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"Forest–grass" global vegetation model with forest age structure

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Abstract

In the paper [Ecol. Modell. 124 (1999) 131], a set of "simplest" models of the global vegetation pattern (GVP) was suggested. All these models are based on the simple probabilistic "urn" schemes and their dynamics were sufficiently complex to present nonlinear phenomena such as multiple equilibriums and hysteresis. Although these schemes are simple, sufficiently complex behaviour is implied. Expressed in terms of equations with biologically motivated parameters, only three equilibriums corresponding to "grass ", transition "grass–forest" and "forest" zones exist. Stability domains of these equilibriums do not intersect in the parameter space. Since at each geographical point, the GVP dynamics is described by the same dynamical system with different parameters; then this difference is defined by the change in annual temperature and precipitation. We also assume that at any point there are both tree and grass "seeds". In order to reduce the number of independent parameters, we formulate two additional hypotheses. Let τ_m and τ_l, i.e. the age of maturity and the life span for trees. Then, (1) the ratio $k_\tau = \tau_m/\tau_l$ must be constant for coniferous and deciduous trees and (2) $\tau_m = \tau_{ml}(T)$. Both these hypotheses have been tested. As a result only one parameter, which governs the intensity of competition within a mature tree cohort, remained free and it could be used for the tuning purposes. Since the final GVP substantially depends on the border shape between forest, grass and mixed biomes in the climatic space {temperature, precipitation}; then in order to obtain better coincidence between the real and modelled GVP, we should modify the classic Lieth diagram. After calibrating parameters using climatic and vegetation data we developed a model, which predicts vegetation distribution in satisfactory agreement with observation for the present day. It is also shown that a "relaxation" time (time to reach equilibrium) for a transition zone is more than one order greater than the time for "pure" grass and forests equilibriums. This means that a real transformation of the GVP under climate change is a very slow process.
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Keywords: Vegetation; Global modelling

1. Introduction

The first work in this series (Svirezhev, 1999) was devoted to the development of different semi-

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analytical methods for dynamic modelling of the global vegetation, and a set of "simplest" models of the global vegetation pattern (GVP) was suggested. However, if we want to describe a real GVP we have to set transition probabilities of the models in more concrete forms, which take into account the information about physiological and ecological properties of different vegetation types. In particular, we have to analyse their dependencies on the temperature and precipitation.

In this work, we would like to show that the use of even primitive and maximally simplified models of transition probabilities, which are based on the empirical distribution of vegetation types in the plane {annual temperature–annual precipitation} and some additional general properties of plants, gives the GVP, similar (at least qualitatively) to the real vegetation pattern. We hope that more detailed models of transition probabilities will give the GVP closer to the reality. Note that our approach allows constructing the dynamic GVP that, in turn, allows describing transition processes in the global vegetation under climate change.

All these models are based on some simple probabilistic "urn" schemes. Nevertheless, these simple schemes imply sufficiently complicated dynamics described by the system of integro-differential equations with partial derivatives. A reduction to two age cohorts, juvenile (young) and mature trees, gives us two ordinary differential equations:

$$\frac{\mathrm{d}p_2}{\mathrm{d}t} = -Ap_2 + ap + bp_2p - cp_2^2,$$

$$\frac{\mathrm{d}p}{\mathrm{d}t} = (-\varphi_1)(1-p)(lp_2 - p) \tag{1.1}$$

for two-state variables: the "forest function" $p(t)$, i.e. the fraction of areas covered by forest, and the fraction of areas covered by mature trees, $p_2(t)$. It is obvious that $0 \le p_2(t) \le p(t) \le 1$. System Eq. (1.1) depends on six parameters: A, a, b, c, l and φ_1 which, in turn, can be expressed through more biologically motivated and measured values:

$$A = m_2 + \gamma_2 - a_2,$$

$$a = \frac{1}{2}\tau_\mathrm{m}, \quad b = \gamma_2 - \pi_{12}, \quad c = \pi_{22} - \pi_{12},$$

$$a_2 = \frac{1}{2}\left(\frac{1}{\tau_\mathrm{l} - \tau_\mathrm{m}} - \frac{1}{\tau_\mathrm{m}}\right),$$

$$l = 1 - \left(\frac{\varphi_2}{\varphi_1}\right), \quad \varphi_i = \beta_i - \gamma_i, \quad i = 1, 2. \tag{1.2}$$

Substantively, if $\tau_\mathrm{m} < \tau_\mathrm{l}/2$, then $a_2 < 0$.

How can all these values be interpreted? The values τ_m and τ_l are the age of maturity (age of first reproduction) and the life span (some maximal age) for trees, respectively. The value m_2 is the natural mortality for mature trees, the value π_{12} the probability of young tree winning in competition against a mature one (during 1 year) and π_{22} the probability of survival of one mature tree at the expense of another (this is some measure of competition among mature trees). The value γ_1 is the probability of grass winning in competition against young trees and the value β_1 the probability of a opposite result. The values γ_2 and β_2 are the analogous probabilities but for the "grass–mature tree" pair.

