THE PRINCIPLE OF SPACE-FOR-TIME SUBSTITUTION IN PREDICTING *BETULA* SPP. BIOMASS CHANGE RELATED TO CLIMATE SHIFTS

USOLTSEV, V. A.[2,3] – LIN, H.[1,4,5,6*] – SHOBAIRI, S. O. R.[1*] – TSEPORDEY, I. S.[3] – YE, Z.[1,4,5,6] – ANEES, S. A.[7]

[1]*Research Center of Forestry Remote Sensing & Information Engineering, Central South University of Forestry and Technology, Changsha 410004, China*
(e-mail: Omidshobeyri214@gmail.com)

[2]*Ural State Forest Engineering University, 620100 Yekaterinburg, Siberian tract, 37, Russia*

[3]*Botanical Garden of the Ural Branch of the Russian Academy of Sciences, 620144 Yekaterinburg, ul. 8 Marta, 202a, Russia*

[4]*Key Laboratory of Forestry Remote Sensing Based Big Data & Ecological Security for Hunan Province, Changsha 410004, China*
(e-mail: 1053460198@qq.com)

[5]*Key Laboratory of State Forestry Administration on Forest Resources Management and Monitoring in Southern Area, Changsha 410004, China*

[6]*Changsha Changchang Forestry Technology Consulting Co., Ltd., Changsha 410004, China*
(e-mail: loyzer@163.com)

[7]*Beijing Key Laboratory of Precision Forestry, Forestry College, Beijing Forestry University, Beijing 100083, P. R. China*
(e-mail: anees.shoaib@gmail.com)

[*]*Corresponding authors*
e-mail: linhui@csuft.edu.cn; Omidshobeyri214@gmail.com

(Received 19th Feb 2022; accepted 20th May 2022)

Abstract. Human society faces problems of a global scale today, as a result of which the priorities of environmental research are shifting to the macro level, and ecology has entered the era of "big data". The authors have created a database of 1,717 model trees of *Betula* spp. with measured indicators of diameter at breast height (DBH), tree height, age, and aboveground biomass growing in the territory of Eurasia. Regression models for aboveground biomass components are calculated, including the dendrological indices mentioned, and two climate indicators as independent variables. Based on the theory of space-for-time substitution, the obtained patterns of changes in aboveground biomass in the territorial climatic gradients of Eurasia are used to predict changes in biomass due to climate shifts. In accordance with the law of the limiting factor by Liebig, it is established that in sufficiently moisture-rich climatic zones, an increase in temperature by 1°C with a constant amount of precipitation causes an increase in biomass, and in water-deficient zones — its decrease. In warm climatic zones, a decrease in precipitation by 100 mm at a constant average January temperature causes a decrease in biomass, and in cold climatic zones — its increase.

Keywords: *hydrothermal gradients, biomass components, allometric models, mean January temperature, annual precipitation*

DOI: http://dx.doi.org/10.15666/aeer/2004_36833698

Introduction

Most of the environmental problems that human society faces today can only be solved on a global scale, and the priorities of environmental research are shifting to the macro level. Ecology has entered the era of "big data", "big science", and "big theories" (Niu et al., 2020). In the context of global climate shifts, understanding the development of forest ecosystems in terms of their ability to absorb atmospheric carbon is of increasing interest. In localized gradients of natural zones formed as a result of long-term vegetation evolution, changes in the biological productivity of vegetation cover occur (Kosanic et al., 2018; DeLeo et al., 2020).

These climatically determined spatial gradients of the productivity of trees and stands can be used to predict its changes in time under the influence of expected climate shifts based on the theory of space-for-time substitution. This term means using current patterns observed in spatial gradients to understand and model the same patterns in prospective time gradients that are currently unobservable (Blois et al., 2013). Methods based on space-for-time substitution are used in different fields; in particular, for the study of long-term nutrient cycling and plant succession (Johnson and Miyanishi, 2008) or for the prediction of biodiversity (Fitzpatrick et al., 2011), and there are encouraging results in this regard (Pickett, 1989; Blois et al., 2013).

