ABSTRACT
This paper presents the results of application of landscape-ecological methods for evaluation of biotic regulation of the carbon cycle in forest ecosystems. Methods for constructing analytical and cartographic empirical-statistical models for identification of forest associations and zonal/regional types of forest formations capable of stabilizing the continental biosphere under changing climate are described. Possible biotic regulation of the carbon cycle under known scenarios of future greenhouse warming is suggested. The maps on the carbon content and its changes in the forests of the Oka river basin are presented.

KEY WORDS: ecosystem, biogeocoenoses, climatic changes, empirical statistical modeling, cartographic approach, ecological prediction.

INTRODUCTION
Understanding mechanisms of sustainability of the continental biosphere under changing climate is connected, in many respects, with studying the biotic regulation of the carbon cycle in the soil–vegetation–atmosphere system. These problems have already been highlighted in quite a number of papers both in Russia and abroad [Gorshkov, 1994; Climate..., 1996; Aber et al, 2001; Celniker, 2006; et al]. However, while a strong emphasis is placed on a procedure for determination of carbon pools in different components of phytobiota and in soil, as well as on the functioning of the carbon cycle and the current carbon content in forests, wetlands, and other ecosystems, problems of quantitative assessment of responses of different biotic components of the carbon cycle to global climatic changes are illustrated to a much lesser extent. Thus, there are actually no predictions of the climatogenic dynamics of factors effecting biotic regulation of CO₂ content in the atmosphere.

Further development of the concept of biotic regulation may be achieved through studies of local-regional mechanisms of the biological cycle that provides stability of natural environment in accordance with the Le Chatelier’s principle. Biogeocoenoses (landscape facieses), i.e. ecosystems of the topological level, is the most complex and active part of natural environment, i.e., its functional “core” [Sochava, 1974]. This elementary unit of geographical ecology accepted in Russia corresponds to the categories “site,” “ecoelement,” and “landtype phase” in classifications of Australia-Britain, Canada, and USA, respectively [Klijn and Udo de Haes, 1994]. Spatial diversity of biological cycles is created primarily by structural heterogeneity of biogeocoenoses. The concept of biotic regulation of the carbon cycle in the biosphere has not been yet developed in such statement of the problem. The forest cover is one of the leading factors providing for the stability of the continental...
biosphere. Forest ecosystems are the most potent regulators and stabilizers of natural biogeochemical cycles [Sukachev, 1972], including the carbon cycle and the temperature regime of the atmosphere [Gorshkov, 1994]. Global-scale deforestation is considered one of the main causes of the increasing greenhouse effect.

BACKGROUND

This problem was addressed in the previous regional environmental forecast studies of forest ecosystems in the headwater area of the Volga River basin [Kolomyts, 2008]. It has been empirically established that the main channel of connections of regional and local ecosystems with the background climatic system passes through the summer soil moisture which is the most powerful ecological factor predetermining ecosystem territorial distribution and main functional parameters. In turn, this factor itself depends mainly on the average July temperature, while its association with the average January temperature is non-significant. The leading climatic factor of future ecological reconstructions is temperature change during the vegetation period.

Biotic regulation of the carbon cycle under changing climate is determined by the shifts in small biological cycles (phytomass production and degradation). A temporal lag of these functional changes is relatively small. Climatogenic shifts in the rates of phytomass production appear during the first several years in the taiga zone and are completed within a year in the sub-zone of broadleaf forests [8]. Changes in decomposition rates are of the same order, however the total duration of carbon presence in the forest litter, coarse woody debris, and mobile soil humus may take several decades.

THE LANDSCAPE-ECOLOGICAL APPROACH TO THE PROBLEM

The problems of forecasting forest ecosystem dynamics under changing climate have been poorly developed. International prognostic developments [Climate..., 1995; Aber et al, 2001; etc] are mainly small-scale and, hence, cannot reveal basic mechanisms accounting for the spatial variability of responses of forest communities to the same background climatic factors. In addition, behavior of local ecosystems under climatic changes has been poorly studied. The so-called models of landscape mosaic [Forman, 1995] deal with comparatively small areas of the forest cover selected on the basis of functional characteristics of structurally homogeneous areas. However, these models are spatially limited because they describe only typical sites in typical biomes, rather than the entire topological diversity of the ecosystems.

We offer the approach to analysis of biotic regulation phenomena from a broader landscape position. It allows one to identify diverse types of this regulation mechanism determined by the spatial distribution of biogeocoenoses under different zonal/regional conditions. This makes it possible to find the origins of the mechanisms of the phytobiota effect on the carbon exchange between the earth surface and the atmosphere and to identify mechanisms that ensure the resistance of terrestrial ecosystems to climatic changes.

The local landscape-ecological prediction presented herein is based on construction of discrete empirical-statistical models of much more complicated geo-(eco-) systems [Rozenberg, 1984; Kolomyts, 2008]. These models describe behavior of geo-(eco-) systems as the indivisible complex formations in the aspect of the Sukachev’s biogeocoenoses concept [Sukachev, 1972]. They make it also possible to work with a small number of the most informative characteristics. The results obtained are probably not as accurate as, for instance, at simulation modeling [Aber et al, 2001], but they have a higher level of spatial resolution.

