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Abstract

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GEOPHYSICS

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ON THE THEORY OF THE INFLUENCE OF CLIMATIC FACTORS ON PHOTOSYNTHESIS

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As is known, the process of photosynthesis is associated with the assimilation by plants of carbon dioxide contained in the air, with absorption of the energy of solar radiation. The kinetics of photosynthesis has been studied in a number of investigations (see ([3])), in which it has been established that the dependence of the rate of assimilation of carbon dioxide on the magnitude of photosynthetically active radiation can be represented in the form

$$A = \frac{\alpha Q}{1 + \frac{\alpha}{A_m} Q}, \tag{1}$$

where A is the rate of assimilation; A_m is the rate of assimilation at sufficiently large values of radiation; Q is photosynthetically active radiation; α is a coefficient of proportionality.

Let us consider the case of a plant cover of height H, with the amount of photosynthesizing leaf surface per unit area of the cover in a layer of unit height equal to s. The assimilation in a thin horizontal layer of such a cover of height dz will be equal to

$$dA = \frac{\alpha Q s \, dz}{1 + \frac{\alpha}{A_m} Q}. \tag{2}$$

The amount of radiation in the plant cover varies with height, decreasing from its greatest values at the upper boundary of the cover. We shall assume that, in a thin layer in the cover, the decrease in the amount of photosynthetically active radiation is proportional to its magnitude, the density of the cover, and the thickness of the layer dz, i.e., that

$$dQ = \gamma Q s \, dz, \tag{3}$$

where γ is a coefficient of proportionality.

Assuming that at the upper boundary of the plant cover $Q = Q_H$, we obtain

$$Q = Q_H e^{-\gamma s(H-z)}, \tag{4}$$

where z is height.

The value of the rate of assimilation at large amounts of radiation depends on the conditions of diffusion of carbon dioxide. Experimental investigations have shown (see ([3])) that, for the comparatively low concentrations of carbon dioxide observed under natural conditions, the value A_m is approximately proportional to the concentration of carbon dioxide. Thus, it may be assumed that

$$A_m = \beta c, \tag{5}$$

where β is a coefficient of proportionality depending on temperature and some other factors; c is the concentration of carbon dioxide in the free air at the given level in the plant cover.

From (2), (4), (5) we obtain the equation

$$\frac{dA}{dz} = \frac{\alpha s Q_H e^{-\gamma s(H-z)}}{1 + \dfrac{\alpha Q_H e^{-\gamma s(H-z)}}{\beta c}}. \tag{6}$$

It follows from this that the assimilation value of the plant cover as a whole is determined by the formula

$$A_H = \int_0^H \frac{\alpha s Q_H e^{-\gamma s(H-z)}\, dz}{1 + \dfrac{\alpha Q_H e^{-\gamma s(H-z)}}{\beta c}}, \tag{7}$$

in which c is an unknown function of z.

To determine the dependence of c on height, the following considerations may be used. The change in the rate of assimilation in the plant cover with height is determined by the change in the vertical turbulent flux of carbon dioxide, i.e.,

$$\frac{dA}{dz} = \frac{d}{dz}\left(\rho k \frac{dc}{dz}\right) \tag{8}$$

(ρ is the density of air).

We shall assume that in the plant cover the coefficient of turbulent exchange k is proportional to height, i.e. $k = k_1 z$. Then we obtain

$$\frac{dA}{dz} = \rho k_1 \frac{dc}{dz} + \rho k_1 z \frac{d^2c}{dz^2}. \tag{9}$$

From (6) and (9) we find the differential equation

$$\frac{d^2c}{dz^2} + \frac{1}{z}\frac{dc}{dz} = \frac{\alpha s Q_H e^{-\gamma s(H-z)}}{\rho k_1 z \left[1 + \frac{\alpha Q_H e^{-\gamma s(H-z)}}{\beta c}\right]}, \tag{10}$$

which should be solved under the boundary conditions:

A. At $z = H$, $c = c_H$.

$$\tag{11}$$

The value c_H is then determined from the formula

$$A_H = \rho D_H (c_\infty - c_H),$$

where D_H is the integral coefficient of turbulent diffusion above the plant cover, and c_∞ is the concentration of carbon dioxide in the air at a sufficient height above the plant cover.

B. At $z = 0$ the vertical flux of carbon dioxide at ground level is determined by its rate of entry from the soil, A_0.

The nonlinear differential equation (10) can in the general case be solved numerically, after which the integral (7) can also be calculated by numerical methods. In a number of particular cases equation (10) is substantially simplified, which makes it possible to obtain simple analytical solutions.

Of interest are solutions for limiting cases, when assimilation is determined mainly by diffusion and does not depend on radiation, and when assimilation depends little on the change in the concentration of carbon dioxide in the plant cover.

