

Carbon Balance in Forest Ecosystems and Biotic Regulation of Carbon Cycle under Global Warming: Landscape-ecological Predictive Modeling

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Abstract It is outlined the concept of biotic regulation of carbon cycle in biosphere with the help of a study of local mechanisms in the small biological cycle. The prognosis of changes of biological cycle and biotic regulation of the carbon cycle according to the HadCM3 scenario of global warming are presented. Two mutually antithetical phenomena of carbon cycle biotic regulation will be developing on the Russian Plain. The extreme south of the forest zone will be the field of significant additional accumulation of carbon in atmosphere. The main positive biotic regulation of carbon cycle, according to the Les Chatellier's principle, will be performed by broadleaf-coniferous forests of high plains in the nemoral-forest sub-zone and in the southern belt of sub-taiga zone. Local and regional maps of carbon balance are presented as well.

Keywords Global Warming, Forest Ecosystems, Carbon Balance, Predictive Modeling

1. Introduction

Global anthropogenic impact on climate and the resultant large-scale biosphere processes have created an urgent ecological problem. The development of local (topological) and regional aspects of the concept of continental biosphere stability is one of the most important ways to solve it. This approach is based on studying the biotic regulation of the carbon cycle and moisture exchange in the soil-vegetation-atmosphere system that ensure the stability of natural ecosystems[30, 89, etc.]. This problem has been addressed by many authors[1, 3, 9, 37, 41, 46, 69, 84, 88, 89, etc.]. High emphasis is placed on development of a procedure for determination of carbon pools in different components of phytobiota and in soil, as well as creation of a database on the current carbon content in forest, marsh, and other ecosystems, with territorial generalizations by natural and administrative regions. Biosphere processes determining the "work" of the carbon cycle under various natural conditions and under anthropogenic successions are also considered in detail.

The problems of quantitative assessment of responses of different biotic components of the carbon cycle to global climatic changes are illustrated much less. Accordingly, there are actually no predictions of the climatogenic dynamics of factors effecting the biotic regulation of

carbon dioxide content in atmosphere. Meanwhile, solution of these problems is necessary for revealing mechanisms that provide stability of various zonal-regional subdivisions of continental biosphere under the forthcoming global warming.

The stability of biosphere and its patterns connections with realization of known Le Chatelier's principle on the regional-local level, i.e. in scale of minor biological cycle. According to this principle, the state of the environment will be stable if a spontaneous increase in the CO₂ content of the atmosphere is accompanied by the corresponding increase in carbon uptake by the terrestrial and marine biota. This is how biotic regulation occurs. The Le Chatelier's principle is violated when the biota becomes a carbon source instead of sink; i.e., it itself releases CO₂ into the atmosphere in response to an external influence. Simultaneously, the water vapor content of the atmosphere increases, which leads to additional global climate warming that is even greater than the initial (carbon) signal[29]. This situation goes beyond biotic regulation of the environment, with adaptation of species and communities to the changing conditions, as well as their stabilizing selection, becoming a priority[30].

The forest cover is one of the leading factors providing for the stability of the continental biosphere. Boreal forests play an important role in the global carbon cycle. Forest ecosystems are the most potent regulator and stabilizer of natural bio-geochemical cycles[76], including the carbon cycle, as well as the temperature regimen of the atmosphere[77]. There are indications in the literature that evaluation of sources and sinks of carbon in boreal forests

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of the world interfere with the uncertainty in the data available from Russian forests[36]. Some authors state that the current understanding of ecological processes in boreal forests is far from well[68].

2. The Contemporary State of the Problem

Methodological aspects of the prognostic dynamics of forest ecosystems and shifts in their carbon balance accompanying climatic changes are intensely developed worldwide[1, 10, 61, 69, etc.]. In general, these prognostic models may be called empirical-simulation ones. Almost all of them are global or superregional and are mainly based on remote-sensing methods for collecting the initial information used to describe the relationship between vegetation and climatic parameters. The models may be divided into two groups.

The first group comprises the so-called biogeographic models MAPSS, DOLY, BIOME2, etc., which mainly predict the successional replacement of forest-forming species and the corresponding changes in the ranges of the zonal/regional types of biomes. Examples are small-scale prognostic maps of the main plant formations in the United States for the years 2030 and 2095 based on two climatic models, HadCM2SUL and CGCM1.

The second group comprises prognostic biogeochemical models describing the physical and chemical processes in plants and soil that determine the primary net production, as well as the carbon fluxes, accumulation, and loss. These are, e.g., the models TEM, CENTURY, and BIOME-BGC[59] characterizing climate-related changes in the parameters of the biological cycle. The VEMAP (Vegetation/Ecosystem Modeling and Analysis Project, members 1995) program has been used to calculate productivities and carbon contents of the main biomes of the United States for the scenario of doubling the atmospheric CO₂ concentration according to the prognostic climatic models OSU, GFDL, and UKMO[1]. Simulation models have yielded similar scenarios for Russia[52].

In the framework of the VEMAP, biogeographic and biogeochemical concepts have been mechanistically united to form a cross-model for three climatic scenarios[20, 61]. However, the authors themselves agree that such prognostic models are somewhat inadequate and think that predictions should be based on more detailed data on the structural and functional organization of ecosystems.

All these prognostic developments are small-scale and, hence, cannot reveal basic mechanisms accounting for the spatial diversity of the responses of forest communities to the same background climatic factors; in addition, the behaviour of local ecosystems under conditions of climatic changes has been poorly studied. The so-called patch models[21, 22] deal with comparatively small areas of the forest cover selected on the basis of the functional characteristics of structurally homogeneous ranges. However, these models are spatially

limited because describe only typical sites in typical biomes (the bottom-down approach), rather than the entire topological diversity of ecosystems.

Purely computational simulation models of the response of forests to climatic factors are also being intensely developed[12, 13, 52, 66, 73, 89]. Parameters of the biological cycle are first calculated for an individual tree or the dominant forest-forming species. The type of the habitat conditions expressed in the averaged hydrothermal and soil characteristics is regarded as an integrated ecological factor. The relationships found in this way are then extrapolated to large regions or entire natural zones for which predictions are made.

Despite the considerable success of simulation modeling, its substantial drawbacks are also obvious. Describing, rather schematically, the main terrestrial biomes (the tundra, coniferous forest, etc.), they are essentially "dimensionless"; i.e., they are models with lumped parameters. These models cannot reproduce the spatial mosaic of the predicted functional parameters at the regional and local levels because they do not take into consideration the multifold ecological role of the terrain (forest management data are insufficient for this purpose).

The class of simulation (lattice, fractal, etc.) models pertains to the well-known metapopulation theory based on Turing's model of dissipative structures[25, 81]. The metapopulation theory has recently been found to contradict the results of experiments and, hence, has been criticized[35]. We believe that simulation models serve as a kind of "beacons" reflecting some invariant characteristics of the ecological space. This is their, undoubtedly important, role; however, this type of simulation alone will not do for geographic ecology.

Methods for carbon balance assessing in forest ecosystems are often based on forest inventory data[10, 16, 27, 39, 56, 78, 90]. Remote sensing data are widely used for this purpose as well[18, 43]. On the other hand, there is no unified technology of determining carbon stocks using these data, so that there may occur an essential disagreement in results obtained from different authors[36]. Case studies in using multi-spectral Landsat data to estimate carbon stocks in forests have appeared not very successful. Some another study have shown that the regional estimates of biomass may be made from the use of remote methods such as LiDAR that can measure forest canopy height directly over large regions[17]. There are examples in the literature that refer to the use of direct measurements at experimental test sites to estimate carbon balance in major regions: for example, in forest-tundra of Russia[86], or in Amazon-river basin[62]. In such studies, authors usually noted spatial heterogeneity of terrestrial sources and sinks of carbon.

We believe that the simulation models serves as a kind of "beacons" reflecting some invariant properties of ecological space. This is their, undoubtedly, important role; however, this type of modeling alone will not do for landscape (geographical) ecology.

3. The Landscape-Ecological Approach to the Problem

The main characteristic of this approach is that the phenomenon of biotic regulation is considered at the local (topological) level in landscape terms, thereby allowing for diverse types of this regulation determined by the spatial distribution of biogeocoenoses (landscape facies)ⁱ 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 those mechanisms that ensure the resistance of geo(eco-)systems to climatic changes.

Landscape-ecological models describe the behaviour of geo(eco-)systems as the indivisible complex formations – in the aspect of Sukachev's doctrine about the biogeocoenoses [75, 76]. They make it possible to obtain the results operate with a higher level of the special resolution as compared with, for example, simulation models (see above), and to come out for higher special resolution and broader generalizations.

The landscape-ecological approach is based on the construction of *discrete empirical statistical models* of natural ecosystems. These models describe the category of self-organizing systems, which can adequately describe stabilizing selection as a response of the biota to climatic perturbations exceeding the adaptation threshold. In these models, the results of field observations are used as an empirical basis for modeling itself, rather than as reference data for testing results of calculations. This, first, minimizes the effect of the subjective factor in developing the model; second, provides a considerably higher spatial resolution than, e.g., simulation modeling; and, third, gives empirical grounds for wider geographic generalizations.

Too little literature is devoted to forest models that use natural holistic biogeocoenosis as an elementary unit. Models often consider biomes[1], classes of forests[6, 40], communities of forest plants[58], forest tree types[4, 5, 11, 19, 33, 53], abundance of trees[55], and so on.

Environmental factors for models are climate, soil and topographic features, but they are frequently treated as a mechanistic set of influential factors that are not organized in a form of a natural system. Even when an attempt is made to some selection of forest land types (sites, habitats), it produces a very formal basis[24, 34, 65].

Without consideration of a system of ordered interactions in landscapes, we may get restricted and formal answers.

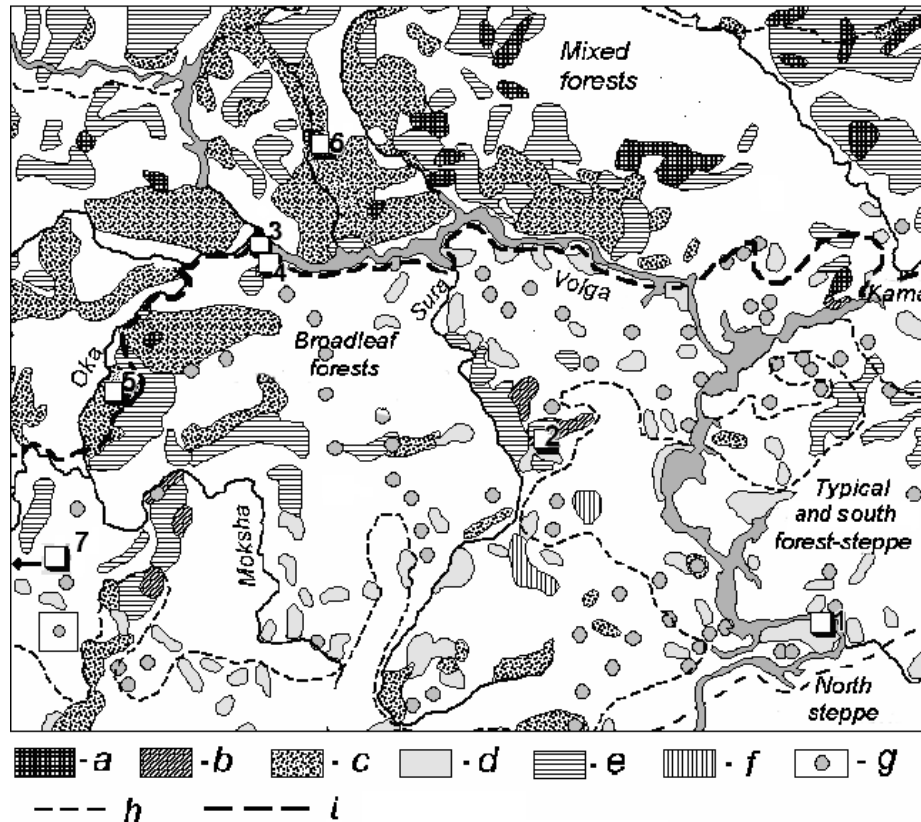
The given report gives an account of the numerical methods and results of regional and local landscape-ecological prognoses developed by the authors[47, 48–51]. These methods are used for numerical paleoreconstructions for the first time. The ways and efficiency of using these principles in assessment of the past and future states of natural eco-systems are demonstrated as well. At the same

time, in contrast to the known methodical approaches, an unambiguous character of transformation of geo(eco-) systems is assumed at a fixed value of geophysical trend, when a new state may have features of not one but several states existing in the given moment of time.