FIELD DATA FOR MODELING

Materials of large-scale landscape-ecological surveys carried out by the authors at six experimental test sites of the Middle and
**ENVIRONMENT**

Fig. 1. Landscape couplings of the predicted carbon balance dynamics in forest biogeocoenoses under different zonal/regional conditions of the Middle and Upper Volga Regions, according to the scenarios of HadCM3 model.

| ΔC(Fa) – carbon balance (t/ha); TE, E, T, TA-A, Saq – local sites (see in the text); solar exposed slopes: sun – sunny, shad – shady and neutral |
| --- |
| **A. Zhguli low-mountain range, south forest-steppe (at its south boundary), pine and oak-linden forests** |
| ΔC(Fa) | TE | E | T | TA-A | Saq |
| --- | --- | --- | --- | --- | --- |
| 0 | -50 | -40 | -30 | -20 | -10 |
| **B. High-plan farewell Shchelokovsky Farmstead (high right bank region of by-Volga river), north forest-steppe (at its north boundary), oak and linden forests** |
| ΔC(Fa) | TE | E | T | TA-A | Saq |
| --- | --- | --- | --- | --- | --- |
| 0 | -50 | -40 | -30 | -20 | -10 |
| **C. By-Volga high plain, high right-bank region of by-Sura river (By-Sura), middle forest-steppe, pine and oak-linden forests** |
| ΔC(Fa) | TE | E | T | TA-A | Saq |
| --- | --- | --- | --- | --- | --- |
| 0 | -50 | -40 | -30 | -20 | -10 |
| **D. High-plan uralishche (stow) Green Town (high right-bank region of by-Volga river), north forest-steppe (at its north boundary), boundary between forest-steppe and sub-taiga zones, mixed and conifer forests** |
| ΔC(Fa) | TE | E | T | TA-A | Saq |
| --- | --- | --- | --- | --- | --- |
| 0 | -50 | -40 | -30 | -20 | -10 |
| **E. By-Oka-Terrace biosphere reserve (lowland Middle left-bank region of by-Oka river), south boundary of sub-taiga zone, mixed, conifer, broad- and small-leaved forests** |
| ΔC(Fa) | TE | E | T | TA-A | Saq |
| --- | --- | --- | --- | --- | --- |
| 0 | -50 | -40 | -30 | -20 | -10 |
| **F. Okata ha forested lowland in the Lower by-Oka region (vicinity of the town Vyksa), south outpost of sub-taiga zone, spruce-pine forests** |
| ΔC(Fa) | TE | E | T | TA-A | Saq |
| --- | --- | --- | --- | --- | --- |
| 0 | -50 | -40 | -30 | -20 | -10 |
| **G. Kerzhensky Reserve (trans-Volga outwash forested lowland), south strip of sub-taiga zone, pine and spruce forests of south-taiga appearance** |
| ΔC(Fa) | TE | E | T | TA-A | Saq |
| --- | --- | --- | --- | --- | --- |
| 0 | -50 | -40 | -30 | -20 | -10 |

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Upper Volga Region (1987–1998) were used in a method specifically developed for the forecast analysis. These test sites contain a wide range of zonal plant formations, from the southern forest-steppe to mixed forests (Fig. 1). Each of these test sites characterizes a particular regional ecosystems, with the corresponding conventional name (Zhyguli, Shchelokovsky Farmstead, By-Sura, Green Town, etc.).

Six facies groups that represent general diversity of forest types and test sites have been isolated based on 45–50 sample areas in each of the test sites. The facies groups were located along the vector of the local landscape couplings (microcatenae) in the direction of edaphic moistening increase: from the eluvial (E) and the transeluvial (TE) types of local sites (geotopes) through the slope transit (T) and the transaccumulative (TA) to the accumulative (A) and superaqual (Saq), according to the classification [Glazovskaya, 1964].

A similar system of landscape couplings is characteristic of the mesorelief types at the regional level couplings [Polynov, 1956]. The flat interfluve (placor) group was isolated within the biogeocenoses (this group occupies eluvial locations and represents a local type of zonal bioclimatic norm for a given ecoregion). The biogeocenoses of other geotopes were considered extrazonal, reflecting background condition of other regions, often considerably distant.

The following phytomass parameters (t/ha) were used for calculation of the carbon balance: (1) skeletal tree-shrub phytomass, BS; (2) root mass, BR; (3) total green mass, BV; (4) forest litter mass, ML; (5) debris – dead skeletal mass (brushwood and dead-wood), WD; (6) humus in soil organic-mineral layers, HU.

The regional climate scenarios for the period to 2100 were taken from one of the most extreme global coupled atmosphere ocean general circulation models (AOGCMs) [Climate..., 1996] – HadCM3, version A2 (Hadley Centre of Climate Research, UK) [Pope et al, 2000]. Ecological prediction by this model permits one to evaluate the forest ecosystems feedback to global climatic changes that may exceed the level of tree endurance and cause the disintegration of both nemoral and boreal forests within large areas.

The entire forecast period in our analysis included five intervals (20–25 yrs duration): 1985–2010, 2010–2030, 2030–2050, 2050–2075, and 2075–2100. The period of meteorological observation for 1881–1985 represented the baseline. Recent global warming began at the end of this period [Climate ..., 1996]. The model forecasts a 5.5–7.0°C increase of the mean July temperature in the Middle Volga Region by the end of the 21st century. According to this scenario, the annual precipitation will remain virtually unchanged; therefore, the humidify factor $C_{hum}$ will decrease from 0.95 to 0.36 in the southern forest-steppe of the Zhyguli region and from 1.37 to 0.65 in sub-taiga of the Volga region. Thus, until the year of 2100, the thermo-arid climatic trend will be developing in the entire Middle Volga Region. We have assumed this scenario as the basis for our analysis of climatogenic dynamics of the functional parameters of forest ecosystems.