Without loss of generality, we can assume that $\beta_1 = \gamma_2 = \pi_{12} = 0$, then $b = 0$, $-\varphi_1 = \gamma_1$, $k = \gamma_1/\beta_2$, $c = \pi_{22} = \pi$. We also assume that $m_2 = 1/(\tau_l - \tau_m)$ then $A = \tau_l/(2\tau_m(\tau_l - \tau_m))$. Under these assumptions, we get from Eq. (1.1)

$$\frac{\mathrm{d}p_2}{\mathrm{d}t} = \frac{1}{2\tau_m}(p - \alpha p_2 - \mu p_2^2),$$
$$\frac{\mathrm{d}p}{\mathrm{d}t} = \gamma_1(1-p)(lp_2 - p), \tag{1.3}$$

where $\alpha = A/a = 1/(1-k_\tau)$, $k_\tau = \tau_m/\tau_l$, $\mu = c/a = 2\tau_m\pi$, $l = 1 + (\beta_2/\gamma_1)$. The full analysis of this system including the existence and stability of equilibriums corresponding to different vegetation pattern configurations and their dependence on system parameters was carried out in the work cited above. We use them here in another form.

2. Local successions "grass ⇒ forest" and "forest ⇒ grass": transitions through an intermediate form in a parameter space

These assumptions have allowed simplifying the original model; nevertheless, the system demonstrates how the stable vegetation equilibrium changes from pure grassland to an age-structured forest (and vice versa) through an intermediate forest–grassland community depending on parameter evolution. Note we implicitly assume that they are potentially related to climate. This is illustrated by direct calculations of stability conditions for all three (possible) equilibriums in the system Eq. (1.3):

a) $p^* = p_2^* = 0$: if $\alpha > l$ (or $k_\tau > (l-1)/l$), then only a grassland is stable.
b) $p^* = l((l-\alpha)/\mu)$; $p_2^* = (l-\alpha)/\mu$: if $(l-\mu)/l < \alpha < l$, then an intermediate community "forest–grass" is stable.
c) $p^* = 1$; $p_2^* = (1/2\mu)(\sqrt{\alpha^2 + 4\mu} - \alpha)$: if $\alpha < l - \mu/l$ and $\alpha > 1 - \mu$, then only a forest is stable. It is obvious that the last inequality is always fulfilled.

Knowing the variable p and p_2, the mean forest age can be calculated as

$$\widehat{\tau} \approx \frac{1}{2}\left[\left(1 - \frac{p_2}{p}\right)\tau_m + \frac{p_2}{p}(\tau_l - \tau_m)\right] = \frac{1}{2}\left[\tau_m + \frac{p_2}{p}(\tau_l - 2\tau_m)\right]. \quad (2.1)$$

In fact, the stability of different equilibriums depends only on three parameters: l, μ and α (in addition, $l, \alpha > 1$); the other two parameters, τ_m and γ_l, influence only the velocity of movement along trajectories. If we assume parameter α is fixed (at least, it has only two different values for two types of forest: coniferous and deciduous), then the stability domains are defined for only two-parametric space. In other words, they can be depicted in the plane $\{\mu, l\}$.

Assuming parameters μ and l are slowly change with the changing climate parameters T and P (for instance, along the curve ad in Fig. 1) then the local vegetation pattern will also evolve.

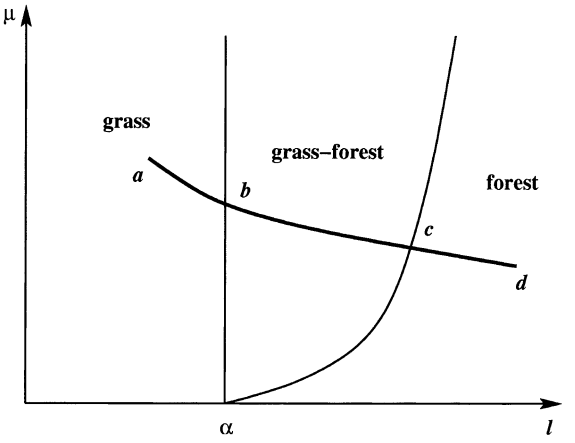


Fig. 1. Stability domains of the solutions corresponding to the states "forest", "forest–grass" and "grass" in the plane $\{\mu, l\}$.

Let the evolution of this pattern under climate change start from the point a when the pattern is a grassland. Climate change causes the change of parameters μ and l, and by the same token, the evolution of an equilibrium pattern, but before the representing point crosses the line $l = \alpha$ (at the point b), the pattern remains grassland. When the representing point crosses the line $l = \alpha$, then a transition structure "grass–forest" appears. In the course of movement from b to c, the "grass–forest" structure remains but the equilibrium forest fraction increases (in a "parabolic" way: $p^* = l(l-\alpha)/\mu(p)$). When the representing point crosses the border between "grass–forest" and "forest" at point c and continues to move to the final point d, only the "forest" pattern will exist. It is necessary to conduct an additional study in order to answer the question: Would the reversible path $dcba$ be the same or not? In other words, is the transition process reversible or irreversible? Since the system is nonlinear, then we have the right to expect the hysteresis phenomenon.

3. The model calibration in a spatial case: some additional hypotheses

Here we assume that no interaction between vegetation of two different spatial macrounits,

which are described the same dynamical system and differ only in their parameter values. We suppose that this difference is defined by a change in climatic variables: mean annual temperature and precipitation. We also assume that any macrounit contains "seeds" of both trees and grass (*panspermia* hypothesis). This allows a trajectory to go out of equilibriums when they become unstable, even if these equilibriums are trivial, for instance, either $p^* = 0$ or $p = 1$. The assumption may be realised in two ways. The first is to introduce some external upper and lower constraints on the variable p so that $\varepsilon \leq p \leq 1-\varepsilon$ where $\varepsilon \ll 1$. The second is to introduce into the right sides of Eq. (1.3) some small random perturbations. This also avoids the trivial equilibrium case.