We developed landscape-ecological models of carbon balance based on direct authors' measurements of phytomass and humus contents in landscape-ecological surveys at experimental test sites that characterize given ecoregion. By using *the principle of catenary organization of local ecosystems*, we may maximally cover the diversity of geomorphological, hydroedaphic, and phytocoenotic features of the ecoregion. As a result, we obtained average values for calculated grids of carbon balance of various regions that were very close to similar averages from sampling test sites of the same regions. This approach served as a basis for revealing substantiated carbon balance spatial variability of regional forest ecosystems at a high significance level.

Regional retrospective landscape-ecological prognosis developed by the authors is characterized by qualitatively new level of spatial resolution as compared with the existing paleogeographical reconstructions and their prognostic interpretation for the territory of the Russian Plain[82, 83], with a much deeper scenario analysis. Besides, the use of annual humidify factor but not only the temperature or precipitation used generally[15, 37] resulted in more objective assessments of the future landscape-ecological conditions in the region on the basis of retrospective prognosis.

The landscape-ecological approach to modeling the functional parameters of local ecosystems is based on Timofeeff-Ressovsky's biochorological concept[79] concerning the spatial organization of the matter and energy cycles by the living matter in biogeocoenoses as discrete, elementary structural units of the biosphere. According to theoretical developments in this field, the biosphere is regarded as a statistical ensemble of biogeocoenoses as biochorological units that weakly interact with one another but have a highly ordered internal organization (due to stabilizing selection). Each ecosystem at the level of facies or their groups is assigned specific functional characteristics related to the structure of local matter and energy fluxes. This approach permits the prediction of the behavioural patterns of forest communities under different geomorphological and edaphic conditions on the basis of comprehensive empirical data collected in the course of field studies, while retaining the statistical methods of their analysis. Therefore, the prognostic models of local geographic space may include the mechanisms of the biotic regulation of the carbon cycle, which is a new aspect of solving this problem.



Forests: *a* – fir, silver fir and black alder; *b* – broadleaf-pine, sometimes with fir; *c* – pine and fir-pine; *d* – broadleaf; *e* – birch-aspen and birch-lime; *f* – birch and pine-birch; *g* – extra-scale areas of broadleaf forests; *h* – boundaries between the natural zones/sub-zones; *i* – Main Landscape Border of the Russian Plain. Other meanings: 1–6 – test site numbers (explanation in the text)

Figure 1. Forest formations on headwater of the Volga river basin and arrangement of experimental test sites

Combining the biogeographic and biogeochemical approaches into a single operational system of landscape ecological prediction entails estimation of changes in the parameters of the biological cycle and carbon balance of forest biogeocoenoses at every stage of their climatogenic successions. This allows the spatial diversity of the local functional response of the forest cover to background climatic signals to be described in more detail and the corresponding diversity of the biotic regulation of the carbon cycle to be revealed. The methodical developments and results of simulation modeling may also be used in developing the empirical statistical models.













The biotic regulation of the carbon cycle under conditions of global climate changes is determined by climatogenic changes in the parameters of the internal exchange and balance of plant matter in ecosystems. It has been found [48] that the relationships of landscape zonal systems with climatic characteristics (mainly air temperature and precipitation) cannot be used for developing local prognostic models with spatially distributed parameters. The main mediator of the relationships of structural and functional characteristics of topological-level ecosystems with climate is soil moisture content in summer, which is the most potent ecological factor determining the territorial organization of biogeocoenoses. For forest formations of the Volga basin, the July reserve of productive soil moisture has been found to be closely related to the Vysotsky–Ivanov’s annual atmospheric

humidity factor, which, in turn, is strongly, significantly correlated with the mean air temperature in July [49].

Results of forest landscapes modeling should be expressed not only in analytical schemes, but also as maps. Some tendency of increase in number of spatially explicit forest landscape models may be noted. Until 2000, these are DISPATCH, FIRE-BGC [44], LANDMAN, FORMOSAIC, SAFE FORESTS, DELTA, LANDISIM [7, 34] and models with no title. From 2000, the number of spatially explicit models further increased: LADS, VDDT/TELSA, SEM-LAND, EMBYR, HARVEST, MAPSS и MC1, DISTRIB, BFOLDS, FIN-LANDIS, LANDSUM, RMLANDS, Q-LAND, FATELAND, LANDIS-II [32, 54], and other models with no title.

In parallel with models of forest landscape, methods of predictive modeling was developed (see for reviews [4, 14, 23, 31]). These models are often based on simplified binary characteristics of ecosystems (e.g., presence/absence of species), which means a significant loss of information, and therefore low strength of statistical relationships. We use predictive mapping based on a wide set of continuous (not binary) characteristics that describe the structure and functioning of forest ecosystems, as well as an extended system of topographic attributes that was not used earlier by other authors. Based on these relationships, more detailed maps of ecosystem functional parameters were created for base and prognostic periods.

Table 1. Groups biogeocoenoses (landscape facies) of different Middle Volga ecoregions represented by corresponding experimental sites

No. of facial groups	Ecoregions (experimental test sites)			
	Zhyguli low-mountain range (Zhyguli)		High right-bank by-Sura region (By-Sura)	
1	Light steppified pine forests on the steep sunny slopes		Pine and spruce-pine forests on the upper parts of slopes of sabulous ancient-alluvial plain	
2	Subors and pine-broadleaf forests on the steep neutral and shadowy slopes		Pine-broadleaf and aspen forests on the flat watershed of second moraine plain	
3	Maple-lime oak and aspen forests with nut grove on the shadowy slopes of middle steepness		Oak-lime and aspen forest with nut grove on the loamy high watersheds (ecosystems of the flat-interfluves)	
4	Elm-maple-lime forests on the gently sloping watersheds (ecosystems of the flat-interfluves)		Spruce-pine forests on the lower parts of slopes of sabulous-loamy ancient-alluvial plain and high flood-plain	
5	Shadowy broad-leaf forests on the lower parts of steep slopes		Spruce-lime-oak and pine-birch-aspen forests on the gently concave slopes of high sabulous-loamy interfluves	
6	Lime, maple and aspen forests of the bottoms of small deep valleys		Swamped spruce-pine forests on the interfluve depressions of moraine and out wash sabulous-loamy plain	













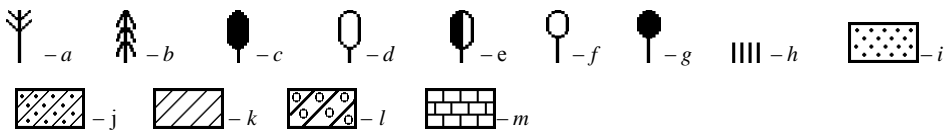
No. of facial groups	Ecoregions (experimental test sites)			
	High right bank region of by-Volga river (Green Town)		High right bank region of by-Volga river (Shchelokovsky Farmstead)	
1	Pine forests and subors on the sandy hilly watersheds		Maple-lime oak forests on the near-watershed sunny loamy slopes	
2	Spruce forests and spruce-lime oak forests on the flat sandy interfluves		Lime and aspen forests on the shadowy and neutral loamy slopes;	
3	Spruce-lime oak forests and birch forests on the flat sabulous-loamy watersheds (ecosystems of the flat-interfluves)		Maple-lime oak forests on the gently sloping loamy watersheds (ecosystems of the flat-interfluves)	
4	Spruce-pine forests on the gentle sandy slopes		Maple-lime oak forests on the transit sunny loamy slopes	
5	Pine and spruce forests on the depressions of sandy interfluves and on above-floodplain terraces		Oak, lime, and aspen forests on the transit shadowy and neutral loamy slopes	
6	Swamped floodplain small-leaf forests of the valleys of small rivers		Oak and lime forests on the lower parts and bottoms of loamy slopes	

Table 1. Continued

No. of facial groups	Ecoregions (experimental test sites)			
	Oka-Tesha forested lowland (Vyksa)		Trans-Volga outwash forested lowland (Kerzhenets)	
1	Pine and spruce-pine forest with lichen and green moos on the apexes of sandy ridges		Pine forests with spruce and birch on sandy ridges	
2	Spruce-pine forests with red bilberries on the loamy-sandy gently-wavy watersheds and slopes		Pine forests with birch and spruce on slightly-undulating interfluves of sandy ancient-alluvial plain	
3	Spruce and spruce-pine forest with wood sorrel on the sandy flate-interfluve and gently slopes (with small depth of loam occurrence)		Spruce and spruce-birch forests on high interfluves of sabulous-loamy moraine-outwash plain	
4	Oak-pine-spruce forests with nemoral herbage the well drained sandy-loamy slopes and their foots		Spruce-oak-lime and small-leaved forests on high flood-plain and above-floodplain terraces	
5	Pine and spruce-pine forests with bilberries and long moos on the sandy-loamy gently-concave slopes		Coniferous and small-leaved forests on the depressions of moraine-outwash plain	
6	Pine and black alder forests with sphagnum and long moos on the loamy small stream valleys and floodplain depressions		Swamped mixed forests on the floodplain depressions and small stream valleys	

No. of facial groups	Ecoregion (experimental test site)				
	By-Oka-Terrace biosphere reserve (OTBR)		No. of facial groups	By-Oka-Terrace biosphere reserve (OTBR)	
1	Pine-birch forests, with aspen and lime, on gently bulging sandy interfluves and high parts of slopes		4	Lime-aspen-birch forests on high and middle parts of sandy-loamy slopes (with small depth of carbon eluvium)	
2	Pine-spruce and spruce-pine forests on the gently sandy-loamy watersheds		5	Spruce and spruce-pine forests on middle and lower parts of sandy-loamy slopes	
3	Pine-lime-oak and pine-Lime forests on sandy-loamy watersheds (with small depth of carbon eluvium)		6	Swamped coniferous and small-leaved forests on the floodplain depressions and small stream valleys	



Convention meanings to symbols of biogeocoenosis groups (for all tables and figures). Dominant forest stand: a – pine; b – spruce; c – oak; d – lime, elm; e – broadleaf kinds without the division; f – birch, aspen; g – black alder. Grass cover: h – forb-meadow steppe. Soil formatting rocks: i – sandy; j – sandy loam; k – middle and heavy loam; l – sandy-loamy moraine with small boulders; m – carbon bedrock

It is known that, to mitigate global climate change consequences, one may initiate new low-cost forests in Africa, South America, and Asia, and, during 100-year period of time, global carbon sequestration by these plantations might result in 5% to 25% of carbon emission[8]. These authors believe that these evaluations are more detailed than previous ones. However, they remain within the planetary scale, which makes them very superficial. In our study, we examined variants of planting different forest types in the Oka-river basin of an area about 240 000 km², and have constructed forecast maps of carbon balance for these variants. In a summary, evaluation results of a regional extent have been obtained. Based on them, identified types of forest plant communities were recognized that might potentially provide the greatest carbon sequestration under global warming.

We tested an original approach to calculating and drawing large-scale raster maps of the discrete parameters of the biogeocoenosis biological cycle based on geomorphometric methods[70, 72] at different variants of climatic prediction for Middle Volga regions. This approach can be used more widely in prognostic analysis.

The prediction of the changes in metabolism and carbon balance should be based on the phenomenon of the thermo-arid climatic trend, which will be progressing throughout the 21st century in the entire central zone of the Russian Plain and in Eurasia as a whole[2, 37, 49]. The disbalance of the biological cycle caused by soil dehydration in summer will lead to irreversible "savannization" of the entire wide zone of broadleaf and mixed forests in the Middle and Upper Volga Regions accompanying by catastrophic decomposition of forest communities in forest and steppe zonal ecotones.

These results may be regarded as a prerequisite for prognostic functional modeling and determining the mechanisms of the regulation of the carbon cycle by the forest cover during the forthcoming climate changes. A basis for local ecological prediction with spatially distributed parameters is provided by a set of the trajectories of climatogenic successions in forest communities (subject to the modifying effect of the terrain), which have been determined for each ecoregion.