METHODS OF FORECAST ANALYSIS

The Le Chatelier’s principle for stability of natural environment is expressed by the following postulate [Gorshkov, 1994]: the state of environment will be stable if any spontaneous increase of CO$_2$ content in the atmosphere is accompanied by an equal enhancement of carbon utilization by the terrestrial and ocean biota. An apparent violation of the Le Chatelier’s principle is the transformation of biota from the carbon sink into the carbon source, i.e., the situation when biota releases CO$_2$ into the atmosphere under external influence.

The potential of biotic regulation has been assessed using hydro-thermal ordination of metabolic characteristics of forest topoecosystems under different zonal/
regional and local conditions (an empirical simulation of anticipated climatogenic changes of biological cycle). The ordination was performed by soil temperature at the depth of 50 cm and by summer productive moisture reserves of the 0–50 cm soil layer.

As can be seen from Table 1, the correlation is not always high, though quite significant ($P < 0.05$). At a weak connection, the latter can be interpreted only as a certain general tendency of changes of given parameters under the influence of the geophysical trend.

To assess changes of the carbon content in different biotic components, we used the so-called forestry method based on the dynamics of live and dead phytomass. This method gives the best results at balance assessments of the carbon cycle components for long periods of time [Celniker, 2006]. The change $\Delta C(Fa)$ of the carbon flow in the soil-plant-atmosphere system was calculated as follows:

$$\Delta C(Fa) = \Delta C(WD) + \Delta C(ML) +$$

$$+ \Delta C(HU) - \Delta C(BS) - \Delta C(BV) - \Delta C(BR). \quad (1)$$

This balance equation was used to calculate possible changes of the carbon flows between the soil-plant cover and the atmosphere for different periods of the forecast for each

| Table 1. Examples of calculation models that describe changes of biogeocoenotic biological cycle parameters of different regional ecosystems in the Middle Volga Region under trends of changes in soil temperature and soil moisture content during the vegetation period |
| --- |
| **Model type (calculation formula)**) | **Regional ecosystems (see Fig. 1)** | **Parameters (see in the text)** | **Coefficients** | **Statistical characteristics **)** |
|  |  |  | $b_0$ | $b_1$ | $b_2$ | $R$ | $P$ | $S_y$ |
| By-Sura | BV | $b_0 + b_1x_1 + b_2x_2$ | 21.93 | -0.7415 | -0.7135 | 0.664 | 0 | 3.09 |
| HU | $b_0 + b_1x_1$ | 5.99 | 0 | 55.77 | 0.696 | 0 | 20.29 |
| Zeleny | BR | $b_0 + b_1x_1 + b_2x_2$ | 8.712 | 5.838 | -0.0678 | 0.582 | 0.1 $\times 10^{-1}$ | 17.92 |
| Shchelokovsky Hutor | HU | $b_0 + b_1x_1$ | 16.34 | -0.2402 | 0.07426 | 0.713 | 0 |
| ML | $b_0 + b_1x_1 + b_2x_2$ | 27.18 | -2.333 | 0.04896 | 0.717 | 0 | 6.51 |
| Shchelokovsky Hutor | WD | $b_0 + b_1x_1 + b_2x_2$ | 642.1 | -114.7 | 5.142 | 0.936 | 0 | 2.21 |
| Zhyguli | ML | $b_0 + b_1x_1 + b_2x_2$ | 44.08 | -0.3611 | 0.00091 | 0.699 | 0 | 17.75 |
| Shchelokovsky Hutor | BS | $b_0 + b_1x_1 + b_2x_2$ | -34.93 | 0.9472 | 0.00403 | 0.769 | 0 | 90.49 |
| HU | $b_0 + b_1x_1$ | 12.5 | 0.1712 | 0 | 0.649 | 0 | 9.31 |
| Kerzhenets | WD | $b_0 + b_1x_1 + b_2x_2$ | 22.85 | -0.2588 | 0.00149 | 0.72 | 0 | 12.78 |
| HU | $b_0 + b_1x_1$ | 8.84 | 0.0091 | 0.0006 | 0.851 | 0 | 8.03 |
| Prioksko-Terrasny reserve | BS | $b_0 + b_1x_1 + b_2x_2$ | 244.6 | 0.3956 | -0.00312 | 0.557 | 0.7 $\times 10^{-1}$ | 71.4 |
| ML | $b_0 + b_1x_1$ | 25.31 | 0.0159 | 0.00042 | 0.577 | 0.4 $\times 10^{-3}$ | 16.32 |
| Zhyguli | BS | $b_0 + b_1x_1 + b_2x_2$ | 3.706 | 15.42 | 0 | 0.611 | 0 | 39.3 |
| BR | $b_0 + b_1x_1$ | 1.768 | 26.26 | 0 | 0.614 | 0 | 12.25 |
| Zeleny | ML | $b_0 + b_1x_1 + b_2x_2$ | 0.0845 | 35.08 | 0 | 0.506 | 0 | 16.0 |
| Gorod | WD | $b_0 + b_1x_1 + b_2x_2$ | -4.389 | 64.63 | 0 | 0.642 | 0 | 7.0 |

*) $x_1$ – soil temperature at 50 cm depth ($t_{50}$); $x_2$ – stored soil moisture in 0–50 cm layer (W-50).
**) $R$ — coefficient of correlation; $P$ – significance level (the Pearson criterion); $S_y$ — coefficients of standard deviation. Significant arguments in equations of multiple regression are shown in the bold font.
group of facies in all examined six regional ecosystems (mentioned above). Each member of the right part of the equation (1) may have both positive and negative values. At positive values, the first three members of the equation provide for an increase of CO₂ emission from the soil-plant cover to the atmosphere, while the other three members provide for a decrease of this flow. In this case, the dead phytomass pool acts as an additional carbon source, while the live phytomass plays the role of its sink (i.e., deposit).