The problem is how to calibrate the model using only the geographical distribution of annual temperature and precipitation. Before this, we formulate and test one hypothesis.

There are two characteristic times for trees: τ_m and τ_l, i.e. the age of maturity and the life span. We assume that: *both the age of maturity and the life span are defined by the operation of one "biological clock"*, the rate of which may depend on local climate. According to this assumption, the ratio of these characteristic times, $k_\tau = \tau_m/\tau_l$, *must be constant* (at least, for such high taxonomic levels as *genus*, etc.). In order to test the hypothesis, we use a correlation between the first reproduction age and the life span for approximately 100 plant species clustered into three groups: deciduous (shrubs + angiosperms), coniferous and monocarpics (Harper, 1994). It is easy to show with sufficient accuracy that the ratio $k_\tau = \tau_m/\tau_l$ is a constant for each group. It is obvious that $k_\tau = 1$ for monocarpics (later on we exclude such a vegetation type). Two other constants are $k_\tau^{\mathrm{d}} = 0.01$ for deciduous (shrubs + angiosperms) and $k_\tau^{\mathrm{c}} = 0.06$ for coniferous (on the average, with a sufficiently broad range of variability). As a result, we reduce the number of defining parameters since k_τ accepts only two values: k_τ^{d} and k_τ^{c}.

Further, it is natural to assume that the maturity age of trees depends on the annual temperature: the higher the temperature, the lower is the maturity age. The dependence was taken in the form $\tau_m = R/(T - T_{\mathrm{cr}})^{\lambda}$. The constants R and λ are to be determined for each of two classes: coniferous and deciduous (except monocarpics). The critical value T_{cr} is the minimal annual temperature for existence of any vegetation, taken to be -16 °C. This threshold could be explained by the soil permafrost phenomenon, which is one of the main restrictions on forest expansion into waste areas of the tundra in North Eurasia and North America. Generally speaking, the value of T_{cr} depends on the current climate and may change with the evolution of mean annual temperature. Moreover, for different authors the distribution of forest, grass and transitional biomes on the Earth's surface is calculated in different ways, with the critical temperature varying from one map to another. Nevertheless, we believe this parameter to be constant and obtain its value from the well-known Lieth diagram (Lieth, 1975), which shows the location of different vegetation types on the plane of annual temperature and annual precipitation. Identifying other constants was carried out using expert statements (Utkin et al., 1985; Shvidenko, 1999).

Larch (mainly *Larix kajanderi* and *L. gmelini*) grows in Russia covering an area of about 2.6 million km^2 and generates the northern tree line globally. It occurs in regions where the average annual temperature changes from between -8 and -10 °C (forest islands in tundra) to between $+4$ and $+5$ °C (planted forest in steppe). The reproduction period (for a tree, which is growing unhindered) starts after 40–45 years in the North and after 15–20 years in the South. The average life span is equal to about 400–420 years in the extreme North and 140–150 years in the South.

Birch (*Betula pendula*) can grow from the Arctic Circle (between -4 and -5 °C) down to the subtropics (between $+10$ and $+12$ °C). Reproduction age starts after 15–20 years in the North and 8–10 years in the South. The life span is 140–150 years and 70–80 years in the North and South, respectively.

These data resulted in the following dependencies of maturity age on temperature (it is interesting that these dependencies will be close,

therefore we will use one mean expression for them):

$$\tau_m = \frac{178}{(T - T_{cr})^{0.85}}. \quad (3.1)$$

4. Calibration of the model in a spatial case: using Lieth's diagram

The most difficult problem is to connect the climatic data with the parameter $l = 1 + \beta_2/\gamma_1$, which defines both the equilibriums and their stability. For this, we use the simplified Lieth diagram (see Fig. 2). In the diagram the border between tundra and an intermediate pattern "tundra–coniferous forest" passes along the curve AB. The border between an intermediate pattern and coniferous forest (taiga) passes along the curve CD. At a temperature $T_{ch} \approx 6$ °C, coniferous forests are replaced by deciduous ones (in reality this transition is smoother). We see that the picture is "tilted", and for $T > T_{ch}$ the border between grass (steppe) and an intermediate pattern "deciduous forest–steppe" passes along the curve GH. The border between forest–steppe and deciduous forest passes along the curve EF. The same borders are between tropical forest and savannah. The "tilting" reflects the different reaction of vegetation with respect to a precipitation gradient in the polar and tropical regions.

Certainly, the approximation is very rough. However, it describes the real distribution of the major biomes in climate space {temperature, precipitation} with a good qualitative accuracy, and the borders are very similar with those used in the work of Brovkin et al. (1998).