A comparative analysis of the accuracy of various methods for determining the biological productivity of tree species has shown that models performed at a tree level give a lower error in estimating biomass per unit area compared to models performed at a stand level (Zeng et al., 2018). Allometric models of tree biomass are particularly relevant when assessing biomass in stands of mixed species composition (Shuman et al., 2011).

In Australian conditions ranging from dry ecotopes to tropical rainforests, simple allometric models of aboveground biomass for a combination of *Eucalyptus* and closely related species explained 84-95% of the total biomass variation. However, the effectiveness of the model improved only very slightly when such indicators as tree height, basic wood density, and climate variables were included in the model as independent variables. The loss of forecasting efficiency was <1% if generalized models were used instead of species-specific models. The use of generic multi-species models did not significantly distort the biomass forecast in 92% of the 53 tested species. In addition, the overall efficiency of predicting biomass at the stand level was 99%, and the average absolute prediction error was only 13% (Paul et al., 2016). In Tanzania's dry-to-wet conditions, the generic allometric model of aboveground biomass explained 95% of its variation. However, for a more accurate assessment of the biomass, it is recommended to calculate models taking into account the growing conditions (Mugasha et al., 2012).

The inclusion of territorial values of temperature and precipitation as additional independent variables in allometric models of tree biomass improved the accuracy of estimates and made it possible to predict changes in biomass in Chinese forests during climate shifts (Zeng et al., 2017; Fu et al., 2017). Warming by 1°C has been shown to increase the aboveground biomass of a tree by 0.9 % and to decrease the root biomass by 2.3%; an increase in precipitation by 100 mm causes the decrease in aboveground and underground biomass by 1.5 and 1.1%, respectively (Zeng et al., 2017). In these studies, the territorial differences in climate are extrapolated to the predicted climate shifts over time in accordance with the principle of space-for-time substitution (Zeng et al., 2017; Fu et al., 2017). However, such models are presented as single studies on regional levels (Lei et al., 2016; Forrester et al., 2017; Zeng et al., 2017; Fu et al., 2017).

It is known that the production of plant biomass is limited by a factor that is in minimum or excess in relation to its needs according to the principle of limiting factor (Liebig, 1840). At the polar limit of birch distribution in Siberia, the limiting factor is temperature, but as we move south, the heat deficit decreases and the role of moisture deficiency increases. At the same time, the change of the limiting factor occurs in the subzone of the middle taiga (Fonti, 2020).

In this study, we intend to: (a) identify the most efficient structure of the allometric model of biomass on the example of *Betula* spp. in Eurasia, (b) identify how the aboveground biomass of trees is related not only to the dendrometric indicators of trees, but also to the territorial average values of temperatures and precipitation at a transcontinental level, (c) to establish whether the effect of the law of the limiting factor is manifested when modeling changes in the biomass of trees of forest-forming species on the territory of Eurasia in relation to geographically determined changes in temperatures and precipitation; and (d) to show to what extent the constructed climate-conditioned models of biomass, sensitive to temperature and precipitation in territorial gradients, can be used to predict its changes in temporal gradients based on the principle of space-time substitution.

The genus *Betula* spp. is included in *Betulaceae* family. This family has 120-150 species (Grimm and Renner, 2013). Majority of species are present in northern climatic zones and have a wide natural distribution area on the Eurasian continent, ranging from the Atlantic to Pacific coasts. Birch is among ten common species in Russia. There are several species in the common birch category from the section *Albae* Rgl.: silver birch (*B. pendula* Roth.), downy birch (*B. pubescens* Ehrh.), mountain birch (*B. tortuosa* Ldb.), Japanese white birch or Siberian silver birch (*B. platyphylla* Suk.) (Hynynen et al., 2009).

Materials and Methods

To solve these problems, the database on the biomass of forest-forming species of Eurasia in the amount of 15,200 trees (Usoltsev, 2020) is used. From it, 1,717 sample trees of *Betula* spp. were selected with measured values of the DBH, tree age and height and components of aboveground biomass (*Table 1*). The genus *Betula* spp. is represented by some vicarage species, mainly *B. pubescens* Ehrh., *B. pendula* Roth, and in smaller numbers by *B. maximowicziana* Regel, *B. ermanii* Cham., *B. platyphylla* Suk., *B. costata* Trautv., and *B. dahurica* Pall.).