At negative values of the above parameters, the results are quite the opposite. Thus, the overall balance of changes of carbon exchange between biogeocoenoses and the atmosphere is described by \( \Delta C(Fa) \), which shows whether this group of forest ecosystems consumes additional amount of CO₂ from the atmosphere due to the shifts in the biological cycle induced by global warming or, on the contrary, becomes a source of additional CO₂ emissions.

New methods of geomorphometry were used in the cartographic part of the forecast analysis [Shary, 2001; Shary et al, 2002]. Multidimensional environment-forming properties of relief allow interpolation and extrapolation (substantiated during the analysis) of the data measured (or calculated) on representative test sites, thus significantly extending the boundaries of the analyzed territory. The currently known methods of a quantitative relief description are confined to six basic morphometric values. Herein, we used a system of 18 parameters introduced by P. A. Shary [Shary et al, 2002].

At the local level, large-scale mapping (1:50–100,000) was based on predetermined, statistically significant linkages of the structural and functional characteristics of local ecosystems with morphometry of the relief. Morphometric parameters were derived from the NASA data (SRTM3, Shuttle Radar Topography Mission at resolution 3° arc seconds or 90 m on equator, http://dds.cr.usgs.gov/srtm/version2_1/SRTM3/) on the earth surface elevations as matrices with a cell size (grid spacing) of 50 m recalculated into the Gauss-Kruger projection for the 9th 6° zone. For instance, the following multiple regression equations (with the corresponding Spearman correlation coefficient \( r_s \) and the level of significance \( P \)) were obtained for the Zhyguli ecoregion:

The total C sources of the baseline period –

\[
C_{base} = 222.6 - 55.6 \cdot GA - 25.6 \cdot Q - 12.6 \cdot H; (r_s = 0.87, P < 10^{-6});
\] (2)

the change in the total C stocks by 2050 –

\[
\Delta C_{2050} = -99.8 + 47.1 \cdot GA + 25.3 \cdot Q + 18.0 \cdot H; (r_s = 0.88, P < 10^{-6}).
\] (3)

Here, \( H \) – mean curvature; designations of other predictors are given in the note to Table 3.

Regional maps were constructed using the NASA satellite data on the relief: the matrices of earth surface elevations obtained as a result of implementation of SRTM project (SRTM30, Shuttle Radar Topography Mission, at resolution 30° arc seconds or 900 m on equator, http://dds.cr.usgs.gov/srtm/version2_1/SRTM30/).

The Oka river basin was taken as the model territory at the regional level. The matrix for this basin was transformed into the Kavraysky VII INT projection for the European Russia with a 900 m grid. In advance, the statistical analysis of spatial differentiation of changes in the total C content had been performed for predictive periods for the plant formations and their combinations using program "Analytical GIS Eco" [Shary, 2001].

Transition from the local to the regional level of forecast with construction of maps at 1:2,500,000 scale was carried out using our method of induction-hierarchic extrapolation. The method utilizes the
empirically established phenomenon of poly-zonality of local geo-(eco-) systems as a form of their response to global climatic changes [Kolomyts, 2008]. The regional systems of local zonality were isolated based on the identified patterns of the influence of local geomorphological and edaphic factors on the background regional-bioclimatic environment. These regional systems are composed of the vector rows of flat interfluve and extrazonal biogeocenoses (see above) that correspond to the vector of the predicted climate changes. These rows may serve as a model of the main trends of ecosystem changes.

The procedure of extrapolation was as follows. Each type/subtype of plant formations distinguished on the small-scale geobotanic map was correlated with a certain group of biogeocenoses from their flat interfluve and extrazonal series in a given ecoregion. This series characterizes the regional spatially ordered system of local zonality (microcatena). Then, each range of a given formation represented as a poly-vector set of mesocatenae was broken into mesosites, i.e., the links of the chain of the regional landscape couplings (E → TE → T → TA, A; see above), with division of the TE and T locations into two solar-exposure gradations (sunny and shady). New methods of geomorphometric statistics were applied. Then, it was possible to create an intermediate map of mesoscale sites for the entire forested area of the region. For the Oka river basin, such map was compiled using multiple regression equations applied to the data of the test sites Shelokovsky Farmstead, Green Town, Vyksa, Kerzhenets, and the Prioksko-Terrasny reserve.

Assuming that in accordance with the B.B. Polynov’s conception of landscape couplings [Polynov, 1956] a mesocatena is a homomorphic image of microcatenae, we aggregated the biogeocenoses of all isolated groups at each test sites into mesogeotopes of a corresponding geobotanical range. Thus obtained the regional phytocatenae mosaic was, then, supplemented with the baseline or predictive metabolic parameters of the biogeocoenoses serving as local representative members of different zonal-regional types/subtypes of the geographic environment. The described algorithm of induction-hierarchic extrapolation is a fundamentally novel method of regional predictive mapping based directly on the materials of field landscape-ecological surveys.