The first of these cases corresponds to the condition $\alpha Q \gg A_m$, i.e. to a state of "light saturation" in the plant cover at all levels. Then—

then equation (10) takes the form

$$\frac{d^2c}{dz^2} + \frac{1}{z}\frac{dc}{dz} = \frac{s\beta c}{\rho k_1 z}. \tag{12}$$

The solution of this equation has an especially simple form when $A_0 = 0$. From this solution one obtains the formula

$$A_H = \frac{\rho D_H c_\infty}{\left[1 + \frac{\rho D_H}{\sqrt{\rho k_1 \beta s H}} \frac{I_0\left(2\sqrt{\frac{\beta s H}{\rho k_1}}\right)}{I_1\left(2\sqrt{\frac{\beta s H}{\rho k_1}}\right)}\right]}, \tag{13}$$

where I_0 and I_1 are Bessel functions of imaginary argument.

A comparatively simple solution is obtained in the case where the change in the concentration of carbon dioxide in the plant cover has little effect on the rate of assimilation. Under such conditions the quantity c in formula (7) may be considered equal to c_∞. Then we obtain

$$A_H = \frac{\beta c_\infty}{\gamma} \ln \frac{1 + \frac{\alpha Q_H}{\beta c_\infty}}{1 + \frac{\alpha Q_H e^{-\gamma s H}}{\beta c_\infty}}. \tag{14}$$

Using equations (13) and (14), one can obtain formulas for determining the productivity of the plant cover and the magnitude of the leaf surface that ensures the greatest productivity. The productivity P is equal to the difference between assimilation and the expenditure of biomass (mainly for respiration), which may be considered proportional to the leaf surface, i.e., equal to $\varepsilon s H$ (the proportionality coefficient ε will be different for different plant species in accordance with leaf thickness and other morphological characteristics). Thus, for the two cases considered above we obtain

$$P = \frac{\rho D_H c_\infty}{\left[1 + \frac{\rho D_H}{\sqrt{\rho k_1 \beta s H}} \frac{I_0\left(2\sqrt{\frac{\beta s H}{\rho k_1}}\right)}{I_1\left(2\sqrt{\frac{\beta s H}{\rho k_1}}\right)}\right]} - \varepsilon s H; \tag{15}$$

$$P = \frac{\beta c_\infty}{\gamma} \ln \frac{1 + \frac{\alpha Q_H}{\beta c_\infty}}{1 + \frac{\alpha Q_H e^{-\gamma s H}}{\beta c_\infty}} - \varepsilon s H. \tag{16}$$

Equation (16) is similar to a formula previously obtained by Monsi and Saeki ([2]).

Let us consider the dependence of productivity on the total leaf surface sH. From equations (15) and (16) it is evident that the quantity P first increases with increasing sH, then reaches a maximum and begins to decrease. In this case, from the condition $dP/d(sH) = 0$, we find that the greatest productivity of the plant cover in the second case is attained at

$$sH = \frac{1}{\gamma} \ln \frac{\alpha Q_H}{\varepsilon} \left(1 - \frac{\varepsilon}{\beta c_\infty}\right). \tag{17}$$

It is easy to show that, in this case, at the lower boundary of the plant cover (at $z = 0$) the conditions of the "compensation point" hold, i.e., the condition that assimilation equals biomass expenditure. A similar supposition was previously expressed by Saeki ([4]), who confirmed it with experimental data.

It may be thought that under natural conditions, with a sufficient supply of moisture to plants, the leaf surface of the vegetation cover should approach the value corresponding to the conditions of greatest productivity.

When the amount of moisture in the soil is insufficient, the magnitude of the leaf surface is limited by the magnitude of possible transpiration, which, in this way, also limits the assimilation and productivity of the vegetation cover.

For xerophilous vegetation under conditions of a dry climate, the transpiration value T may be taken as equal to (see (1))

$$T = \Delta\omega = \rho D'(q_s - q)sH, \tag{18}$$

where D' is the coefficient of diffusion of water vapor entering the free air from the leaves; q_s is the specific humidity of air saturated with water vapor; q is the specific humidity of the air outside the vegetation cover; $\Delta\omega$ is the amount of water in the soil available for transpiration.

Assuming that, under conditions of a dry climate, the greatest productivity of the vegetation cover occurs at the greatest possible transpiration, we find that the optimal value of the leaf area in this case is

$$sH = \frac{\Delta\omega}{\rho D'(q_s - q)}. \tag{19}$$

The equations presented make it possible to estimate the influence on photosynthesis of various climatic factors.

To use these equations in calculations of photosynthesis and, in particular, to determine the most advantageous leaf surfaces, it is necessary to know the values of the parameters entering into the equations.

Some of these parameters, such as, for example, the amount of photosynthetically active radiation Q_H, can be determined for various regions by using materials from work on radiation climatology. With respect to other parameters, the literature contains only approximate estimates for particular cases, which is insufficient for detailed calculations. In this connection it is advisable to carry out experimental investigations, chiefly in order to refine the available data on the maximum rate of photosynthesis of various plants under light saturation (A_m), to estimate the attenuation of solar radiation in various vegetation covers (γ), and to determine the parameters characterizing turbulent exchange in the vegetation cover (k_1) and the conditions of leaf ventilation (D'). A more precise determination of the indicated parameters will make it possible to substantiate the choice of one or another scheme for an approximate or exact solution of equations (7) and (10) for various concrete cases.

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Note: Figure translations are in progress. See original paper for figures.