4. Empirical Material for Modeling

Landscape-ecological forecast analysis was based on the materials of large-scale landscape-ecological surveys carried out by the authors (1987–1996) at seven experimental test sites (ranges) of the Middle and Upper Volga Region (Figure 1). These test sites embrace the main diversity of zonal transitions on the boreal ecotone of eastern sector of the Russian Plain:

(1) The zonal ecotone of forest and steppe – oak forests and steppified pine forests of the Zhyguli low-mountain range (the region of “Samarskaya Luka” National Nature Park);

(2) The sub-taiga/forest-steppe ecotone – mixed and broadleaf forests of the high right-bank by-Sura region (territory of “Chavash Forest” National Nature Park);

(3–4) The boreal-nemoral forest ecotone – coniferous, mixed and broadleaf forests of high-plain by-Volga region (the right-bank region of the Volga River) in the vicinity of Nizhny Novgorod; this compound ecotone system consists of two subsystems: (3) erosion loamy plain with maple-lime oak and aspen forest (stow “Shelokovsky Farmstead”) and (4) moraine-outwash plain with spruce, pine and spruce-lime oak forests (stow “Green Town”);

(5) Outwash forested lowland of the Oka-Tesha region (the right-bank strip of the Oka River) – pine forests and subors near the boundary between the mixed forest zone and the nemoral-forest sub-zone (surroundings of the town Vyksa, Nizhny Novgorod region);

(6) Moraine-outwash lowland on the trans-Volga region (north of Nizhny Novgorod) – spruce and pine forests in the southern strip of the zone of mixed forests (“Kerzhensky” Nature Reserve).

(7) By-Oka-Terrace biosphere reserve – OTBR (lowland Middle left-bank region of by-Oka river), south boundary of sub-taiga zone; mixed, conifer, broad- and small-leaved forests.

Each of these test sites characterizes a particular *regional ecosystem*, with the corresponding conventional name (Zhi-guli, by-Sura, Shelokovsky Farmstead, Green Town, Vyksa, Kerzhnets, OTBR).

Six facial groups distinguished for each regional ecosystem (Table 1) cover the major topological (local) diversity of forest types and are located in the vector system of landscape couplings (catenas) – in the direction of edaphic moistening increase: from eluvial (E) and transeluvial (TE) types of local sites (geotops) through slope transit (T) and transaccumulative (TA) types to riverain accumulative (A) and bed supraqual (Saq) one, according to classification[26, 64]. The eluvial-accumulative sites on the interfluvial padings (E-A) also have the excessive edaphic moistening. According to the Vysotsky’s conception[60, 74], a group of *flat-interfluvial (placor) facies* on eluvial sites, as local zonal representative, was distinguished in each system of landscape coupling. The rest ecosystems formed as a result of various refractions of this back-ground under the effect of local geomorphological and hydro-edaphical factors[74]. In the latter case, a certain ensemble of so-called *extrazonal natural complexes* is formed[60]. They are the representatives of other zonal-regional types of geographical environment, not only neighbouring but also quite distant.

Empirical information collected on 40–50 sample areas for each test site included about 80 characteristics of the structure-functional state of forest topoecosystems. Let us list the main measured and calculated discrete parameters of the small biological turnover, with indication of their designations: *BS* – skeletal tree-shrub phytomass; *BV* – total green photosynthetic mass; *BR* – root mass; *WD* – dead skeletal mass (brushwood and dead-wood); *ML* – forest litter mass; *HU* – labile humus mass.

Table 2. Examples of the calculate models, describing the changes of the biological cycle parameters on biogeocoenoses of different regional ecosystems of the Middle Volga Region under the trends of soil temperature and soil moisture content in vegetation period

Model kind (calculate formula) *)	Regional ecosystems	Parameters	Coefficients			Statistic characteristics **)		
			b_0	b_1	b_2	R	P	S_y
$y = b_0 + b_1x_1 + b_2x_2$	By-Sura	BV	21.93	-0.742	-0.7135	0.664	0	3.09
		HU	5.99	0	55.75	0.696	0	20.29
	Green Town	BV	11.2	0.4756	-0.0289	0.406	$1.5 \cdot 10^{-2}$	0.11
		BR	8.712	5.838	-0.0678	0.582	$0.1 \cdot 10^{-3}$	17.92
		HU	16.34	-0.24	0.07426	0.713	0	
	Shchelokov.Farmstead	ML	27.18	-2.333	0.04896	0.717	0	6.51
$y = b_0 + b_1x_1 + b_2x_1^2$	Shchelokov.Farmstead	WD	642.1	-114.7	5.142	0.936	0	2.21
	Kerzhenets	ML	88.39	-15.03	0.7225	0.575	$0.5 \cdot 10^{-3}$	8.85
$y = b_0 + b_1x_1 + b_2x_2^2$	Zhyguli	ML	44.08	-0.361	0.00091	0.699	0	17.75
	Shchelokov.Farmstead	BS	-34.93	0.9472	0.00403	0.769	0	90.49
		HU	12.5	0.1712	0	0.649	0	9.31
	Kerzhenets	WD	22.85	-0.259	0.00149	0.72	0	12.78
		HU	8.84	0.0091	0.0006	0.851	0	8.03
	OTBR	BS	244.6	0.3956	-0.0031	0.557	$0.7 \cdot 10^{-3}$	71.4
HU		25.31	0.0159	0.00042	0.577	$0.4 \cdot 10^{-3}$	16.32	
$y = \exp(b_0 + b_1/x_1)$	Zhyguli	BS	3.706	15.42		0.611	0	39.3
		BR	1.768	26.26		0.614	0	12.25
	Green Town	ML	0.0845	35.08		0.506	0	16.0
		WD	-4.389	64.63		0.642	0	7.0
	Vyksa	ML	0.3274	46.81		0.798	0	0.34

The hydrothermal trends for the period up to 2150 were taken by one from the extreme climate prediction models of general atmospheric circulation AOGCMs – HadCM3, Version A2[28, 65]. Ecological prognosis by this model permits to evaluate the forest ecosystem reaction on such global climatic changes which may exceed the level of tree endurance and cause the disintegration of both nemoral and boreal forests on the large spaces. The entire forecast period includes five steps: years 1985–2025, 2025–2050, 2050–2075, 2075–2100 and 2100–2150. Period of meteorological observation 1881–1985 is a basis. Recent global warming was begun from the end of this period[37]

5. The General Direction and Methods of Predictive Analysis

The research strategy consists in identifying the local mechanisms of the biotic regulation of the carbon cycle on the basis of the predicted changes in the discrete parameters of the biogeocoenosis biological cycle in forest biogeocoenoses for specific variants of climate prediction. The objects of the prognostic analysis should be forest ecosystems with a protective status or a slight degree of disturbance, on the one hand, but with highly contrasting local geomorphological and hydrothermal conditions, on the other hand. It is necessary to quantitatively estimate the responses of different carbon pools in forest biogeocoenoses

to global climate changes and predict their functional parameters pertaining to the biotic regulation of the atmospheric CO₂ content either according or contrary to the Le Chatelier principle. This will make it possible to determine the most probable role of boreal and sub-boreal forests in reducing the greenhouse effect of the atmosphere in the course of global climate warming and to estimate to what degree forests of the temperate zone can actually maintain the stability of the biosphere under conditions of climate changes.

Having solved this problem, we will be able to determine the spectrum of the main forest formations of boreal and nemoral forests, some of them improving the stability of the terrestrial ecosystem cover and others, conversely, enhancing its destabilization under the conditions of the predicted thermo-arid climatic trend in the given region. The given objective is one of the key issues of modern global ecology that remain open questions thus far, which, in particular, causes heated debates about the Kyoto Protocol.

Prognostic ecological maps should reflect the local diversity of changes in the biological cycle and carbon pools. This diversity is accounted for by the spatial variation of the hydrothermal and edaphic conditions of geo(eco-)systems. Special attention should be paid to the mechanisms and consequences of the biotic regulation of the carbon cycle in forest and steppe zonal ecotones, where forest communities are always under the hydrothermal conditions that are close

to critical ones and, hence, are the most sensitive to climate changes.

In global ecology, it has already been understood that the spatial variation of carbon fluxes mainly related to the distribution of forests should be taken into consideration. The changes are expressed as peaks and troughs of CO₂ emission in mature forest ecosystems. This results in flows of biogenic elements between local ecosystems, which are part of the biotic regulation of the environment[30]. We suggest methodical approaches that agree with these theoretical views.

The material of large-scale landscape-ecological surveys in experimental test sites (see below) characterizing different zonal-regional conditions were used for preliminary estimation of the pattern of climate-related changes in the discrete parameters of the biological cycle in forest ecosystems at the local level.

The resultant comprehensive discrete data allowed us to implement the biochorological approach, enunciated by Timofeyeff-Ressovsky back in the 1960th, as a tool for prognostic landscape ecological study and to develop analytical and cartographic empirical statistical models of the changes in the biological cycle and carbon balance with spatially distributed parameters[67, 70]. The prediction was based on (a) our methods of empirical statistical modeling of topological-level ecosystems and discrete metabolic parameters and (b) hydrothermal ordination of these parameters in the space of local landscape series (catenae) for different zonal conditions. Functional ordination permitted, in a way, an empirical simulation of anticipated climatogenic changes of biological turnover in boreal and nemoral forests.

5.1. Analytical Methods

The thermo- and hydroedaphic ordination of metabolic characteristics of topoeosystems was made by two geophysical parameters: the temperature of soil 50 cm deep (t_{50}) and summer productive moisture reserves in the 0–50 soil layer ($W-50$). This parameter is connected with the atmospheric humidification most closely. The functional characteristics of forest ecosystems show the highest correlation with these parameters as well. As one can see (Table 2), correlation connections are not always rather high though quite significant (Pirson's test of significance, $P \ll 0.05$). At the weak connection, the latter can be interpreted only as a certain general tendency of changes of the given metabolic parameter under the influence of geophysical trend on the background of significant "noise" effect of other factors of the local order.

For estimating changes in the carbon contents of individual biotic components and forest biogeocoenoses in general, we used the traditional forest management method[46, 80] based on the estimation of the dynamics of live phytomass and necromass (and the humus mass), which yields the best results in CO₂ balance calculations over long periods of time. This method gives the best results at balance assessments of the carbon cycle components for long periods

of time. The change $\Delta C(Fa)$ of the mass of carbon flow in the system of soil-plant-atmosphere can be presented as follows:

$$\Delta C(Fa) = \Delta C(Rm) - \Delta C(NPP), \quad (1)$$

where Fa is CO₂ flow above the plant cover; Rm is CO₂ emission as a result of vital activity of soil and above-ground saprotrophs (mainly bacteria and fungi) which decompose humus, forest litter, and skeletal dead mass; NPP is pure primary production of biogeocoenoses (above-ground + root). Using the considered discrete parameters of minor biological cycle, the above equation can be written in expanded form:

$$\Delta C(Fa) = \Delta C(WD) + \Delta C(ML) + \Delta C(HU) - \Delta C(BS) - \Delta C(BV) - \Delta C(BR) \quad (2)$$

This balance equation was used to calculate possible changes of carbon flows between soil-plant cover and atmosphere in different periods of prediction (by HadCM3) for each facies group in all seven regional ecosystems (see above). The carbon contents in different phytomasses and in labile humus of soil were calculated using conversion coefficients, based on the known literature sources[39, 46, 63, etc.]. The values of some of these coefficients (e.g., by BV, ML and HU) were differentiated by each experimental test site and by each of facies group on a test site depending on the zonal and local conditions of habitat.

Each member of the right part of the equation (2) may have both positive and negative values. At positive values, the first three items give an increase of CO₂ emission from soil-plant cover into atmosphere and the other three give a decrease of this flow. In the latter case, the dead mass pool acts as an additional carbon source, while the live phytomass plays the role of its sink (deposit). With negative values of the above parameters, the picture is quite the opposite: in the reduced branch of biological turnover, carbon dioxide release into atmosphere decreases, while the autotrophic biogenesis becomes less intensive and consumes less CO₂, thus compensating for the resulting deficiency of carbon dioxide in the atmosphere.

As a result, the total balance of changes of carbon exchange between biogeocoenoses and atmosphere $\Delta C(Fa)$ is formed, which must show whether this group of forest biogeocoenoses consumes additional amount of CO₂ from atmosphere due to the shifts in biological turnover induced by the global warming or, on the contrary, becomes a source of its additional emissions. In the former case, there is a negative feedback directed at realization of the Le Chatelier's principle for stabilization or even weakening of the primary thermo-arid climatic signal; in the latter case, there is a positive feedback, which leads to intensification of the greenhouse effect of atmosphere and, consequently, the warming itself.