MODELING RESULTS AND THEIR DISCUSSION

Predictions by Analytical Models

The main results of the empirical-statistical prediction are given below (they are described in more detail in our previous publications [e.g., Kolomyts, 2008; Kolomyts and Rozenberg, 2009].

1. The decomposition part of the biological cycle, as a rule, is more sensitive to climatic changes than the productivity part [Kolomyts, 2009]; therefore, the decomposition part should react to climatic changes first. At the same time, during sufficiently long periods of time, the maximal (by absolute values) changes occur not in the decomposition part of the cycle, but in its autotrophic biogenesis part. The skeletal tree-shrub phytomass (BS), mainly increment of woody biomass, represents the greatest part of the shifts of productivity (Table 2). By 2100, changes of the total carbon content ($\Delta C(BS)$) in its extreme values will range from $\sim (37-62) \ t/ha$ in E and TA of oak-linden forests of the Zhiguli and Shelokovsky Farmstead to $+ (95-100) \ t/ha$ in TE and E of coniferous-broadleaf forest of the Nizhnyi Novgorod Volga region. The extreme values of changes $\Delta C(Fa)$ will comprise from $\sim (78+100) \ t/ha$ to $+(115+120) \ t/ha$. These values represent the potential range of climatogenic changes of the carbon flows in the live skeletal phytomass and in the biogeocoenoses in general. The baseline values for the first, second, and the third regions were 140–190, 134–2,112, and 180–243 t/ha, respectively. Therefore, in the coming century, the content of carbon...
Table 2. The forecasted component and balance changes in the carbon content (t/ha) relative to the baseline period in flat interfluvue forest biogeocoenoses under different zonal-regional conditions of the Middle and Upper Volga Regions

| Parameters (see in the text) | Base values | Changes in predicted periods |
|------------------------------|-------------|------------------------------|
|                              |             | 2010 | 2030 | 2050 | 2075 | 2100 |
| a) Zhyguli                   |             |      |      |      |      |      |
| BS                           | 82.78       | -23.05 | -27.32 | -31.55 | -37.53 | -43.69 |
| BV                           | 4.39        | -1.60  | -1.77  | -1.93  | -2.10  | -2.26  |
| BR                           | 30.25       | -11.90 | -14.08 | -16.13 | -18.06 | -19.72 |
| WD                           | 10.24       | -6.98  | -7.53  | -8.02  | -8.45  | -8.80  |
| ML                           | 5.24        | 3.56   | 4.90   | 6.34   | 7.78   | 8.99   |
| HU                           | 61.47       | -10.54 | -15.29 | -18.62 | -20.65 | -21.66 |
| Balance                      | 198.61      | -50.51 | -61.09 | -69.91 | -77.29 | -83.11 |
| b) By-Sura                   |             |      |      |      |      |      |
| BS                           | 123.42      | -18.99 | -14.77 | -10.84 | -3.31  | 2.90   |
| BV                           | 5.17        | -0.60  | -0.61  | -0.84  | -0.93  | -1.13  |
| BR                           | 40.40       | -8.88  | -8.04  | -7.82  | -6.46  | -5.64  |
| WD                           | 4.90        | -1.06  | -1.23  | -1.46  | -1.71  | -1.91  |
| ML                           | 5.88        | -1.28  | -1.60  | -2.03  | -2.45  | -2.79  |
| HU                           | 31.64       | -9.76  | -11.09 | -11.45 | -13.53 | -14.76 |
| Balance                      | 211.41      | -40.56 | -37.34 | -34.42 | -28.39 | -23.33 |
| c) Green Town                |             |      |      |      |      |      |
| BS                           | 134.14      | 13.73  | 26.61  | 38.16  | 49.82  | 60.19  |
| BV                           | 6.59        | 1.90   | 2.32   | 2.65   | 3.01   | 3.30   |
| BR                           | 39.48       | 4.44   | 7.99   | 11.09  | 14.28  | 17.06  |
| WD                           | 4.06        | -3.46  | -3.63  | -3.73  | -3.80  | -3.84  |
| ML                           | 5.48        | -0.13  | -1.00  | -1.60  | -2.05  | -2.38  |
| HU                           | 11.16       | -1.71  | -2.28  | -2.65  | -3.11  | -3.43  |
| Balance                      | 201.36      | 14.77  | 30.0   | 43.91  | 58.15  | 70.9   |
| d) Prioksko-Terrasny reserve |             |      |      |      |      |      |
| BS                           | 155.09      | -27.14 | -27.85 | -27.76 | -27.99 | -27.91 |
| BV                           | 6.00        | -1.98  | -1.88  | -1.89  | -1.87  | -1.88  |
| BR                           | 42.41       | -4.11  | -4.30  | -4.28  | -4.34  | -4.32  |
| WD                           | 15.66       | -7.44  | -7.19  | -7.21  | -7.15  | -7.17  |
| ML                           | 7.48        | 6.58   | 9.44   | 9.58   | 12.69  | 11.14  |
| HU                           | 12.79       | 2.84   | 2.52   | 2.55   | 2.48   | 2.51   |
| Balance                      | 239.43      | -31.24 | -29.25 | -29.0  | -26.17 | -27.61 |
| e) Kerzhensky reserve        |             |      |      |      |      |      |
| BS                           | 84.7        | -13.00 | -12.64 | -11.86 | -11.85 | -11.15 |
| BV                           | 4.41        | 1.21   | 1.19   | 0.82   | 0.86   | 0.60   |
| BR                           | 17.08       | -9.44  | -9.81  | -11.68 | -11.60 | -12.59 |
| WD                           | 7.85        | 0.40   | 0.26   | -0.31  | -0.40  | -0.64  |
| ML                           | 10.15       | 3.91   | -4.16  | -4.71  | -4.73  | -3.45  |
| HU                           | 13.69       | -2.45  | -3.41  | -3.50  | -3.66  | -4.09  |
| Balance                      | 137.88      | -27.19 | -29.09 | -33.24 | -31.38 | -31.32 |
stored in the skeletal phytomass of the forest ecosystems of the Middle Volga region may change by ±(25–50)% and more on average compared to the baseline values. This fact points to quite a significant regulating role of the regional mixed and nemoral forests' productivity in their carbon exchange with the atmosphere.