We assume that the dependence $l = l(T, P)$ is presented in the form, which is linear with respect to P:

$$l = b_0(T) + b_1(T)P. \quad (4.1)$$

Taking into account the stability conditions of Section 2, we can write the relations between l and other parameters along the curves AB, CD, EF and GH in the form:

a) at AB:

$$l_g = \frac{1}{1 - k_\tau^c}, \quad T < T_{ch}, \quad (4.2)$$

b) at CD:

$$l_f = \frac{1}{2(1 - k_\tau^c)} \left(\sqrt{1 + 8\pi(1 - k_\tau^c)^2 \tau_m(T)} + 1\right), \quad T < T_{ch}, \quad (4.3)$$

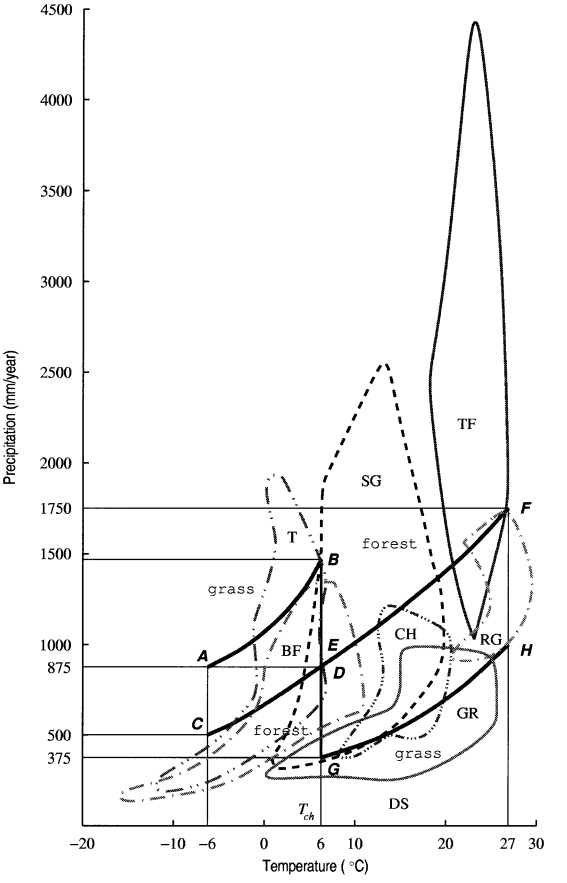
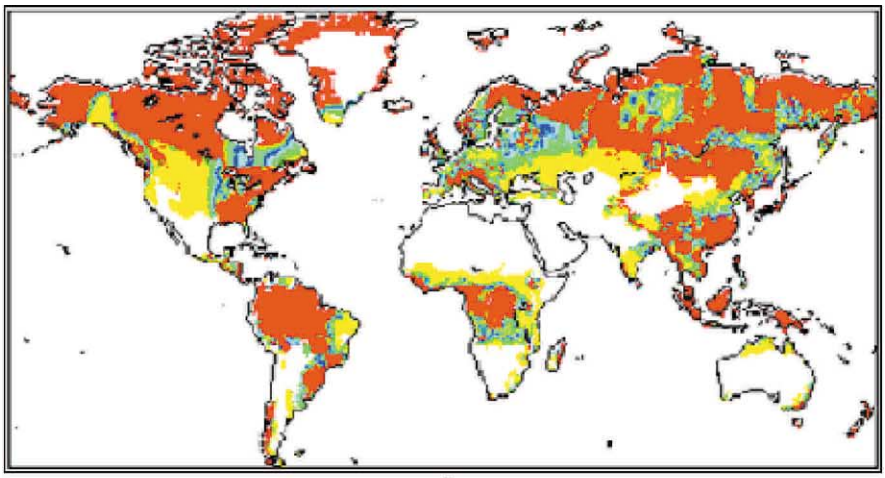
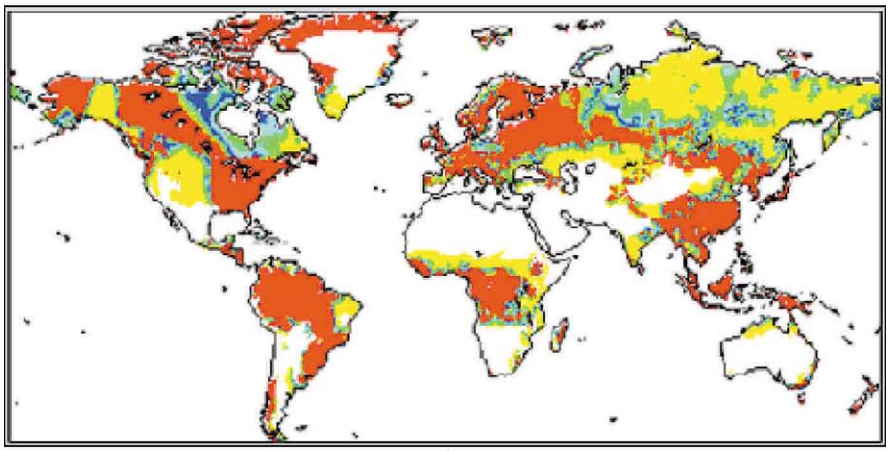