Such carbon balance of local ecosystems for all of the five predicted periods is presented in Figures. 2, 3 and 4. The zero balance shows the maintenance of the base level of influence, for which the following condition is accepted: the direct and reverse carbon flows between biogeocoenoses and atmosphere are balanced. The negative and positive carbon

balances show that the biotic regulation of carbon cycle is directed at additional destabilization of biosphere in the first

case and at maintenance of its stability in the changing climate in the second case.

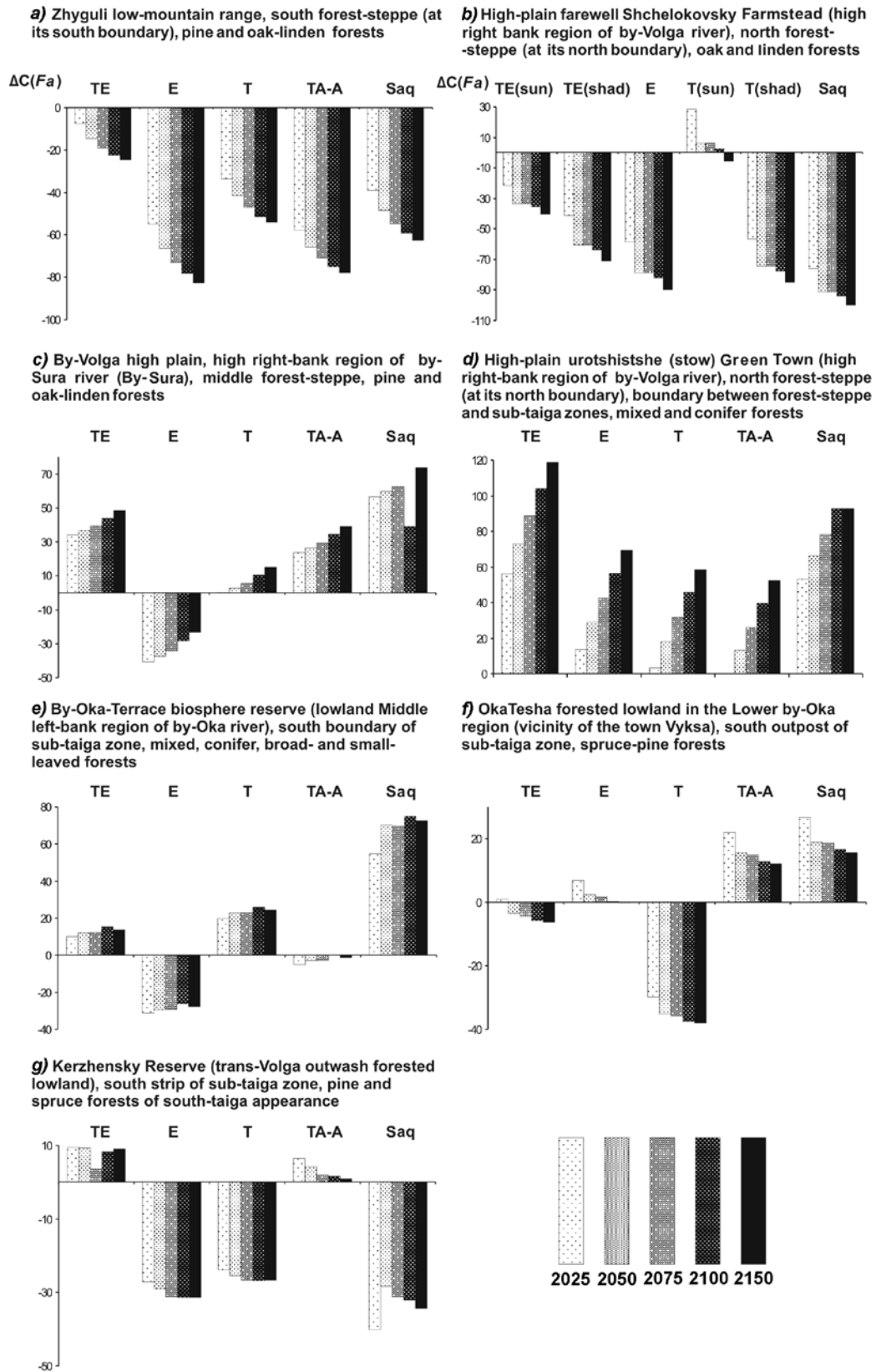


Figure 2. Landscape couplings of predicted C balance dynamics in forest biogeocoenoses under different zonal/regional conditions of the Middle and Upper By-Volga regions, according to the scenarios of HadCM3 model

$\Delta C(Fa)$ – carbon balance (t/ha). TE, E, T, ... – local sites (see in the text). Solar exposed slopes: sun – sunny, shad – shadow and neutral.

Table 3. Equations of the connections of carbon content change ($\Delta C(Fa)$) in forest formations of the Oka river basin to year of 2075 with most important environment factors, according to HadCM3 model

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

Foot-note. Predictors in regression equations are: Z – absolute elevation; MCA – maximal catchment area; GA – gradient (degrees) of the slopes; k_{max} – ridge geometrical forms (maximal curvature); Q – insolation (instant intensity of direct solar irradiation); T – average July temperature

5.2. Cartographic Methods

The new methods of geomorphometry were used in the cartographic part of predictive analysis of carbon balance [72, 75]. At the local level, the 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 (SRTM project) on 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 Spirman correlation coefficient r_s and the level of significance P) were obtained for the ecoregion of the Zhyguli low-mountain range:

(a) total C sources of the base period –
 $C_{\text{base}} = 222.6 - 55.6 \cdot GA - 25.6 \cdot Q - 12.6 \cdot H;$
 $r_s = 0.87, P < 10^{-6};$ (3)

(b) the change in total C stocks by 2075 –
 $\Delta C_{2075} = -99.8 + 47.1 \cdot GA + 25.3 \cdot Q + 18.0 \cdot H;$
 $r_s = 0.88, P < 10^{-6}.$ (4)

Another equations were obtained for the plain ecoregion of By-Oka-Terrace reserve:

(c) total C sources of the base period –
 $C_{\text{base}} = 243.69 - 92.82 \cdot MCA - 41.62 \cdot kh + 22.31 \cdot Z;$
 $r_s = 0.48, P < 10^{-2};$ (5)

(d) the change in total C stocks by 2075 –
 $\Delta C_{2075} = -5.25 + 10.18 \cdot MCA + 8.07 \cdot Q - 3.21 \cdot kA;$
 $r_s = 0.50, P < 10^{-3}.$ (6)

Here is: Z – absolute elevation; Q – slope illuminance with position of the Sun at the southern azimuth (instant intensity of direct solar irradiation); GA – steepness of slopes, H – mean landform curvature; kh – horizontal curvature showing flux convergence regions, with the growth of carbon deposits (see also Foot-note to the Table 3); MCA – maximal catchment area; kA – total accumulation curvature, separates zones of relative accumulation and removal from areas of relative transit ($\Delta C(Fa)$ is maximum in the transition zone).

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 SRTM30 project, USA-Italy-Germany (Shuttle Radar Topography Mission,

the project of radar survey of relief by Shuttle, 2000). The Oka river basin was taken as a model territory of the regional level. The matrix for this basin was transformed into the Kavraysky VII INT projection for the European Russia with the spacing of 900 m. As a preliminary, 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 «GIS Eco» [70]. Multiple regression equations used for construction of the predictive maps are presented in Table 3.

Transition from the local to regional level of prediction, with construction of maps on the scale of 1:2,500,000, was carried out using our *method of induction-hierarchic extrapolation*. This method is based on the empirically established *phenomenon of polyzonality of local geo(eco-)systems* as a form of their response to global climatic changes [48, 49]. The revealed regularities of refraction of zonal-regional climatic background by local geomorphological and hydroedaphic factors provide a basis for consideration of the so-called regional systems of local zonality. These are made up of the vector rows of flat-interfluvial and extrazonal biogeocoenoses (see above), that is adequate to the vector of the predicted climate changes. These rows may serve as a model of the main trends of ecosystem rearrangements.

The procedure of extrapolation is as follows. Each type/subtype of plant formation distinguished on a small-scale geobotanic map correlates with a certain group of biogeocoenoses from their flat-interfluvial/extrazonal series in the given ecoregion. This series characterizes the regional spatially ordered (micro-catenary) system of local zonality. Then, each areal of the given formation, represented as a polyvector multitude of mesocatenas, is divided into mesosites, i.e., the links of the chain of regional landscape couplings (sites $E \rightarrow TE \rightarrow T \rightarrow TA, A$; see above), with division of the TE and T locations into two solar-exposure gradations (sunny and shady). With this purpose, the new methods of geomorphometric statistics are used. An intermediary map of meso-scale sites is created for the whole forested area of the region. For the Oka river basin, such a map was formed on the basis of multiple regression equations by the materials of test sites Shelokovsky Farmstead, Green Town, Vyksa, Kerzhenets, and OTBR.

Taking, in accordance with the B. B. Polynov's conception of landscape couplings [64], mesocatena as a homomorphic image of microcatena, we distribute the available biogeocoenoses of all groups distinguished on each testing ground by mesosites of the corresponding geobotanic areal. Thus obtained regional phyto-catenary mosaic is then supplemented with basic or predictive metabolic parameters of biogeocoenoses taken already as local representatives of some or other zonal-regional types/subtypes of geographic environment. The described mosaic of induction-hierarchical extrapolation is a fundamentally novel method of regional predictive mapping based directly on the materials of field landscape-ecological surveys.

6. Results and Their Discussion

6.1. Prognoses of Carbon Balance by Analytical Models

Our calculations have demonstrated that the sensitivity of some or other parameter of the biological cycle to external impact is not adequate to the scope of changes, which occur in it in the course of this impact. The main results of empirical-statistical prediction are given an account below

1. The decomposition part of biological cycle is the most sensitive to climatic impacts [51]; nevertheless, during sufficiently long periods of time *the maximal (by absolute values) changes occur not in this branch but in autotrophic biogenesis: general net production of forest communities*. Moreover, skeletal tree-shrub phytomass (BS), mainly wood gain, is the great part of the shifts of productivity and carbon content. Such regularity is typical of all considered forest ecosystems (Table 4).

In 2100, the changes of total carbon content in its extreme values will range from $-(78 \div 100)$ t/ha at the zonal ecotones of forest and steppe (test sites Zhyguli and Shelovsky Farmstead) to $+(115 \div 120)$ t/ha in coniferous-broadleaf forests near the northern boundaries of the nemoral-forest sub-zone (Green Town). The changes of carbon content in BS will be accordingly $-(25 \div 40)$ t/ha and $+(85 \div 105)$ t/ha. It means, that in the coming century, the content of carbon conserved in skeletal phytomass of forest ecosystems of the Middle Volga River may change for $\pm(25 \div 50)\%$ and more of the base value on the average. This fact points to quite a significant regulating role, which the productivity of mixed and nemoral forests of the regions must play in their carbon exchange with atmosphere.

2. The global warming will induce in some cases an abrupt drop and in other cases as much significant increase of forest productivity, and that will be directly reflect on the carbon balance and will turn out to be the key link of the mechanism of biotic regulation of the carbon cycle. Zonal-regional contrasts of biotic regulation of carbon cycle may be evaluate by the value $\Delta(Fa)$ for the eluvial (flat-interfluvial) topoecosystems (see Table 4). On the territory of southern and middle forest-steppe there is an unambiguous and quite

clear decline of the production potential of forest communities. Carbon deposit in skeletal phytomass will reduce most quickly in flat-interfluvial mesophilic elm-lime and oak forests of erosion-loamy uplands (see Figures 2, *a, b*, and 3, *a, b*). Their role as a sink of atmospheric carbon will diminish.

3. The productivity of marginal forest communities at the zonal ecotone of forest and steppe will decrease most of all. In the skeletal tree-shrub pool of flat-interfluvial broadleaf forests of the Zhyguli mountain range, the loss of carbon content in 2050 will be from 2–6 to 26 t/ha and from 9–14 to 34 t/ha, respectively, and in the end of the 21st century this deficiency will reach 32 and 39 t/ha. As is seen, the climate prediction models are not very much different. Simultaneously, the rate of decay of skeletal dead mass (debris) and humus will significantly increase, though the forest litter mass will grow due to the increasing deficit of precipitation (see Table 5, *a*). As a whole, the detritus branch here will contribute to further accumulation of CO₂ in atmosphere and, jointly with the production branch, will induce *the progressing disturbance of the Les Chatelier's principle at the southern boundary of the forest belt, resulting in intensification of the global warming*.