2. Global warming will induce, in some cases, an abrupt drop or, in other cases, an increase of similar magnitude of forest productivity, which will directly affect the carbon balance. Zonal-regional contrasts of biotic regulation of the carbon cycle may be evaluated by the value $\Delta(Fa)$ for the eluvial (flat interfluve) ecosystems (see Table 2).

Within the territory of the southern and the middle forest-steppe, there will be an unambiguous and quite clear decline of the productivity potential of forest communities. Carbon deposition in the skeletal phytomass will decrease most quickly in flat interfluve mesophilic elm-lime and oak forests of eroded-loamy uplands (see Fig. 1, A–C). Their role as a sink of atmospheric carbon will diminish. The rates of carbon sequestration in the skeletal phytomass within the aqueous-glacial plains of the nemoral-forest sub-zone, the most hydromorphic A and EA–Saq birch-spruce-pine forests will be markedly reduced. At the same time, the rate of carbon sequestration of xeromorphic biogeocoenoses, particularly of forest-meadow-steppe communities on steep sunny slopes and that of pine steppified forests of well-drained watersheds, will change little; therefore, their contribution to the changes in the carbon balance will be insignificant.

At the same time, soil moisture deficit of the zonal forest-steppe ecotones will increase under global warming and impede decomposition and mineralization of the above ground dead organic matter. This will result in the increase of forest litter mass $ML$ and debris $BW$. However, there will be even greater mineralization of the humus mass $HU$ resulting in additional $CO_2$ emissions to the atmosphere (see Table 2, a).

The primary productivity and reserves of living organic matter of the mixed and dark coniferous forest biogeocoenoses of the forest-steppe zone (at the northern boundary) and of the southern strip of the sub-taiga zone will increase (and quite significantly). Accordingly, conservation of atmospheric carbon in the perennial skeletal phytomass of these topoccosystems will also increase and, as a consequence, the significance of this phytocoenotic pool as a carbon sink will increase as well (see Table 2, c, and Fig. 1, D). On the other hand, the thermo-arid trend will intensify the processes of decomposition of dead organic matter even further and, correspondingly, will reduce its mass (including the forest litter) and the humus mass as well. These processes will result in additional release of $CO_2$ from the soil-plant cover to the atmosphere.

On the outwash forested lowlands of the sub-taiga zone, the thermo-arid trend will induce a decrease of the total annual forest production, which must result in a lower amount of $CO_2$ bound by photosynthesis. Changes in the detritus part of the biological cycle will be more explicit and intensive. Soil temperature rise and soil drying will increase abruptly degradation of dead organic matter with higher degree of its utilization and additional release of $CO_2$ to the atmosphere (see Table 2, e, and Fig. 1, F, G).

3. Under global warming, two mutually antithetical phenomena of carbon cycle biotic regulation in the soil-vegetation-atmosphere system will be developing on the Russian Plain. The extreme south of the forest zone will be the source of significant additional emissions of carbon to the atmosphere. Accordingly, the natural balance of the carbon cycle as one of the leading stabilizing mechanisms of the continental biosphere will be disturbed. It will inevitably accelerate the process of degradation and disappearance of marginal forests in the southern and typical forest-steppe. The flat interfluve conifer and mixed
forests of the sub-taiga outwash lowlands will play similar negative role in the change of the carbon balance.

The main positive biotic regulation of the carbon exchange between the terrestrial ecosystems and the atmosphere reducing the greenhouse effect (according to the Le Chatellier’s principle) will be performed by mixed and coniferous forests of high plains in the nemoral-forest sub-zone and in the southern strip of the sub-taiga zone. Excessively moist forests and extremely dry pine forests of sub-taiga outwash lowlands will be of secondary importance. Probably, this is the only group of formations of boreal forests that will essentially support the stability of continental biosphere under global warming.

Predictive Scenarios in Cartographic Expression

As examples, let us consider the cartographic models of the carbon balance of forests for the period up to 2050. The fragments of $C_{base}$ and $\Delta C(Fa)$ maps of the Zhyguli forests are presented at the local level (Fig. 2). In the baseline period,

![Cartographic models of carbon balance](image_url)
Fig. 3. The fragments of the maps on the total carbon content and its forecasted changes within the territory of the Oka river basin.

a. The distribution of the carbon content at the end of the baseline period (1985). The carbon stocks (t/ha):
1 – 10.2–15.0; 2 – 15.0–19.3; 3 – 43–130; 4 – 130–160; 5 – 160–200; 6 – 200–423; 7 – the northern area of steppes

b. The changes in the total carbon stocks for the forecast period of 2050 relative to the baseline (t/ha):
1 – (–1.3)÷0; 2 – 0÷5.5; 3 – (–115)÷(–89); 4 – (–89)÷(–38); 5 – (–38)÷(–12); 6 – (–12)÷0; 7 – 0÷38; 8 – 38÷63; 9 – 63÷115. 1, 2 – fragmentary large tracts of forest among agricultural land; 3–9 – forest areas. 10 – the northern area of steppes
the highest total carbon stocks are typical of the gentle near-watershed shady slopes of the Zhyguli with the least catchment area. In the forecast period, these locations, as well as the bottoms of small valleys, will be characterized by the maximal CO₂ emissions. On steep slopes, the initial carbon stocks are minimal and the forecasted release of carbon will be insignificant too.