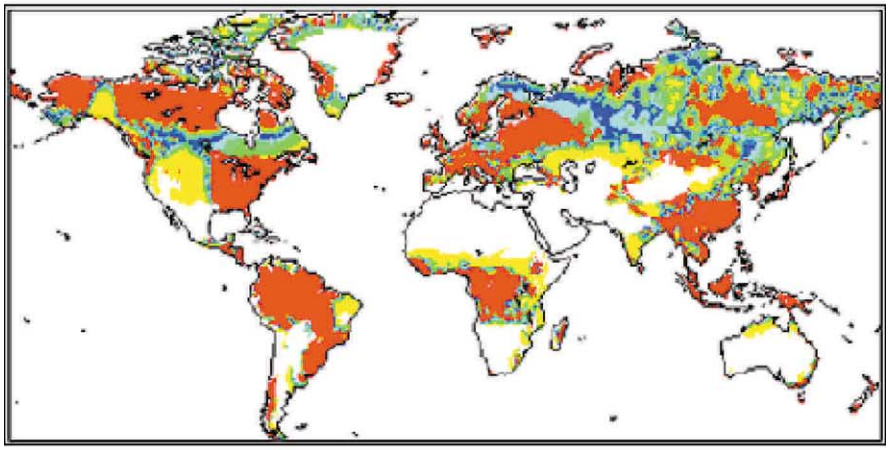
Fig. 2. Vegetation distribution in the climate space {precipitation, temperature}. BF—boreal forest; T—tundra; CH—chaparral; SG—summer-green (deciduous) forest; TF—tropical forest; RG—tropical rain forest; GR—grassland; DS—desert (from Lieth, 1975, with changes).



a)



b)



c)

Fig. 3

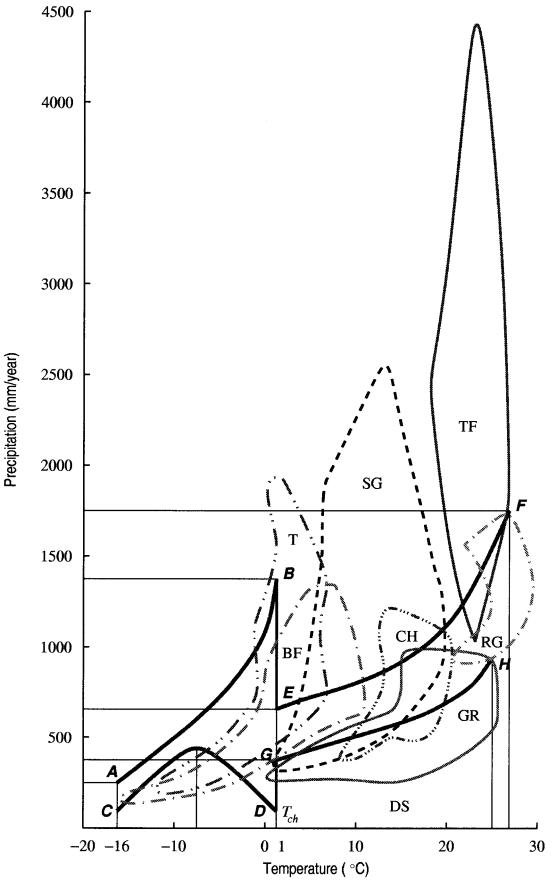


Fig. 4. Vegetation distribution in climate space {precipitation, temperature} with modified borders between "grass", "forest" and "grass–forest". Notations are as in Fig. 2.

c) at EF:

$$l_{\mathrm{f}} = \frac{1}{2(1-k_\tau^{\mathrm{d}})}\left(\sqrt{1+8\pi(1-k_\tau^{\mathrm{d}})^2\tau_m(T)}+1\right), \quad T \geq T_{\mathrm{ch}}, \tag{4.4}$$

d) at GH:

$$l_{\mathrm{g}} = \frac{1}{1-k_\tau^{\mathrm{d}}}, \; T \geq T_{\mathrm{ch}}, \tag{4.5}$$

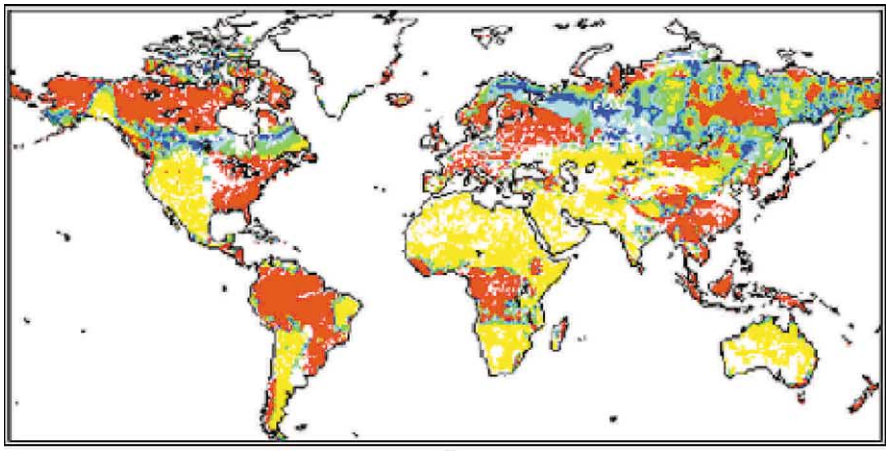
where the dependence $\tau_m(T)$ is defined by formula (3.1). Looking at Fig. 2, we see that there are two values of l for each T calculated by (4.2)–(4.5). These values are sufficient in order to estimate the coefficients b_0 and b_1 in (4.1). Denoting the value of precipitation on the borders by $P_{\mathrm{AB}}(T)$, $P_{\mathrm{CD}}(T)$, $P_{\mathrm{EF}}(T)$ and $P_{\mathrm{GH}}(T)$, we get the following formulas for l:

$$l = \frac{1}{1-k_\tau^{\mathrm{c}}} \times \left\{1 + \frac{\sqrt{1+8\pi(1-k_\tau^{\mathrm{c}})^2\tau_m(T)}-1}{2(P_{\mathrm{AB}}-P_{\mathrm{CD}})} \times (P_{\mathrm{AB}}(T)-P)\right\}, \quad T < T_{\mathrm{ch}}, \tag{4.6}$$