Table 1. *Statistics of sample trees of Betula spp.*

Designation of statistics [(a)]	**Indices analyzed**[(b)]						
	A	***D***	***H***	***Pf***	***Pb***	***Ps***	***Pa***
Mean	40	13.4	14.6	2.56	15.6	87.9	106.2
Min	3	0.2	0.7	0.003	0.003	0.02	0.03
Max	195	48.0	34.5	29.5	230.2	739.5	950.2
SD	21.8	8.1	6.2	3.3	27.7	113.9	141.3
CV, %	54.5	60.0	42.5	129.6	177.7	129.6	133.1
n	1716.0	1716.0	1715.0	1713.0	1715.0	1717.0	1712.0

[(a)] Mean, Min and Max are the average, minimum, and maximum values, respectively; SD is standard deviation; CV is coefficient of variation; n is the number of observations.

[(b)] *A* is tree age, yrs; *D* is stem diameter at breast height (DBH), cm; *H* is tree height, m; *Pf, Pb, Ps* and *Pa* are the biomass of foliage, branches, stem with bark and aboveground biomass in dry condition, kg

The joint analysis of different species is caused by the impossibility of growing the same tree species throughout Eurasia, as a result of which their areas within the genus are confined to certain ecoregions. When entering the transcontinental level of research, we are faced with the obvious fact that no species grows throughout the continent, precisely because of regional differences in climate. Moving from refugia under the influence of geological processes and climate changes, a particular species adapted to changing environmental conditions, forming a series of vicariant species within a genus (Tolmachev, 1962). In other words, differences in traits between species evolved as adaptations to different climates (Laughlin et al., 2021). This gives grounds for analyzing the response of birch trees to changes in climatic characteristics to create one climate-dependent unity within the entire genus *Betula* spp., since the differences in the ecophysiological traits of different species, for example, *B. pendula* vs. *B. platyphylla* vs. *B. costata* are derived from regional climatic features.

The available data of the geographical coordinates of the sample trees are plotted on the maps of the average January temperature (https://store.mapsofworld.com/image/cache/data/map_2014/currents-and-temperature-jan-enlarge-900x700.jpg) and the average annual precipitation (http://www.mapmost.com/world-precipitation-map/free-world-precipitation-map/) (World Weather Maps, 2007) (*Fig. 1*) and are combined with dendrometric indicators of sample trees. In our case, the schematic map of the isolines of mean January temperature, rather than that of the mean annual temperature, was used. With an inter-annual time step, the predominant influence of summer temperature is quite normal (Zubairov et al., 2018). However, against the background of long-term climatic shifts for decades, the prevailing influence is acquired by winter temperatures (Bijak, 2010; Toromani and Bojaxhi, 2010; Morley et al., 2016). In terms of regression analysis, a weak temporal trend of summer temperatures compared to a steep trend of winter ones, means a smaller regression slope and a worse ratio of residual variance to the total variance explained by this regression. Obviously, taking the mean winter temperature as one of the independent variables, we get a more reliable dependence having the higher predictive ability.

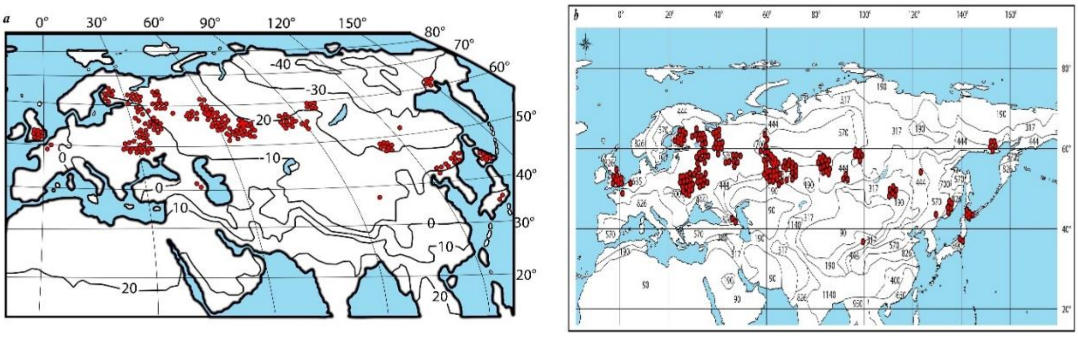

Figure 1. *Allocation of the empirical data of 1,717 sample trees on the maps of the average January temperature, °C (a) and average annual precipitation, mm (b) (World Weather Maps, 2007)*