On the aqueous-glacial plains of the nemoral-forest sub-zone, the moderate hydromorphic birch-spruce-pine forests on the transit sites are able to markedly reduce the tempos of carbon conservation in skeletal phytomass as well (see Figure 2, *c*). Xeromorphic biogeocoenoses, particularly forest-meadow-steppe communities of steep sunny slopes and pine steppified forests of well-drained watersheds, will change few on the base tempos of production, so that their contribution in carbon deposition will be insignificant.

4. On the contrary, a significant increase of productivity is anticipated in high-plain mixed and broadleaf forests of the nemoral-forest subzone and south strip sub-taiga zone. Mixed and dark coniferous forest biogeocoenoses will increase (and quite significantly) both their primary productivity and reserves of living organic matter. Accordingly, conservation of atmospheric carbon in perennial skeletal phytomass of these topoecosystems will increase and, as a consequence, the significance of this phytocoenotic pool as a carbon sink will increase as well (see Figures 2, *d*, and 4, *a*). Positive biotic regulation of the carbon cycle will be widely spread here. This process will be particularly significant in TE xeromorphic and Saq hydromorphic boreal forests, which will play the role of the major carbon sink. In 2050–2075, the value of additional carbon deposit in wood will be here from 36–53 to 77–83 t/ha; in the end of the 21st century, its values will be 75–105 t/ha. Simultaneously, there will be a noticeable activation of decomposition of forest litter and humus. The effect of forest productivity growth, which is positive for the carbon balance, will be reduced to a certain extent by resulting CO₂ emission into atmosphere.

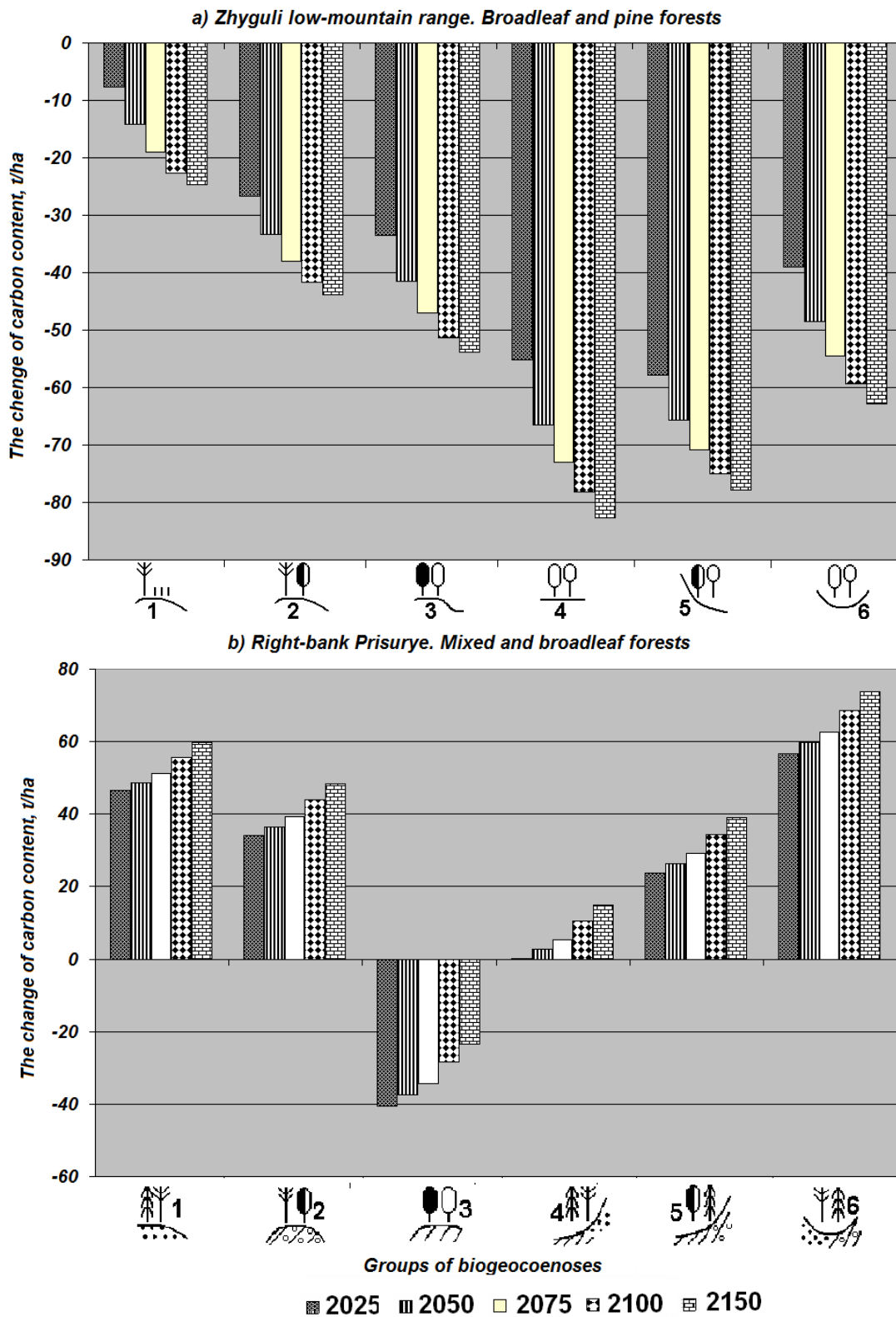


Figure 3. The predicted dynamics of carbon balance in the groups of forest biogeocoenoses on south and typical forest-steppe of the Middle Volga River Region, according to HadCM3 model

2025–2150 – prediction dates. Conventional meanings of biogeocoenose groups see in Table 1.

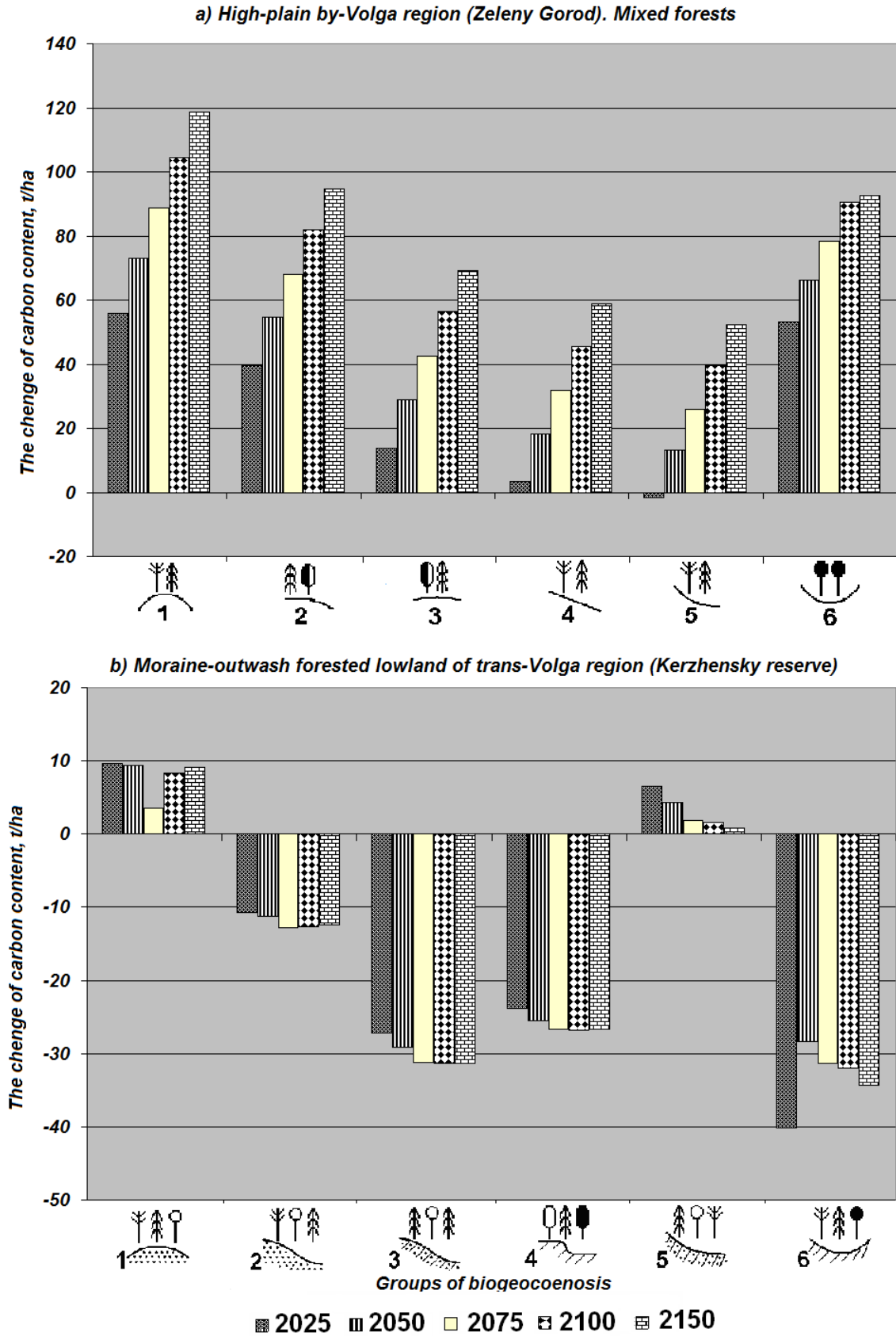


Figure 4. The predicted dynamics of carbon balance in the groups of biogeocoenoses near boundary between mixed forest zone and south-taiga subzone on the Middle Volga river region, according to HadCM3 model

Meanings are as Figure.3.

5. In sub-taiga outwash forested lowlands, the Le Chatelier's principle will be observed only due to the functional shifts of semi-paludal coniferous forests of the lower catena links, where the improvement of hydrothermal conditions of soil will induce a significant increase of productivity (see Figure 2, *f, g*). At the same time, in flat-interfluvial and close to them transit spruce-pine and spruce-oak-lime communities, the autotrophic biogenesis will be weakening against significant activation of decomposition of above-ground dead mass and humus, which will cause here a general tendency of negative biotic regulation of the carbon cycle.

Far more unambiguous and intensive changes may occur in the detritus branch of biological cycle (ΔML) on outwash forested lowlands of more northern sub-taiga region. Soil temperature increase and desertification abruptly activate the degradation of dead organic matter, with higher degree of its utilization and additional release of CO_2 to atmosphere.

6.2. Ecological Consequences of the Biotic Regulation of The Carbon Cycle

The obtained materials give quite a clear idea of the zonal and local regularities of predicted biotic regulation of carbon cycle under global warming. The results of calculations by HadCM3 model characterize in principle the clear expressed dynamics of the effect of forest ecosystems on CO_2 content in the atmosphere. The results of hydrothermal ordination of biological turnover parameters [51] and predicted carbon balance indices (see Tables 4 and 5, Figures. 3 and 4) make it possible to establish spatial regularities of the effect of phytobiota on the carbon cycle not only on the local scale but also at a level of landscape-zonal systems. The general conclusions on biotic regulation of the carbon cycle under global warming are formulated as follows.

Under predicted global warming, two mutually antithetical phenomena of carbon cycle biotic regulation will be developing on the Middle Strip of the Russian Plain. *The extreme south of the forest zone will be the field of significant additional accumulation of carbon in the atmosphere* (see Figure 3, *a*, Tables 4, *a*, and 5, *a*). Accordingly, the natural balance of carbon cycle as one of the leading stabilizing mechanisms of continental biosphere will be disturbed. It will induce local intensification of the greenhouse effect and inevitably accelerate the general process of degradation and disappearance of marginal forests in southern and typical (middle) forest-steppe. The flat-interfluvial coniferous and mixed forests of sub-taiga outwash lowlands will play the same negative role in the changes of carbon balance.

The main positive biotic regulation of carbon exchange between the above-ground ecosystems and atmosphere aimed at reduction of its greenhouse effect (according to the Le Chatelier's principle) will be performed by broad-leaved/coniferous forests of high plains in the nemoral-forest subzone and in the southern belt of the sub-taiga zone (see Figure 4, *a*, Table 4, *c*). Xerophyte 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. The positive role of broadleaf forests will be much less efficient (see Table 5, *b*); besides, their effect will be limited by northern and typical forest-steppe.