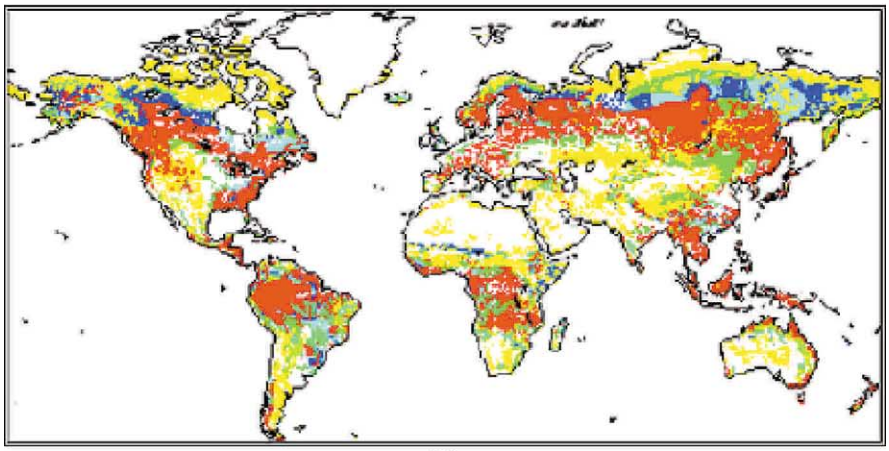
$$l = \frac{1}{1-k_\tau^{\mathrm{d}}} \times \left\{1 + \frac{\sqrt{1+8\pi(1-k_\tau^{\mathrm{d}})^2\tau_m(T)}-1}{2(P_{\mathrm{EF}}-P_{\mathrm{GH}})} \times (P-P_{\mathrm{EF}}(T))\right\}, \quad T \geq T_{\mathrm{ch}}. \tag{4.7}$$

In order to estimate the parameter γ_1, we rewrite the second equation of (1.3) in the following form: $\mathrm{d}p/\mathrm{d}t = (1/t_{\mathrm{suc}})(1-p)(lp_2-p)$. Then the characteristic time of the evolution for the forest function, i.e. the rate of change of area occupied by forest, is equal to $t_{\mathrm{suc}} = 1/\gamma_1$. This value can be interpreted as the time of succession "grass⇒forest" at a given site. It is natural to assume that the time of succession is approximately equal to the life span of trees, τ_l. Then $\gamma_l = 1/\tau_l = k_\tau/\tau_m$ where $k_\tau = k_\tau^{\mathrm{c}}$ for coniferous and $k_\tau = k_\tau^{\mathrm{d}}$ for deciduous forest.

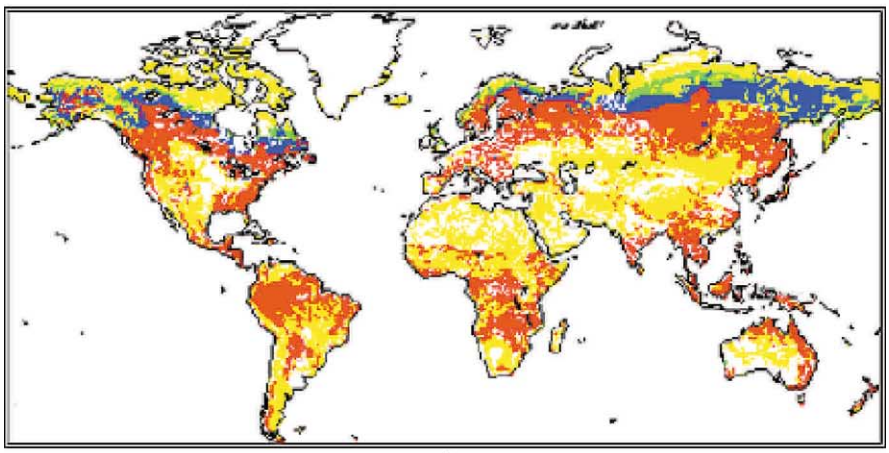
Fig. 3. The equilibrium GVPs: yellow—[0, 5% of forest], green—[5, 50], blue—[50, 85], red—[85, 100], white—deserts and ices. (a) The borders between different vegetation zones on Lieth's diagram are exponential. Tuning parameter $c = 10$. (b) The slope of borders is changed. Tuning parameter $c = 100$. (c) The borders are modified. Tuning parameter $c = 10$.



a)



b)



c)

Fig. 5

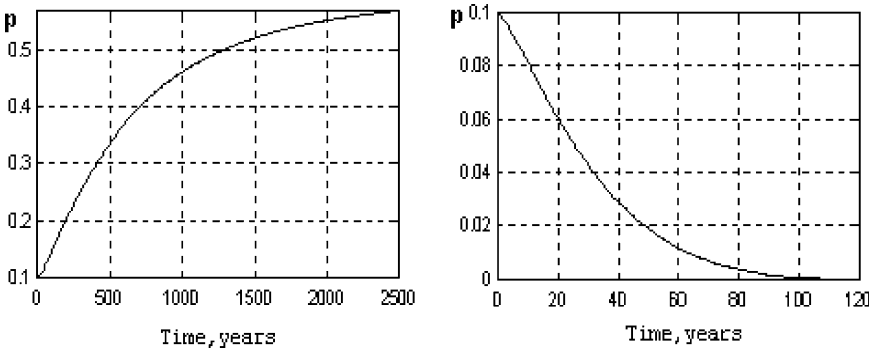


Fig. 6. Convergence to different vegetation equilibriums: the transition zone (left) and the "pure" grass (right); p is the forest fraction.