The choice of winter temperature also has a bioecological background. It is known that each environmental factor has an optimal range of its effects in which it is most effective and beyond which this effect decreases or even has an overwhelming result (Tranquillini, 1955; Burian, 1970; Liepa, 1980; Cárdenas-Pérez et al., 2022). In our case, the winter temperature, in particular, the long-term temperature of January, has the most effective effect on the tree bioomass of forests.

The above-mentioned, previously published models of tree and stand biomass sensitive to climate change were performed at the regional levels and were adapted to regional climatic features (Lei et al., 2016; Forrester et al., 2017; Fu et al., 2017; Zeng et al., 2017). Due to regional allocation, none of them can be extrapolated to the transcontinental level. They give the visions of the local trends of biomass in connection with the local climate and may even be opposite in sign. Therefore, their totality cannot give the performance of what awaits biota and forest cover in particular at the global level.

Our database, which provides initial information on the biomass of trees of forest-forming species of Eurasia (Usoltsev, 2020), makes it possible to show, if not global, then at least trans-continental expectations of upcoming changes in tree biomass under the influence of possible climatic shifts at the continental level. Today we have databases on tree biomass for Eurasia (Falster et al., 2015; Schepaschenko et al., 2017; Usoltsev, 2020), which have many disadvantages, which limits the possibilities of developing empirical predictive models based on them. In particular, due to the lack of data for some regions, these gaps have to be covered by an interpolation technique in the modeling of biomass.

We also mean the limited explanatory possibilities of multiple regression analysis, as a result of which we consistently extract from the total variance of biomass, first of all, the variance that is most explained by the main dendrometric and climatic variables. The residual variance includes both unaccounted factors as well as methodological uncertainties and trivial calculation errors of the harvest data. Naturally, it is impossible to extract and explain the variability of biomass from such a residual dispersion, due, for example, to the unevenness of precipitation by month during the year. As a consequence, we cannot use such models to predict the impact of extreme events (droughts, floods, etc.) on the biomass of trees. Process-based models seem to be more suitable for this purpose (Sato et al., 2010).

Usually, when analyzing the productivity of trees or stands, the influence of a single factor is estimated: either temperature or precipitation (Lieth, 1975; Reich et al., 2014; Russell et al., 2015; Fonti, 2020; Frauendorf et al., 2020; Devi et al., 2020). Estimating biomass by a single climatic factor can lead to contradictory results, since the combined effect of temperatures and precipitation is not taken into account. The presence of the Eurasian database in the maximum ranges of temperatures and precipitation allowed us to assess the combined impact of temperatures and precipitation on the biomass of trees.

The ecologists who are engaged in extracting a climatic signal from the chronologies of tree rings may ask how the temperature of January affects the biomass of a tree when the tree is in winter "hibernation" and why the temperature of June or July, characteristic of the period of active growth, is not accepted? In the context of our research, there is no answer to such the question, since it indicates a substitution of the concept, in this case, the concept of temperature. We install the position of the sample plots with geographically distributed biomass data on the map of geographically distributed winter temperatures (*Fig. 1*) having the aim their conjugate analysis. The current territorial (geographical) distribution of temperatures and precipitation has been formed over millennia, and at the same time, the territorial biodiversity of vegetation cover has been formed in accordance with it (Mohan et al., 2009), including the division of a particular genus into species (Tolmachev, 1962), and this biodiversity determines the structural and functional traits of plant biomass. Since the average January and average annual temperatures are correlated to some extent, the named conjugation of the biomass could be performed both with the average annual and with the average January temperature. We chose the latter for the above reasons.