Thus, far from all formations and associations of boreal forests should be assigned with the role of "the planet lungs", as it is traditionally postulated in Russian and foreign literature. Concentration in the boreal forests of more than 40% of the carbon occurring in all terrestrial biomes [39] still does not mean that all coniferous and mixed forest communities are able to perform global ecological functions of stabilization of the state of biosphere under changing climatic conditions. These functions are significantly differentiated depending on local geomorphological and hydroedaphic conditions, and they may have both positive and negative effects. Coniferous, mixed and broadleaf forests of temperate latitudes may cause such biotic regulation of carbon cycle under global climatic changes that will exert both positive and negative influence on the state of continental biosphere.

6.3. Predictive Scenarios in Cartographic Expression

The maps representing the modern states or variation tendencies of ecosystems may serve as a tool at landscape-ecological prediction. The results obtained for the experimental test sites are presented as maps and matrices of ecosystem parameters. They may be considered as a methodically valuable example for large-scale cartographic modeling with a sufficiently high level of statistic reliability.

As examples, let us consider the cartographic models of carbon balance of forests for the period up to 2075 (see above). At the local level, the 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. The fragments of C_{base} and $\Delta C(Fa)$ maps of the Zhyguli (Samarskaya Luka) and By-Oka-Terrace reserve regions stand are presented at the local level (Figures 5 and 6). Map are created on the base of multiple regression equations, with the corresponding Spirman correlation coefficient r_s and the level of significance P (see above formulas 3–6).

As one can see, for the Samarskaya Luka in the base period the highest total C stocks are typical of the gentle near-watershed shadowy slopes with the least catchment area. In the predicted period, these locations as well as the bottoms of small valleys will be characterized by maximal CO_2 emission. On steep slopes, the initial C stocks are minimal but its forthcoming release will be insignificant.

The local level can be also illustrated by the maps of C_{base} and $\Delta C(Fa)$ for the forest tract of the By-Oka-Terrace biosphere reserve (see Figure 6). The maps were constructed on the basis of connections between the above parameters (the basal and predicted total carbon content) and the most significant environmental factors (see formulas 5–6). In given ecoregion the greatest total carbon reserves in the basal

period are characteristic of weakly sloping near-watershed regions with the lowest water catchment area. In the predicted period, these locations, as well as relatively steep slopes, especially those well heated at the southern azimuth

of the Sun, will be characterized by the maximum CO₂ emission. At the same time, the stands in ravines and thalweg areas will be the pools with the highest carbon deposit.

Table 4. Predicted partial and balance changes in the carbon content (tons/ha) relative to the base period in flat-interfluvial forest biogeocoenoses in different zonal-regional conditions of the Middle and Upper Volga Region, according to the HadCM3 model

Parameters	Base values	Changes in predicted periods				
		2025	2050	2075	2100	2150

Zonal ecotone of forest and steppe (Zhyguli low-mountain range – National Nature Park “Samarskaya Luka”)

BS	101.75	-23.05	-27.32	-31.55	-35.78	-39.66
BV	4.16	-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	5.35	3.56	4.90	6.34	7.78	8.99
HU	113.30	-10.54	-15.29	-18.62	-20.68	-21.66
Balance	265.05	-50.51	-61.09	-69.91	-77.29	-83.11

Right-bank of Sura river, mixed and broadleaf forest – National Nature Park “Chavash Forest” (test site 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

High-plain by- Volga Region, at north boundary of nemoral-forest zone. Mixed forests in the south vicinity of city Nizhny Novgorod (stow “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

Outwash low-land Right-bank of Down Oka river, south boundary of mixed-forest zone. Pure and complicated pine forests (test site Vyksa)

BS	152.75	-36.36	-36.08	-36.11	-36.07	-36.01
BV	9.50	-0.74	-0.89	-0.88	-0.90	-0.93
BR	47.70	-10.60	-11.28	-11.21	-11.31	-11.43
WD	8.50	-0.27	-0.86	-0.80	-0.88	-0.97
ML	12.53	-0.08	-3.03	-3.74	-5.00	-5.19
HU	10.66	1.82	1.31	1.37	1.29	1.19
Balance	241.64	-46.23	-50.84	-51.37	-52.86	-53.34

South strip of mixed-forest zone. Left-bank of middle Oka river. Moraine-erosion plain. Pine-lime-oak forests (By-Oka-Terrace biosphere reserve)

BS	310.18	-27.14	-27.85	-27.76	-27.99	-27.91
BV	11.54	-1.98	-1.88	-1.89	-1.87	-1.88
BR	84.81	-4.11	-4.30	-4.28	-4.34	-4.32
WD	31.96	-7.44	-7.19	-7.21	-7.15	-7.17
ML	14.96	6.58	9.44	9.58	12.69	11.14
HU	22.05	2.84	2.52	2.55	2.48	2.51
Balance	475.5	-31.24	-29.25	-29.0	-26.17	-27.61

South strip of subtaiga zone on the over-Volga Region, moraine-outwash forested lowland. Fir-pine forests (biosphere reserve “Kerzhensky”)

BS	84.7	-13.00	-12.64	-11.86	-11.85	-1.15
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

Foot-note. BS – living skeletal phytomass; BV – verdure mass; BR – root mass; WD – dead skeletal phytomass; ML – forest litter mass; HU – humus mass.

Table 5. Average-weighted (by the area) basic content of organic carbon in soil-vegetation cover (t/ha) and its changes on the nature reserved territories of the Middle and Upper Volga river region, according HadCM3 prognostic climatic model

Periods	Natural reserved territories		
	a) National Nature Park "Samarskaya Luka" (sub-zone of the south forest-steppe, broadleaf and pine forests)	b) National Nature Park «Chavash Forest» (sub-zone of the middle forest-steppe, mixed and broadleaf forests)	c) By-Oka-Terrace biosphere reserve (zone of the mixed forests, at its south boundary; mixed, pine and broadleaf forests)
Base	218.59	174.57	204.52
1985–2025	–44.01 (–20.1)	14.03 (8.0)	1.36 (0.7)
2025–2050	–52.85 (–21.2)	16.78 (9.6)	5.05 (2.5)
2050–2075	–58.40 (–26.7)	19.57 (11.2)	5.16 (2.5)
2075–2100	–62.82 (–18.7)	24.90 (14.3)	8.32 (4.1)
2100–2150	–66.03 (–30.02)	29.56 (16.9)	6.76 (3.3)

Footnote. The predicted deviations (%) of carbon content from basic period is shown in the brackets.

The regional level is represented, as has been mentioned above, by the Oka river basin (Figure 7). Multiple regression equations used for construction of the maps are presented in Table 3. The modern forest cover of this territory under global warming will perform positive (as a whole) carbon cycle regulation. However, the value of such regulation here will not be any significant due to comparatively low changes in the C content in most of the pools including alive skeletal phytomass (see Figure 2, *e, f*). The predictive map also reveals the pronounced contrast and frequent spottiness of the positive and negative values of C balance. Particularly variegated character ($\Delta C(Fa)$ varying from +(65–100) to –(80–136) t/ha) is typical of the meridian band of the right bank of the Oka river downstream, Moksha and Tsna rivers, which makes up the north-west part of the by-Volga High Plain upland and is occupied mainly by complex pine forests and their small-leaved derivatives. Nevertheless, the dominating background here is formed by positive values of $\Delta C = 0–40$ t/ha.

The second region of positive biotic C cycle regulation is the lowland territory of Ryazan’s Meshchera flanked from the south by a bend of the Oka River downstream and occupied by marshy coniferous outwash-plain woodlands. Finally, the eastern slopes of the Smolensk-Moscow ridge and the adjacent left bank of the Middle Oka form the third region with positive ΔC values. Here, mainly broadleaf and spruce forests and derivative birch and aspen forests are prevalent.

Feebly marked negative ΔC values (0 to –12, here and there up to –38 t/ha) will be typical of the two regions: (1) the north-west outpost of the Central Russian Upland, where considerable stands of oak-lime and birch-aspen forests are still maintained, and (2) sub-taiga lowland-outwash left bank of the Klyaz’ma river downstream and the neighbouring right bank of the Volga river, with predominance of broadleaf-spruce and spruce/birch forests. Fragmentary forests on the vast territories of agricultural fields will implement for the most part feebly marked positive biotic regulation of the carbon cycle.

6.4. Virtual Predictive-Ecological Mapping of Carbon Balance

The revealed statistic relations of C balance of different forest formations of the Oka river basin with the most significant predictors (see Table 3) made it possible to construct regression maps of ΔC_{2075} for the period up to 2075 (Figure 8). The maps are of conditional character. Each of them describes virtual reality: the pattern of changes in the C content in the given group of formations provided that it covers the entire basin area. However, such maps present more distinctly the partial contribution of forest communities to C cycle biotic regulation on the territories with different natural conditions. It is particularly important for forestation strategy in the currently deforested regions under anticipated climatic changes. Obviously, at selection of saplings, preference should be given to the varieties providing positive carbon balance.

For the most of forest formations (see Table 4, *b–f*), C deposit increases with the increase of catchment area MCA, i.e. with transition from the E and TE to TA and A types of location. It is particularly typical of the pine and broadleaf-pine forests of the Oksko-Tsninskaya lowland (see Figure 8, *b*), where C accumulation on vast areas amounts to 15 t/ha. At the same time, positive ΔC values are typical of only large river valleys on the Central Russian Upland upstream the Oka river, while C emission prevails on the local watersheds.

In contrast to light-coniferous formations in spruce and broadleaf-spruce forests, C deposit intensifies with altitude Z , whereas in the river valleys spruce forests give feebly marked C emission. At higher illumination of slopes Q (the factor affecting local hydrothermics), C deposit increases in spruce forests and C emission increases in pine and broadleaf-pine forests.

The steepness of slopes GA and maximum curvature k_{max} determining "crest forms" in the relief have positive effect on C accumulation. Exclusion is birch and aspen forests growing in the place of pine forests, which have negative effect. As a result, these secondary formations give the highest CO_2 emissions into the atmosphere for the whole basin: up to 100 t/ha and more (see Figure 8, *d*).

The mean July air temperature as one of their major climatic indices differently affects the C balance of forests. Temperature rise causes a tendency to predominant carbon

emission in the groups of forest formations, which are relatively complex by genesis, and C deposit in comparatively simple groups (see Table 3, a, d).

Predictors of the regression equations describing spatial variability of total C changes may act in different directions;

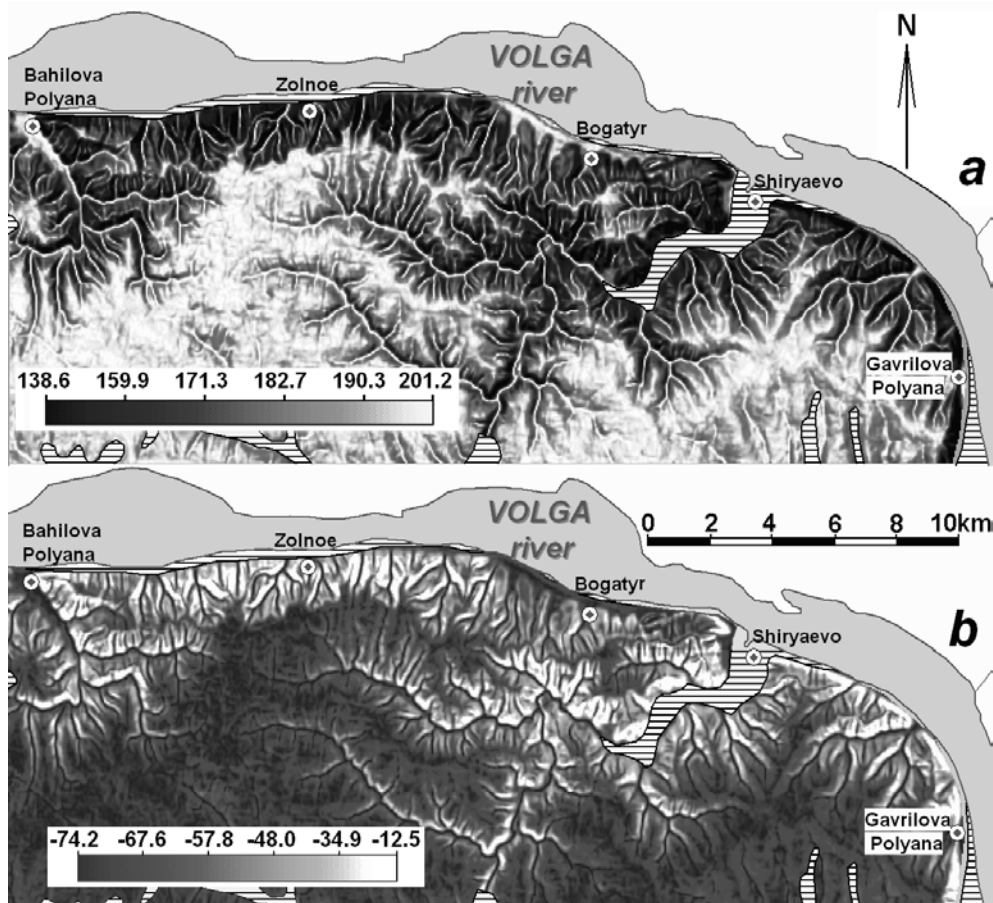


Figure 5. Zhyguli low-mountain ecoregion – National Nature Park “Samarskaya Luka”. Base total C content in forest ecosystems (a) and changes in total C for the predicted period of 2075 (b), in t/ha, according to HadCM3 model

Main predictors for the calculation of maps – insolation, coming to the slopes (illumination), steepness of slope, maximal catchment area. Step of lattice – 50 m. Mean change, calculated by matrix: for 2075 is –65.5 t/ha; for 2150 is –74.0 t/ha.