The regional level is represented, as mentioned above, by the Oka river basin (Fig. 3). Multiple regression equations used for construction of the maps are presented in Table 3. Under global warming, the modern forest cover of this territory will perform positive (as a whole) carbon cycle regulation. However, the scale of this regulation will not be of any significance due to relatively low changes in the carbon content in most of the pools, including the skeletal phytomass (see Fig. 1, E, F).

The forecast map shows also the pronounced contrast and frequent patchiness of positive and negative values of the carbon balance. A particularly patchy distribution of (ΔC(Fa)) varying from +(65–100) to –(80–136) t/ha, is typical of the north-western part of the By-Volga Upland that is occupied by complex pine and small-leaved forests. The other regions of the positive biotic carbon cycle regulation are the swampy forested lowland of Ryazanskaya Meshchera and the eastern slopes of the Smolensk-Moscow ridge; there, broadleaf, spruce, and birch-aspen forests are mainly prevalent.

Weakly marked negative ΔC(Fa) values (0 to –12; occasionally, up to –38 t/ha) will be characteristic to oak-lime and birch-aspen forests of the north-west boundary of the Central Russian Upland, and to broadleaf-spruce and spruce-birch forests of the lowland-outwash left bank of the Klyazma river downstream area and the neighboring right bank of the Volga river. Fragmentary forests on the vast territories of agricultural land will exhibit a weakly marked, for the most part, positive biotic regulation of the carbon cycle.

**Territorial Generalizations of Cartographic Forecast**

It is necessary to assess the contribution of separate groups of forest formations of the Oka river basin to the total biotic carbon cycle regulation (Fig. 4, Table 4). Spruce and broadleaf-spruce forests will actively deposit carbon at relatively dry TE mesosites, where the temperature rise will induce an intense growth of stands (Fig. 4, a). The maximum carbon deposition may be up to

| Groups of plant formations | Regression equations |
|---------------------------|---------------------|
| a) Spruce and broadleaf-spruce forests | ΔC(Fa)₂₀₅₀ = 76.7Z + 46.7T + 24.0Q – 63.8 |
| b) Pine and broadleaf-pine forests | ΔC(Fa)₂₀₅₀ = –24.0Z + 21.0MCA – 7.1Q + 12.1 |
| c) Broadleaf forests | ΔC(Fa)₂₀₅₀ = –76.2T + 42.9MCA + 12.1GA + 5.1 |
| d) Secondary substituting for pine and broadleaf/pine forests | ΔC(Fa)₂₀₅₀ = 83.1kₘₐₓ +76.6MCA + 9.7T – 61.6 |
| e) Secondary substituting for spruce, pine, and broadleaf forests (all secondary forests of basin) | ΔC(Fa)₂₀₅₀ = 37.5MCA – 18.4GA – 10.9T + 12.7 |
| f) Primary and secondary forests of basin (all basin forests on their contemporary areas) | ΔC(Fa)₂₀₅₀ = 28.8MCA + 23.9kₘₐₓ – 7.2T – 7.8 |

Note: Predictors in regression equations are: Z – elevation; MCA –catchment areas; GA – degree of slope; kₘₐₓ – maximal curvature that defines the ‘ridge’ landscape forms; Q – insolation of slopes with the Sun position at the southern azimuth (180º), sun declination 35º; T – average temperature of July.
Fig. 4. The changes in the total C stocks in the groups of plant formations of the Oka river basin predicted for 2050 under different conditions of plain mesorelief

a) Aboriginal formations: 1– spruce and broadleaf-spruce; 2 – pine and broadleaf-pine; 3 – broadleaf; 4 – paludal forest; 5 – flood-plain

b) Secondary small-leaved formations in the place of forests: 1– spruce and broadleaf-spruce; 2 – pine and broadleaf-pine; 3 – broadleaf. E, TE, T, types of mesosites (see in the text); sun and shad – solar exposure (see Fig. 1)
4.6–7.5 th t/km². At the more hydromorphic E and T territories, carbon deposition in the skeletal phytomass will be surpassed by the carbon emissions as a result of drastic intensification of the processes of forest litter decay and humus mineralization. Overall, carbon deposition in dark-coniferous forests will exceed carbon emissions by nearly 70% (see also Fig. 4, a); however, because of an insignificant area of these formations, their contribution to changes in the regional carbon balance will be minor.

Pine and broadleaf-pine formations will also have positive effect on the carbon cycle, i.e., their contribution will be 1.5 times stronger, than that of dark-coniferous forests (see Table 4 and Fig. 4, a). Occupying the greatest areas in the Oka river basin, pine forests will make a considerable positive contribution to the regulation of the carbon cycle. Carbon will accumulate mainly in pine forests on the TE and TA–A elements of the mesorelief. Negative values of the carbon balance should be expected in the light-coniferous forests of flat interfluve sites and of gentle even slopes. Broadleaf forests will serve as minor carbon sinks. The main role in carbon deposition will be played by mesohygrophytic oak-lime forests of river valleys and adjacent slopes, especially those facing north. The E and T mesorelief components will act as CO₂ emitters.