The change of the limiting factor for birch growth as it moves from north to south was mentioned above (Fonti, 2020). In this phenomenon we did not mean climatic indicators in the form of geographically distributed temperatures and precipitation, as in our study, but meteorological data of temperatures and precipitation of specific years and months. Accordingly, our analysis of the factors limiting biomass does not include January temperature meteorological data or average annual precipitation meteorological data, but long-term geographically distributed temperatures and precipitation, the impact of which on biomass is extrapolated to the assumed temporal gradients of temperatures and precipitation through space-for-time substitution. However, there is the other opinion that is an alternative to the principle of a single limiting factor. Drawing an analogy with the distribution of resources in the economy, A. Bloom and co-authors (1985) believe that plants distribute the resources available for growth in such a way that the limiting effect is approximately the same from all resources, and not from the only one of them.

Optimization of the allometric model structure

Based on the analysis of literature sources, the following variants of the allometric model are subjected to comparative analysis:

$$\ln Pi = \mathrm{a}_0 + \mathrm{a}_1 \ln D \tag{Eq.1}$$

$$\ln Pi = \mathrm{a}_0 + \mathrm{a}_1 \ln D + \mathrm{a}_2 \ln H \tag{Eq.2}$$

$$\ln Pi = \mathrm{a}_0+\mathrm{a}_1\ln(D^2H) \tag{Eq.3}$$

$$\ln Pi = \mathrm{a}_0 +\mathrm{a}_1 \ln A +\mathrm{a}_2 \ln D + \mathrm{a}_3 \ln H \tag{Eq.4}$$

$$\ln Pi = \mathrm{a}_0 + \mathrm{a}_1 \ln D + \mathrm{a}_2 \ln H + \mathrm{a}_3 (\ln D)(\ln H) \tag{Eq.5}$$

$$\ln Pi = \mathrm{a}_0 + \mathrm{a}_1 \ln A +\mathrm{a}_2 \ln D + \mathrm{a}_3 \ln H + \mathrm{a}_4 (\ln D)(\ln H) \tag{Eq.6}$$

where Pi is biomass of i-th component of a tree, kg.

Results and Discussion

The initial data on the biomass of trees, the characteristics of which are given in *Table 1,* are processed by the method of multiple regression analysis according to the structure of *models (1)-(6).* The results of the regression analysis are summarized in *Table 2*. The biomass models shown in *Table 2* are valid within the actual ranges of age, stem diameter, and tree height shown in *Table 1.*

Based on the results of comparative regression analysis, the explanatory power of models (5) and (6) for all components of biomass is higher than that of models (1), (2), (3) and (4). The age of a tree, although as an important independent variable in explaining the variability of tree biomass (Qiu et al., 2018), was not statistically significant in this case at $p < 0.05$. In addition, this dendrometric indicator is difficult to measure in tree inventory on large areas compared to the stem diameter and tree height. Therefore, we have involved the model (5) in the procedure of further analysis.