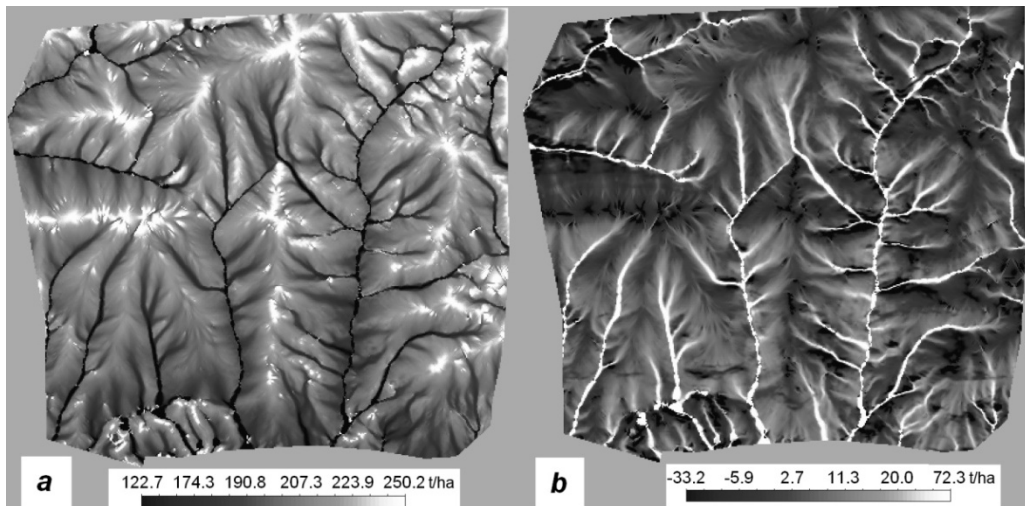


Figure 6. Lowland Middle left-bank region by-Oka river – By-Oka-T errace biosphere reserve. Changes of sum carbon content (carbon deposit, t/ha) to predictive dates 2075 (a) and 2150 (b), in t/ha, according to HadCM3 model

Main predictors – illumination, maximal catchment area and horizontal curvature showing flux convergence regions, with the growth of carbon deposits. Step of lattice – 20 m. Mean change, calculated by matrix: for 2075 is +0.35 t/ha; for 2150 is +0.67 t/ha.

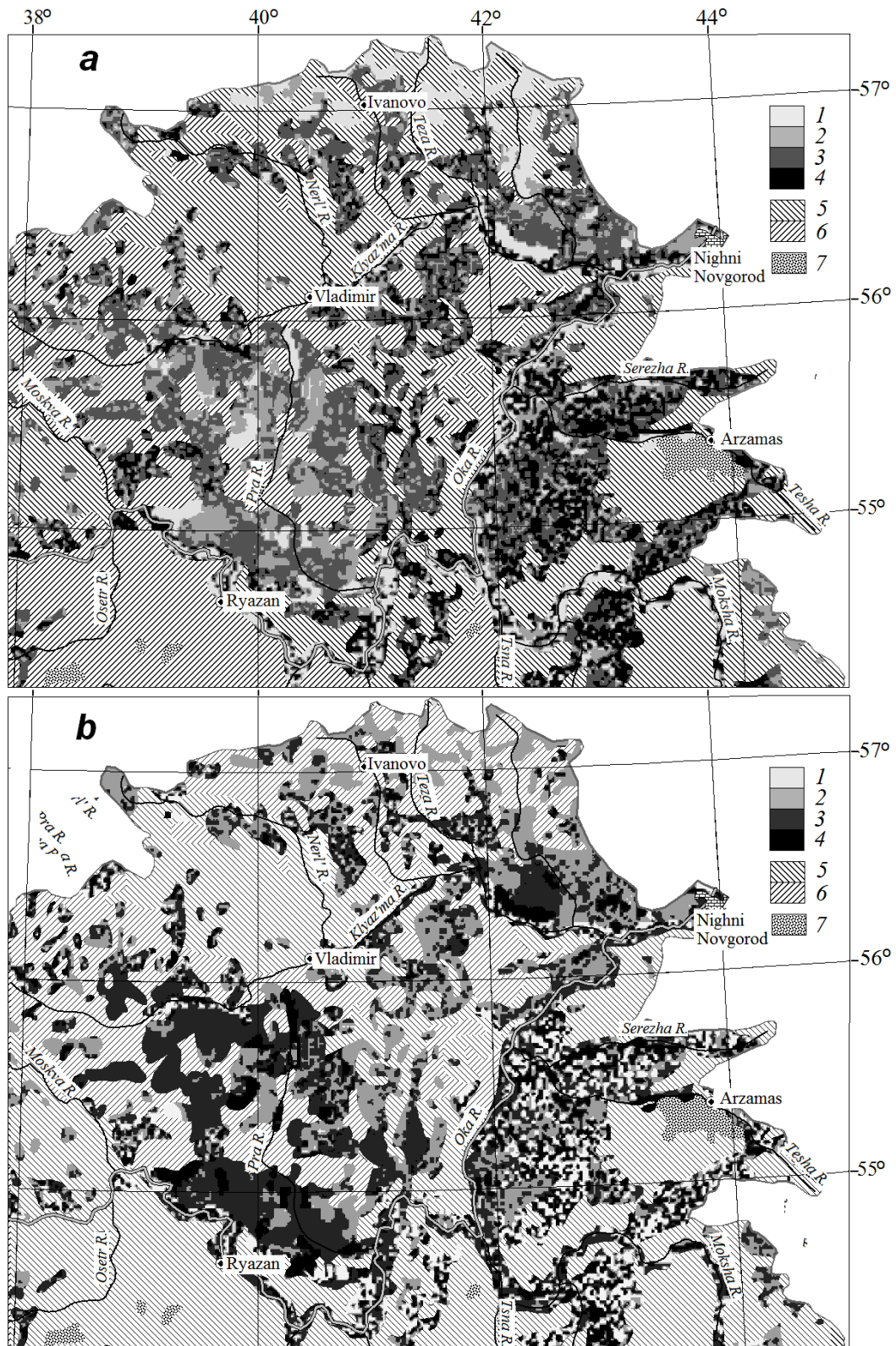


Figure 7. Maps fragments of total carbon content and its predictive changes on the territory of Oka river basin. (a) The carbon content at the end of the basic period (1985), in t/ha: 1 – 10.2 ± 15.0 ; 2 – 15.0 ± 19.3 ; 3 – 43 ± 130 ; 4 – 130 ± 160 ; 5 – 160 ± 200 ; 6 – 200 ± 423 . (b) The carbon balance in the year 2075 according to the global climate model HadCM3 (version A2). Changes in the total carbon reserve compared to the basic period, in t/ha: 1 – $(-1.3) \pm 0$; 2 – 0 ± 5.5 ; 3 – $(-136) \pm (-25)$; 4 – $(-25) \pm 0$; 5 – 0 ± 25 ; 6 – 25 ± 115

Designations: 1 and 2 – fragmentary forests on the area occupied by cultivated fields; 3–6 – forested areas; 7 – plowed patches in steppes.

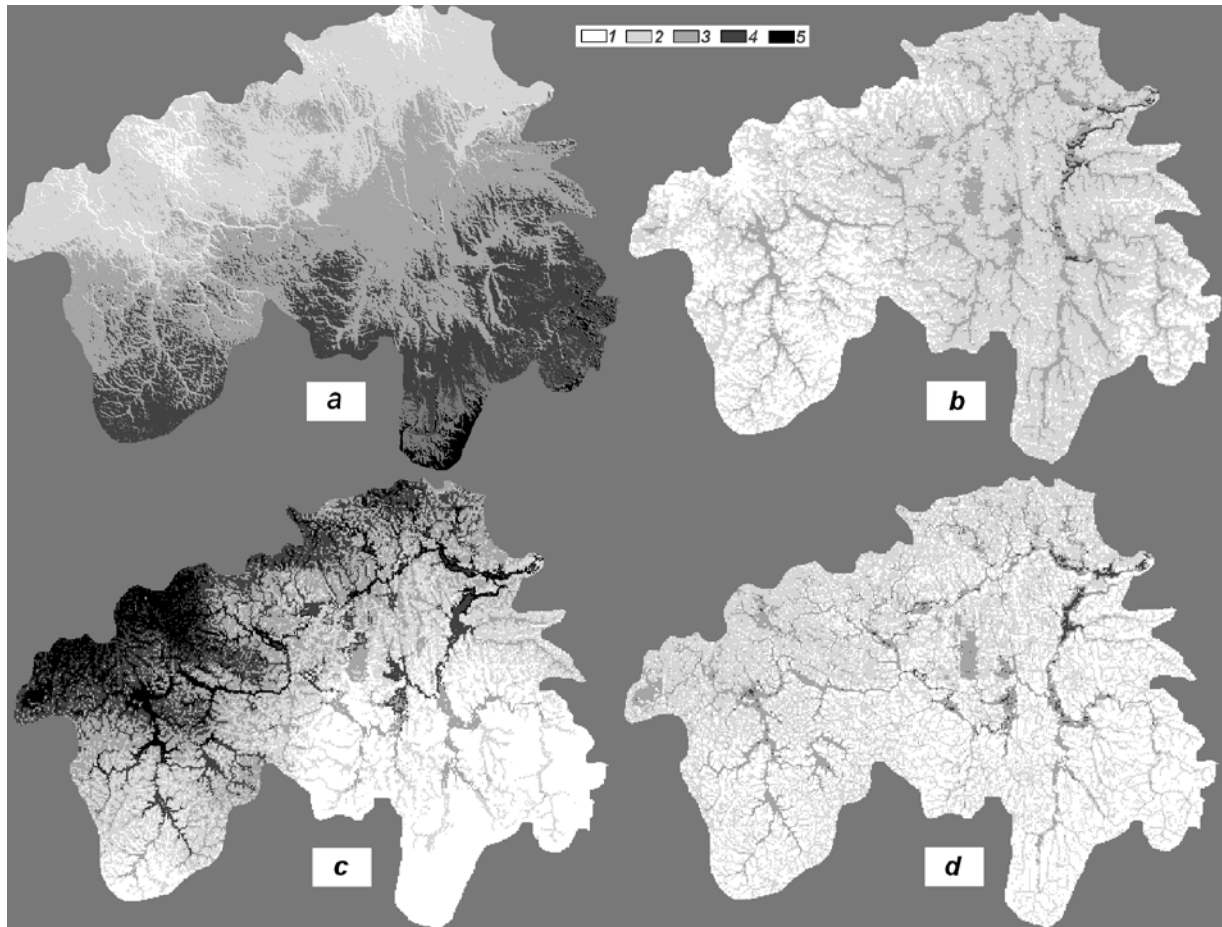


Figure 8. Regression maps of potential C balance in plant formations of the Oka river basin for the predicted period of 2075, according to HadCM3 model

It is admits, that territory of the Oka river basin is completely covered by forests: *a* – spruce and broadleaf-spruce; *b* – pine and broadleaf-pine; *c* – broadleaf; *d* – secondary in the place of pine and broadleaf-pine. Changes in total C content, t/ha: 1 (–136)–0; 2 – 0–15; 3 – 15–30; 4 – 30–45; 5 – 45–115.

