1 - \nu)^2 + 4\nu r_c / r, \\ (1 + \nu)^2 - 4A_l \nu \frac{r_l}{r} &= (1 - \nu)^2 + 4\nu r_c / r. \end{aligned}$$

Thus, the solution of the system (8) for the function Φ_0 looks like:

$$\Phi_0 = A_l \frac{C_{a0}}{r} \frac{2\nu}{1 + \nu + \sqrt{(1 - \nu)^2 + 4\nu r_c / r}}, \text{ where} \tag{9}$$

$$\begin{aligned} \nu &:= \alpha I_{\Phi} \frac{r}{C_{a0}}, A_l = \varepsilon_{\Phi} \sigma(T_l), r = r_c + A_l r_l, r_l = S_l D_a^{-1} + D_c^{-1}, \\ D_c^{-1} &= (D_q + r_{cut}^{-1})^{-1} + r_{mes}, \end{aligned} \tag{10}$$

Let's study the dependence Φ_0 from ν, r .

Transition $\nu \rightarrow \infty$ in (9) is characterized either by a large resistance r , e.g. under soil moisture deficit, or high values of absorbed photosynthetically active radiation I_{Φ} . According to (9), in both the first and second cases $\Phi_0 \rightarrow A_l C_{a0} / r$.

Transition $\nu \rightarrow 0$ is characterized primarily by small values of absorbed photosynthetically active radiation I_{Φ} . According to (9), in this case $\Phi_0 \rightarrow \nu C_{a0} / r = \alpha A_l I_{\Phi}$.

Expression (9) states that the limiting values of the photosynthesis function are as follows Φ_0 are determined by the limit values of limiting resources: radiation I_{Φ} or water potential $\bar{\mu}_s$ of the soil, which determines the resistance D_q^{-1} .

We obtain an approximation of the dependence Φ_0 from ν, r . Let's review $\tilde{f}(\nu, r)$.

$$\Phi_0 = A_l \frac{C_{a0}}{r} \tilde{f}(\nu, r), \text{ where } \tilde{f}(\nu, r) = \frac{2\nu}{1 + \nu + \sqrt{(1 - \nu)^2 + 4\nu r_c / r}}, \nu = \alpha I_{\Phi} \frac{r}{C_{a0}}. \tag{11}$$

Function $\tilde{f}(\nu, r)$, monotonically increasing from (0.0) to the horizontal asymptote $\tilde{f} = 1$ by the $\nu \rightarrow \infty$. Since $r_c / r = r_c / (A_l r_l + r_c) < r_c / r_c = 1$, justly

$$(1 - \nu)^2 < (1 - \nu)^2 + 4\nu r_c / r < (1 - \nu)^2 + 4\nu = (1 + \nu)^2,$$

$$\frac{\nu}{1+\nu} = \frac{2\nu}{1+\nu+\sqrt{(1+\nu)^2}} \leq \tilde{f}(\nu, r) \leq \frac{2\nu}{1+\nu+\sqrt{(1-\nu)^2}} = \frac{2\nu}{1+\nu+|1-\nu|}, \text{ or}$$

$$f(\nu) \leq \tilde{f}(\nu, r) \leq \nu \text{ by the } 0 \leq \nu \leq 1,$$

$$f(\nu) \leq \tilde{f}(\nu, r) \leq 1 \text{ by the } 1 \leq \nu, \text{ where } f(\nu) = \nu(1 + \nu)^{-1}.$$

To approximate $\tilde{f}(\nu, r)$ use a simple function $f(\nu) = \nu(1 + \nu)^{-1}$, $f(\nu) \leq \tilde{f}(\nu, r)$, asymptotically coinciding c $\tilde{f}(\nu, r)$ by the $\nu \rightarrow 0$ and $\nu \rightarrow \infty$. In this case the limit properties of the function Φ_0 are preserved, noted at the end of section 1.3. Φ_0 takes the form of:

$$\Phi_0 = A_l \frac{C_{a0}}{r} \tilde{f}(\nu, r) \approx A_l \frac{C_{a0}}{r} f(\nu) = A_l \frac{C_{a0}}{r} \frac{\nu}{1+\nu} = A_l \left\{ \frac{r}{C_{a0}} + \frac{1}{\alpha l \Phi} \right\}^{-1}, \text{ or}$$

$$\Phi_0 = \left\{ \frac{r_l + A_l^{-1} r_c}{C_{a0}} + \frac{1}{\alpha A_l l \Phi} \right\}^{-1}, c_1 = C_{a0} - r_1 \Phi_0, \text{ where} \tag{12}$$

$$\nu := \frac{\alpha l \Phi}{C_{a0}/r}, A_l = \varepsilon_\phi \sigma(T_l), r = A_l r_l + r_c, \tilde{r} = r_l + A_l^{-1} r_c, \tag{13}$$

$$r_l = D_c^{-1} + S_l D_a^{-1}, D_c^{-1} = (D_q + r_{cut}^{-1})^{-1} + r_{mes} \cdot C_{a0} = c_a^0 + r_l R.$$

Particularly when the vegetation cover is well ventilated $S_l D_a^{-1} \ll D_c^{-1}$ and lack of moisture $D_q \ll D_a/S_l$, $r_{cut}^{-1} \ll D_q \ll r_{mes}^{-1}$, resistance $r_l \cong D_c^{-1} \cong D_q^{-1}$, and

$$\Phi_0 \cong \left\{ \frac{D_q^{-1}}{c_a^0 + D_q^{-1} R} + \frac{1}{\alpha A_l l \Phi} \right\}^{-1}. \tag{14}$$

5 Conclusions

A semi-empirical model of carbon nutrition and photosynthesis of plants, including stomatal resistance and leaf index, is constructed on the basis of a differential-algebraic model. The model is represented by simple algebraic expressions available for further mathematical analysis of the interaction of photosynthesis with other processes in the plant population. It has an adequate set of environmental parameters that takes into account the influence of stomatal regulation on the water regime and photosynthesis of the population.

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