Table 2. *Results of calculation of equations (1)-(6)*

	Dependent variables				
	ln*Pf*	**ln*Pb***	**ln*Ps***	**ln*Pa***	**Model number**
$a_0^{(a)}$	-4.0299	-4.2627	-2.3081	-2.0307	(1)
ln*D*	1.8216	2.4603	2.4248	2.3929	
$adjR^{2(b)}$	**0.822**	**0.902**	**0.962**	**0.964**	
SE	0.627	0.597	0.358	0.343	
$a_0^{(a)}$	-4.0957	-4.4841	-3.5953	-3.1239	(2)
ln*D*	1.7809	2.3215	1.6368	1.7314	
ln*H*	*0.0629*$^{(d)}$	0.2146	1.2170	1.0217	
$adjR^{2(b)}$	**0.822**	**0.903**	**0.988**	**0.983**	
SE	0.626	0.594	0.202	0.236	
$a_0^{(a)}$	-4.6581	-5.1000	-3.3270	-3.0184	(3)
$\ln(D^2H)$	0.6795	0.9171	0.9216	0.9061	
$adjR^{2(b)}$	**0.806**	**0.889**	**0.985**	**0.981**	
SE	0.661	0.639	0.221	0.246	
$a_0^{(a)}$	-3.8661	-4.6041	-3.7678	-3.2592	(4)
ln*A*	-0.1366	*0.0684*$^{(d)}$	0.0996	0.0780	
ln*D*	1.8318	2.2901	1.5956	1.6981	
ln*H*	*0.1133*$^{(d)}$	0.1963	1.1851	0.9978	
$adjR^{2(b)}$	**0.823**	**0.903**	**0.988**	**0.983**	
SE	0.624	0.594	0.198	0.234	
$a_0^{(a)}$	-3.1241	-2.8226	-2.7602	-2.0973	(5)
ln*D*	1.2015	1.3250	1.1392	1.1196	
ln*H*	-0.3935	-0.5683	0.8256	0.5406	
(ln*D*)(ln*H*)	0.2429	0.4168	0.2085	0.2560	
$adjR^{2(b)}$	**0.830**	**0.918**	**0.992**	**0.989**	
SE	0.611	0.547	0.165	0.188	
$a_0^{(a)}$	-2.6896	-2.7559	-2.8711	-2.1360	(6)
ln*A*	-0.2015	*-0.0320*$^{(d)}$	0.0503	*0.0172*$^{(d)}$	
ln*D*	1.2223	1.3248	1.1317	1.1154	
ln*H*	-0.3656	-0.5600	0.8211	0.5407	
(ln*D*)(ln*H*)	0.2665	0.4206	0.2027	0.2541	
$adjR^{2(b)}$	**0.833**	**0.918**	**0.992**	**0.989**	
SE	0.606	0.547	0.164	0.188	

$^{(a)}$The intercept hereafter is adjusted according to logarithmic transformation by Baskerville (1972); $^{(b)}$$adjR^2$ is the coefficient of determination, adjusted for the number of variables; $^{(c)}$SE is the standard error of the equation; $^{(d)}$ these regression coefficients are not reliable at the level of p = 0.05

Designing the model of aboveground biomass sensitive to climate variables

We propose a model of aboveground biomass at the continental level, combining dendrometric indicators of trees (model (5)) and climate variables as independent variables:

$$\ln P_i = a_0 + a_1(\ln D) + a_2(\ln H) + a_3(\ln D)(\ln H) + \\ + a_4[\ln(T+50)] + a_4(\ln PR) + a_5[\ln(T+50)] \cdot (\ln PR) \qquad \text{(Eq.7)}$$

where T is mean January temperature, °C; PR is mean annual precipitation, mm; $[\ln(T+40)]\cdot(\ln PR)$ is a combined variable that characterizes the common effect of temperature and precipitation. The regression coefficients for all biomass components in model (7) are significant at $p < 0.001$. Since the mean January temperature in high latitudes has a negative value, for its logarithmic transformation in model (7), it is modified as $(T+50)$. The results of the calculation of the models (7) are shown in *Table 3*.

Table 3. *Model calculation results (7)*

$\ln(Y)^{(1)}$	$a_0^{(2)}$	$\ln D$	$\ln H$	$(\ln D)\times(\ln H)$	$\ln(T+50)$	$\ln PR$	$[\ln(T+50)]\times(\ln PR)$	$adjR^{2(4)}$	$SE^{(5)}$
$\ln(Pf)$	28.7262	1.2510	-0.4746	0.2452	-7.7748	-5.3644	1.3163	0.847	0.580
$\ln(Pb)$	95.4290	1.3795	-0.6457	0.4143	-27.4814	-15.7630	4.4051	0.925	0.522
$\ln(Ps)$	17.8565	1.1561	0.7954	0.2090	-5.7867	-3.3436	0.9385	0.992	0.162
$\ln(Pa)$	30.6312	1.1461	0.4957	0.2563	-9.1593	-5.3031	1.4839	0.990	0.181

The geometric interpretation of models (7) is obtained by substituting in (7) the average values of D and H taken from *Table 1* (*Figure 2*). As we can see in *Figure 2*, the dependence of all components of the aboveground biomass of equal-sized birch trees on temperatures and precipitation is described by 3D-surfaces of a propeller-shaped form. In cold regions, as precipitation increases, the biomass decreases, but as it moves to warm regions, it is characterized by the opposite trend. As the temperature increases in humid regions, the biomass increases, but as the transition to dry conditions begins to decrease.