Therefore, the resultant account of their interference is required. As a whole, one may say that the higher CO₂ emission, i.e. negative C cycle regulation, at the local level is typical of the near-watershed types of mesosites, particularly those occupied by coniferous-forest communities. Zonal contrasts of the ΔC parameter are most pronounced for broad-leaved formations and to a lesser extent for birch and aspen forests (see Figure 8, *c*). In the north-west region of the Oka river basin belonging to the sub-taiga zone, oak and lime forests will actively take up CO₂ from the atmosphere (up to 50–100 t/ha), thus weakening its greenhouse effect. On the contrary, in the south-east regions of typical and southern forest-steppe, broad-leaved forests will perform negative biotic regulation of the C cycle.

6.5. Territorial Generalizations of Cartographic Prediction for Carbon Balance

It is necessary to assess the contribution of separate groups of forest formations of the Oka river basin to the total biotic C cycle regulation (Figure 9, Table 6). Spruce and broadleaf-spruce forests will actively deposit C at relatively dry TE mesosites, most intensively (2–5 thousand t/km² on

the average) on steep convex slopes, where the temperature rise will induce an intense growth of stands (see Figure 9, *a*). The maximum C deposit may be up to 4.6–7.5 thous. t/km². At the more hydromorphic E and T territories, C accumulation in skeletal phytomass will be surpassed by C emissions as a result of drastic activation of the processes of forest litter decay and humus mineralization. As a whole, C deposit in dark-coniferous forests will exceed C emission by nearly 70% (see also Figure 9, *a*); however, because of insignificant area of these formations, their contribution to the region C balance will be minor.

Pine and broadleaf-pine formations will also have positive effect on the carbon cycle, 1.5-fold stronger in percentage than dark-coniferous forests (see Table 6, *b*, and Figure 9, *a*). Occupying the greatest areas in the Oka river basin, pine forests will make a considerable positive contribution to C cycle regulation, although $+\Delta C$ will decrease via simultaneous CO₂ emission. Carbon will accumulate mainly in pine forests settling down on the TE and TA–A middle-sites. Negative C balance values should be expected in the light-coniferous forests of flat interfluves and gentle even slopes.

Table 6. Change of summary carbon supplies (millions of thons) in plant formations of Oka river basin to 2050, according to HadCM3 model

Groups of forest formations, by[38]	Area, km ²	Base summary carbon	Change of the carbon content			
			deposit	emission	Common sum	
					millions of thons	%
a) Spruce and broadleaf-spruce mixed	2034	37.14	3.02	-1.8	1.22	3.28
b) Pine and broadleaf-pine mixed	26230	481.76	45.77	-23.17	22.6	4.69
c) Broadleaf	4770	84.68	6.76	-4.96	1.8	2.13
d) Secondary substituting for dark-coniferous and mixed	17770	293.26	40.77	-14.79	25.98	8.86
e) Secondary substituting for light-coniferous and mixed	16670	318.7	40.97	-51	-10.03	-3.15
f) Secondary substituting for broadleaf	4911	76.83	0.42	-1.18	-0.76	-0.99
g) Swampy forests	2343	35.18	1.01	-0.17	0.84	2.39
h) Flood-plains	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

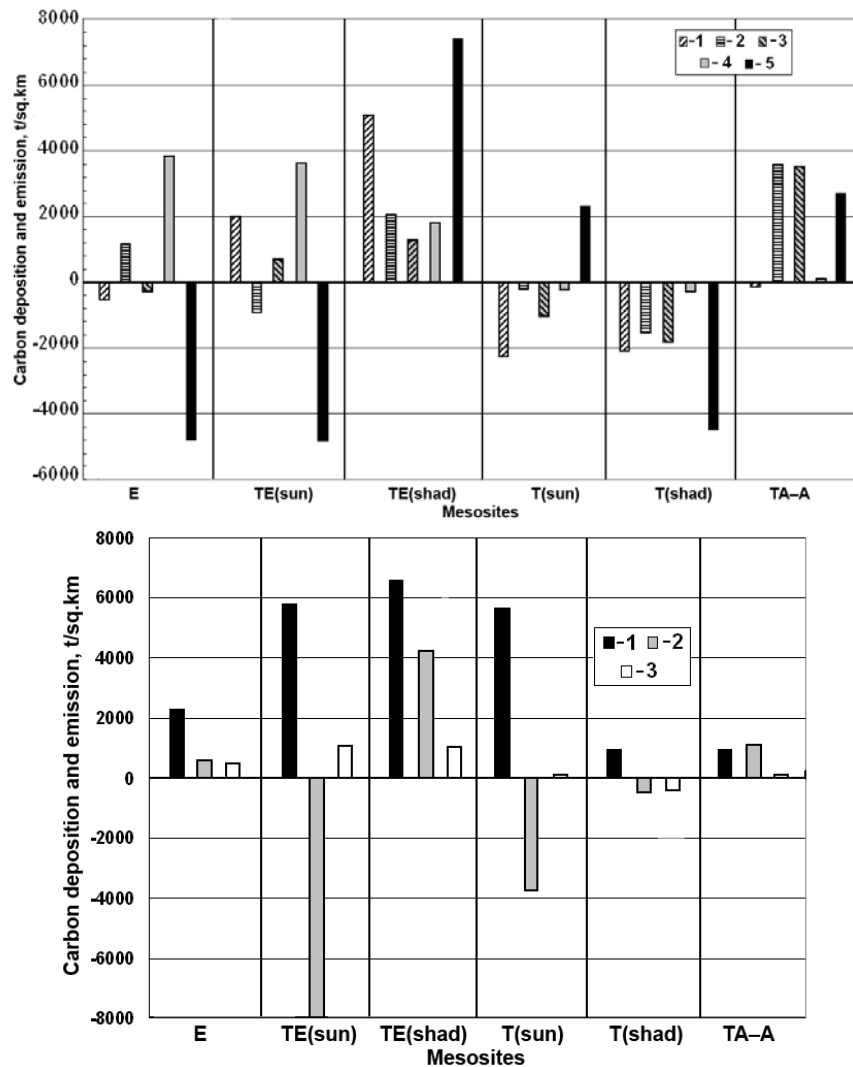


Figure 9. The changes in total C content in the groups of plant formations of the Oka river basin predicted for 2075 under different conditions of plain mesorelief. a) Aboriginal formations: 1 – spruce and broad-leaf/spruce; 2 – pine and broadleaf-pine; 3 – broadleaf; 4 – marsh-forest; 5 – flood-plain. 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 meso-sites (see in the text); sun and shad – solar exposed slopes (see Figure 2).

Broadleaf forests will have both positive and negative effects on the carbon cycle (see above), with the total minor positive balance. The main role in C deposit will be played by meso-hygrophite oak-lime forests of river valleys and adjacent slopes, especially those exposed to north. On the E and T mesosites, CO₂ emission will be dominant. As a whole, the role of native nemoral forests in the C balance of the Oka river basin will be much less as compared with coniferous and mixed forests.

Positive though feasibly marked C cycle regulation must be exhibited by forest-marsh formations (see Figure 9, a). Global warming will drastically increase the productivity of paludal forests. CO₂ consumption for creation of skeletal phytomass will significantly exceed its emission at peat litter decay; therefore, e.g., 3.6–3.8 thous. t/km² of C will have been additionally fixed on swamped watersheds by 2075.

The group of flood-plain forest formations is expected to have the highest territorial contrasts of $\Delta C(Fa)$ parameter. On the shady and neutral gently prominent slopes, soil temperature rise and groundwater level decrease will induce significant activation of productivity. It will give a C deposit value maximal for the whole Oka river basin: up to 7.5 thous. t/km² (see Figure 9, a). Its much lower amount will be accumulated in depression flood-plain forests. At the same time, the communities of eluvial and sunny TE sites will show abrupt intensification of organic decomposition process, which will give additional CO₂ emission within 4.4–4.8 thous. t/km². Resultant contribution of flood-plain forests to the total C balance of the region will be positive.

Secondary small-leaved forests will have the changes in C content different by sign (see Figure 9, b). Birch and aspen forests substituting for sub-taiga dark-coniferous forest associations are in the conditions of higher hydromorphicity of sabulous loamy soils. Thermo-arid signal will induce accelerated growth of stands in these communities. In the upper links of meso-catenas, additional C drainage in skeletal phytomass will have amounted to 5.7–6.6 thous. t/km² by the middle of 21st century owing to good heating and drying of these mesosites. The fact of substitution of secondary birch and aspen forests for spruce and broadleaf-spruce forests, i.e., *permanent presence of initial stages of restorative successions, must contribute to excess accumulation of carbon mass in the growing timber*. This seems to be *the leading role of the boreal forest cover of dark-coniferous taiga and sub-taiga types in positive C cycle regulation* by the Le Chatelier's principle.

On less hydromorphic sandy soils, where small-leaved associations exist in the place of pine and broadleaf-pine forests, positive changes in C balance will become evident only on shady TE slopes, which are relatively more humidified. The forests of E, T and TA mesosites will have quite low $+\Delta C$ values. On the sunny slopes total C emission will amount to 4 thous. t/km² and more. As a whole, restorative small-leaved stages of light-coniferous forests will respond to global warming with the common and quite significant negative C balance (see Table 6, e, and Figure 9, b).

Birch-aspen forests growing in the place of oak and lime forests will quite little change the above described pattern of $\Delta C(Fa)$ dynamics typical of their aboriginal precursors. The upper links of meso-catenas will have a low positive C balance, whereas the lower links will have feasibly marked signs of negative C cycle regulation.

7. Conclusions

Thus, biotical C 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 C balance in the forests of the main water catchment area of the Volga river basin, average weighted by area, may be from $-(21\div 27)\%$ to $+(11\div 17)\%$ of base C content. These figures are quite comparable to the data of other predictive regional estimations. For coniferous, mixed, and other USA forests, the changes in NPP and C content were calculated by predictive biogeochemical models CEN (CENTERE) and TER[1]. It was shown that, according to the scenario of UKMO-1987 climate model (the precursor of HadCM3 model), the doubling of atmospheric CO₂ gives relative C balance values in the range of $-(1.5\div 1.8)$ to $+(7.8\div 12.5)\%$.

Let us compare the obtained results with some materials on the forest cover of Russia as a whole. Based on the modern rates of carbon sink in the Russian forests[85], it may be supposed that total C accumulation in the latter during a 65-year period (1985–2050) must be about 23.1 Gt. Per 1% of the area, which is in proportion, e.g., to the area of the Oka river basin, it will be equal to 231 million tons, i.e. 1.8-fold more than is expected on the territory of this basin by 2050 according to the HadCM3 model (see Table 6, column "Deposit"). As one can see, the results of our predictive modeling of C balance are quite realistic and, though the HadCM3 is considered to be extreme, calculations on its basis give even lower estimates of C content changes in forest vegetation cover.

According to other estimates, carbon reserves in the forests of the Northern hemisphere are 36–108 Mg/ha[17]. The average carbon reserves in the forests of the Oka river basin are 180 Mg/ha. Since our calculations of forest carbon reserves include the carbon of dead phytomass, litter and humus, the data on the basal reserves are comparable.

The necessity of accounting soil carbon in balance calculations is shown in the scientific literature. According to the global estimates, the carbon reserves in above-ground vegetation (550 ± 100 Pg) are of the same order of magnitude as in the atmosphere (800 Pg)[36]. The carbon reserves of soil organic matter exceed 2–3-fold their values in vegetation: 1500–2000 Pg in the upper 1-m soil layer and 2300 Pg in the upper three meters[42, 57]. In essence, the carbon reserve in soil may be considered as a "small geological deposit", because it is on average only 3–4 times less than the fossil fuel reserves of the planet: coal, oil, and gas (5000–10,000 Pg).

The total carbon sink in the Russian forests is 150–200 Mt/yr [85, 87]. It will make 2.34 Mt/yr for 1.17% of the area. The total carbon sink for the period of 65 years will make up to 150.2 Mt. For the forests of the Oka river basin, our model gives a total carbon deposit of 145.8 and carbon emission of 103.1 million tons in 2050. As we can see, the results of our predictive carbon balance modeling are quite comparable with other estimates of carbon reserves in the temperate forests by 2075.

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¹ This elementary unit of geographical ecology accepted in Russia corresponds to categories "Site", "Eco-element", and "Landtype Phase" by classifications of

Australia-Britain, Canada, and USA, respectively [45].