5. Calibration of borders on Lieth's diagram and corresponding equilibrium patterns

The first simple idea of calibrating border precipitation functions on Lieth's diagram is to use an exponential approximation. The border dependence of the annual precipitation (in mm) on temperature is presented in the following form:

$$P_{AB}(T) = 1107e^{0.047T}, \qquad P_{CD}(T) = 633e^{0.047T},$$
$$P_{DE}(T) = 683e^{0.035T}, \qquad (4.8)$$
$$P_{FG}(T) = 283e^{0.047T},$$

which is depicted in Fig. 2. Note that such a "rough" approximation of borders is optional. Later on we shall use more "accurate" approximation, and as a result, we get more realistic GVP. It is important that formulas for l, in which the values of $P_{AB}(T)$, $P_{CD}(T)$, $P_{EF}(T)$ and $P_{GH}(T)$ are given along the new borders, are the same. Now, when the borders were determined, we can calculate the dynamics of the GVP, which is determined by the given borders. For initial GVP we use two different biome maps corresponding to two classifications: the Box classes (aggregated) from TsuBiMo model (Box, 1981, 1995; Alexandrov et al., 1999) and the Olson classes (aggregated) suggested by Olson et al. (1985). These initial distributions are slightly modified so that in regions occupied only by "grass" there is a very low "forest" fraction and *vice versa*, a very low "grass" fraction in "forest" regions. This allows us to take into account spatial propagation of generative material. It is necessary since in the opposite case a solution of the system (1.3) cannot leave the zero initials states $p^0 = p_2^0 = 0$ and $p^0 = 1$, i.e. neither "grass" nor "forest" can spread to a new territory without such sort of mechanism.

The Cauchy problem for the GVP differential equations (1.3) is solved by the method of establishment on each grid cell with different values of free parameter c. The spatial distribution of current climate parameters is taken from the well-known Leemans–Cramer database (Leemans and Cramer, 1991) presented in a special format. The latter has a resolution $0.5^\circ \times 0.5^\circ$ which in turn determines the resolution of our models.

However, even the first model simulations with such type of border approximations demonstrate a high sensitivity to the choice of border form in Lieth's diagram (especially concerning regions with marginal annual temperatures—polar regions and Siberia—and tropical regions where the grass zone seems too narrow). Here, approximation (4.8) is too rough to reflect the real biome distribution with the model predicting forest equilibriums in the polar regions (see Fig. 3a). In the tropical regions, the transition equilibrium is shifted to the prevalence of grassland. As a result,

Fig. 5. The equilibrium GVPs under current climate conditions: yellow—[0, 5% of forest], green—[5, 50], blue—[50, 85], red—[85, 100], white—deserts and ices. (a) Box's biomes map is used as an initial spatial distribution, $c = 100$. (b) Olson's biomes map is used as an initial spatial distribution, $c = 100$. (c) Olson's biomes map: red → blue → green—forests, yellow—all types of grasslands.

we get too large forest areas both in the polar and tropical regions.

Note that functions (4.8) are monotonous. What will be the consequences of changing the slope? The result is the following: either forest occupies the entire Palaearctic region (when the slope increases) or biomes are shifted to the South (in the opposite case). This picture is shown in Fig. 3b where forest appears in the Siberian steppe and taiga is replaced by tundra. Apparently, in order to get better results it is necessary to change the form of borders for $T < T_{ch}$ and, may be to change the value of T_{ch}.

If we consider the different projections of the current GVP onto the climate spaces carried out by other authors (Holdridge, 1947; Prentice, 1990; Esser, 1991; Monserud and Leemans, 1992; Brovkin et al., 1998; Alexandrov et al., 1999), we can see that they differ (some more than others) from Lieth's diagram. It can be explained by the following possible reasons: firstly, the use of different classifications of vegetation and, as a consequence, of different vegetation maps; secondly, a relatively low correlation between the geographical location of vegetation type and the climate characteristics of a site. The latter is caused by large intersections of the domains, which correspond, to different types of vegetation in the climate space. This arbitrariness justifies our use of Lieth's diagram.