Paludal forest formations will provide for the main positive carbon cycle regulation (based on the Le Chatelier’s principle) (see Fig. 4, a). Global warming will drastically increase their productivity. The CO₂ sequestration in the skeletal phytomass will significantly exceed its emissions from peat litter decay; therefore, 3.6–3.8 th t/km² of carbon will be additionally fixed within swamp watersheds by 2050.

The group of floodplain forest formations is expected to have the highest territorial contrasts of ΔC(Fa). On the shady and neutral slopes, soil temperature rise and groundwater level decrease will induce significant intensification of productivity.

The carbon deposition values there will be maximal in relation to the entire Oka river basin, i.e., up to 7.5 th. t/km² (see Fig. 4, a). At the same time, there will be intensification of decomposition in the communities of eluvial and sunny TE sites resulting in additional CO₂ emission of 4.4–4.8 th t/km². The resultant contribution of the floodplain forests to the total carbon balance of the region will be positive.

Secondary small-leaved forests will be associated with changes in the carbon content different in sign (see Fig. 4, b). Birch and aspen forests substituting for sub-taiga dark-coniferous forest associations grow in higher hydromorphic conditions on sabulous loamy soils. Thermo-arid trend will induce accelerated growth of stands in these communities. In the upper links of mesocatenaes, an additional carbon storage in the skeletal phytomass will be 5.7–6.6 th. t/km² by 2050. The fact of substitution of secondary birch and aspen forests for spruce and broadleaf-spruce forests i.e., of the permanent presence of initial stages of restorative successions, must contribute to additional deposition of carbon in the growing timber. This seems to be the leading role of the boreal forest cover consisting of dark-coniferous taiga and sub-taiga types in positive carbon cycle regulation according to the Le Chatelier’s principle.

On less hydromorphic sandy soils, where small-leaved associations exist in the place of pine and broadleaf-pine forests, there will be a significant negative carbon balance (see Table 4 and Fig. 4, b). Birch-aspen forests growing in place of oak and lime forests will make a relatively little impact on the above described pattern of ΔC(Fa) dynamics typical of their aboriginal precursors.

CONCLUSION

Thus, the biotical carbon cycle regulation by temperate coniferous, mixed, and broadleaf forests under global warming may have both positive and negative
effects on the state of terrestrial ecosystems and the biosphere as a whole. By 2050, the carbon balance of the forests of the main water catchment area of the Volga river basin, average weighted by area, may be from \(-21\%\) to \(+11\%\) of the baseline carbon content. These figures are quite comparable to the data of other predictive regional estimations. For coniferous, mixed, and other USA forests, changes in the net primary productivity and the carbon content were calculated by predictive biogeochemical models CEN (CENTERE) and TER [Aber et al, 2001]. It was shown that, according to the scenario of UKMO-1987 climate model (the precursor of HadCM3), doubling of atmospheric CO2 results in relative carbon balance values in the range of \(-1.5\%\) to \(+7.8\%\).

Let us compare the obtained results with some materials on the forest cover of Russia as a whole. Based on the modern rates of the carbon sink in the Russian forests [Zalihanov et al, 2006], it may be assumed that the total C deposition in the forests during a 65-year period (1985-2050) is about 23.1 Gt. For one percent of this area (i.e., an approximate area of the Oka river basin), this parameter will be equal to 231 mln t, i.e. five times greater than forecasted for the territory by 2050 according to HadCM3 model (see Table 4, column "Deposit"). As one can see, the results of our predictive modeling of the carbon balance are quite realistic and, though HadCM3 is considered to be extreme, its calculations give much lower estimates of carbon content changes in the forest vegetation cover.

| Forests (groups of plant formations) | Area, km² | Total carbon (baseline) | Change of the carbon content | Total | millions of thons | % |
|-------------------------------------|-----------|-------------------------|-------------------------------|-------|------------------|---|
|                                     |           |                         | accumulation           | emission |                 |   |
| 1. Spruce and broadleaf-spruce mixed| 2034      | 37.14                   | 3.02                         | -1.8    | 1.22              | 3.28 |
| 2. Pine and broadleaf-pine mixed    | 26230     | 481.76                  | 45.77                        | -23.17  | 22.6              | 4.69 |
| 3. Broadleaf                        | 4770      | 84.68                   | 6.76                         | -4.96   | 1.8               | 2.13 |
| 4. Secondary substituting for dark-coniferous and mixed | 17770 | 293.26                  | 40.77                        | -14.79  | 25.98             | 8.86 |
| 5. Secondary substituting for light-coniferous and mixed | 16670 | 318.7                   | 40.97                        | -51     | -10.03            | -3.15 |
| 6. Secondary substituting for broadleaf | 4911 | 76.83                   | 0.42                         | -1.18   | -0.76             | -0.99 |
| 7. Paludal                          | 2343      | 35.18                   | 1.01                         | -0.17   | 0.84              | 2.39 |
| 8. Flood-plain                      | 9219      | 149.28                  | 6.62                         | -4.45   | 2.17              | 1.45 |
| All groups of forest formations     | 83947     | 1476.83                 | 145.34                       | -101.52 | 43.82             | 2.97 |
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