Let us keep in mind the following empirical facts connected with the situation in the North Eurasia (Bazilevich et al., 1986). When the mean annual temperature lies in the vicinity of 0 °C then a relatively small increase in precipitation (in comparison with precipitation at the northern border of forest) is accompanied by the complete domination of grassland communities at this site. Decreasing temperature to between −8 and −12 °C, we see that the forest border is shifted to higher precipitation values. This is verified by the appearance of coniferous boreal forest (taiga) at these sites. A further decrease in temperature leads, on the contrary, to a shift of the forest border to lower values of precipitation. The regions with higher precipitation are already occupied by tundra. All these empirical observations lead us, firstly, to decrease T_{ch} so that $T_{ch} \approx 1$ °C and secondly, to approximate the border between "forest" and "grass–forest" (transition) zones in the climate space by some unimodal function with single maximum within the interval $[T_{cr}, T_{ch}]$. The simplest form of such a function is the parabola $P_f = a_f T^2 + b_f T + c_f$, and we need three points in order to define its coefficients. We assume that its maximum is situated at $\{T_2 = -8°, P_2 = 400$ mm/year$\}$ and two lateral points are at $\{T_1 = T_{cr}, P_1 = 50$ mm/year$\}$ and $\{T_3 = T_{ch}, P_3 = 70$ mm/year$\}$. Of course, this assumption is very rough, but moving these points in accordance with the data we can obtain a "better" border curve. In order to determine the parabola coefficients, we have to solve the following linear algebraic system:

$$\begin{pmatrix} T_1^2 & T_1 & 1 \\ T_2^2 & T_2 & 1 \\ T_3^2 & T_3 & 1 \end{pmatrix} X = \begin{pmatrix} P_1 \\ P_2 \\ P_3 \end{pmatrix}. \tag{4.9}$$

The solution is $X \approx [-4.73, -69.78, 144.51]$. Note that a change in the grass border from exponential to parabolic form in this temperature interval does not essentially disturb the vegetation pattern.

As $T > T_{ch}$, exponential forms of borders are a good approximation of the real data (as they are shown in Fig. 4.

Finally, the border curves can easily be written as

$$\begin{aligned} P_{AB}(T) &= 1235.3e^{0.05T}, \\ P_{CD}(T) &= -4.73T^2 - 69.78T + 144.51, \\ P_{EF}(T) &= 431.5e^{0.05T}, \\ P_{GH}(T) &= 255.4e^{0.05T}. \end{aligned} \tag{4.10}$$

So, all the parameters of the model were identified, except $c = \pi_{22} = \pi$, which is the so-called "free parameter" for the user experiments.

6. Dynamics of the global vegetation and equilibrium vegetation patterns

It is interesting that in the equatorial regions the GVP depends weakly on the form of borders in Lieth's diagram. On the contrary, the GVP in the northern regions is sensitive to moving borders as mentioned in the previous section. If the response

of the GVP on the change of borders in Lieth's diagram is analysed more carefully we can see that their movement has the greatest influence on the width of the transition zone "grass–forest" in the geographic space.

The worst agreement between model simulation and real GVP can be seen in northern Greenland, where a coniferous forest is predicted instead of tundra and arctic desert. More detailed investigation has allowed us to understand the reason for such a disagreement between the model and reality. Here precipitation is too low and the equilibrium with low annual temperature always lies in the forest domain of Lieth's diagram. Also, attention is paid to the Siberian coast of the Polar ocean, which is covered by the transition zone with a relatively high percent of forest in spite of all efforts to "improve" Lieth's borders (see Fig. 3c). It can be explained by the insufficient accuracy of the model calculations in areas with low temperatures.

Note that variations in the tuning parameter c, which describe the intensity of competition within the mature tree cohort do not strongly change the GVP, influencing only the fraction of young forest (when c increases it increases, too).

It is interesting to point out that taking Olson's classes of Earth's vegetation as the initial forest distribution has no impact on the final "grass–forest" equilibrium configuration despite some important differences (stronger patchiness in Olson classification, for example) between Box and Olson distributions (Fig. 5a and b). For comparison, the Olson biome map for the contemporary climate is shown in Fig. 5c.

Thus, Fig. 3c and Fig. 5a and b show sufficient approximation of the model simulation to the real vegetation distribution, and therefore we are confident in the ability of the model to simulate accurately the GVP under CO_2 doubling climate scenarios.

It is clear that we have to integrate the model equations at each geographical point until equilibrium is reached in order to get the map of the equilibrium GVP. The additional result is a time taken to reach equilibrium. If in order to establishing of "pure" equilibriums, such as "grass" and "forest", 30–50 years are necessary then the establishing time of "mix" equilibrium in the transition zone is about 1500–2000 years. This means that a real transformation of the GVP, which is really described by local (but continuous) shifts of border between forest and grass biomes and formation of new transition zone, is a very slow process Fig. 6.

7. Conclusions

Although simple probabilistic "urn" schemes of the dynamics of GVP imply sufficiently complex behaviour, its simplified equations with biologically motivated parameters have only three equilibriums corresponding to " grass ", transition "grass–forest" and "forest" zones. Stability domains of these equilibriums are not intersected in the parametric space. After calibrating parameters with climatic and vegetation data, we obtain a model which simulates forest and grass distribution in acceptable agreement with reality under current climatic conditions. Certainly, we could use more detailed vegetation structure (like Olson's map) but it would make the model more cumbersome having increased both the number of equations and number of uncertainties in the process of calibration.

Since the final GVP depends (substantially) on the form of borders between forest, grass and mixed biomes in the climatic space {*temperature, precipitation*}, we modified the classic Lieth diagram in order to obtain the better agreement between the real and model GVP. It was also shown that a "relaxation" time (time to reach an equilibrium) for the transition zone of more than one order of magnitude greater in comparison with time for "pure" equilibriums, "grass" and "forest", was needed. This means that a real transformation of the GVP under climate change is a very slow process.

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