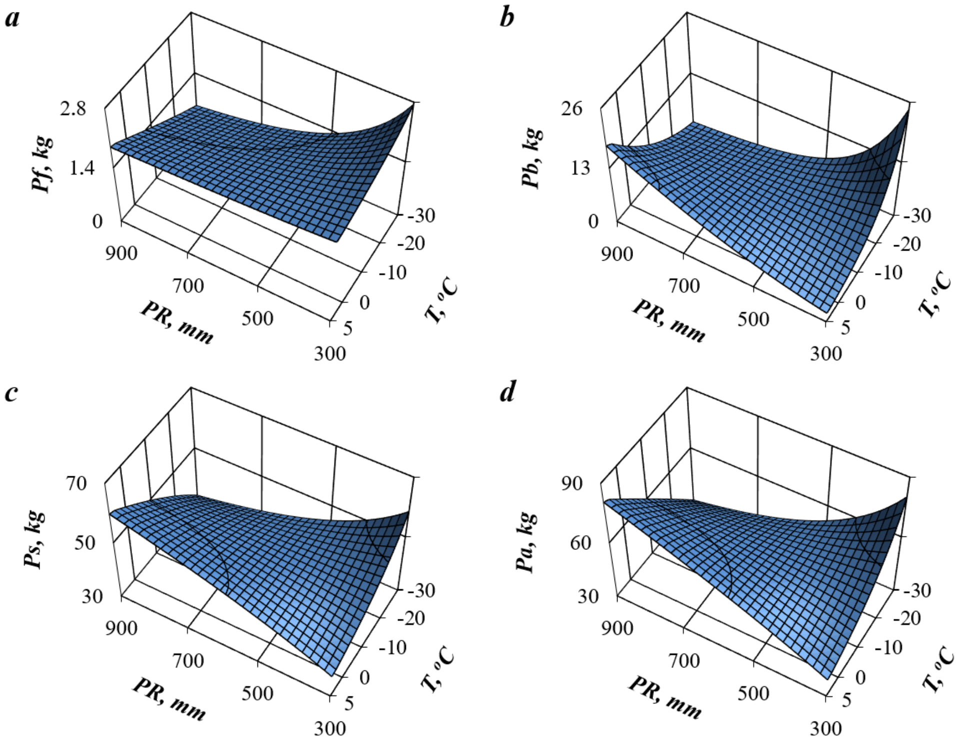

Figure 2. *Calculated changes in aboveground birch biomass of trees (D=13.4 cm; H=14.6 m) according to the model (7) due to the mean January temperature (T) and mean annual precipitation (PR). The designations of the components of the biomass hereafter: a, b, c, d are foliage, branches, stems over bark, and aboveground biomass respectively, kg*

Predicting Betula spp. biomass change related to climate shifts on the base of the principle of space-for-time substitution

Let us consider the described patterns in a different perspective, implementing the concept of space-time substitution and the principle "What will be happened, if...?". In other words, we will find out how the tree biomass will react if, with constant territorial temperature and precipitation gradients, we assume a temporal temperature change of 1°C or annual precipitation of 100 mm. Taking the first derivatives of the two-factor surfaces presented in *Figure 2*, we obtained the regularities of changes in the biomass at the given increments of temperature and precipitation.

Figure 3 shows the change in tree biomass (Δ, %) with a temperature increase by 1°C in different climatic zones (territorial gradients) characterized by different temperature and precipitation ratios. It is assumed that precipitation changes only geographically, and the temperature as a result of the expected climate change increases by 1°C at different territorial temperature levels, designated as -30Δ...+5Δ. For all components of biomass, a general pattern of the Eurasian scale is obtained: in moisture-rich climatic zones, an increase in temperature with a constant amount of precipitation causes its increase (red areas of the surfaces in *Figure 3*), and in the moisture-deficit zones its decrease (blue areas of the surfaces in *Figure 3*).

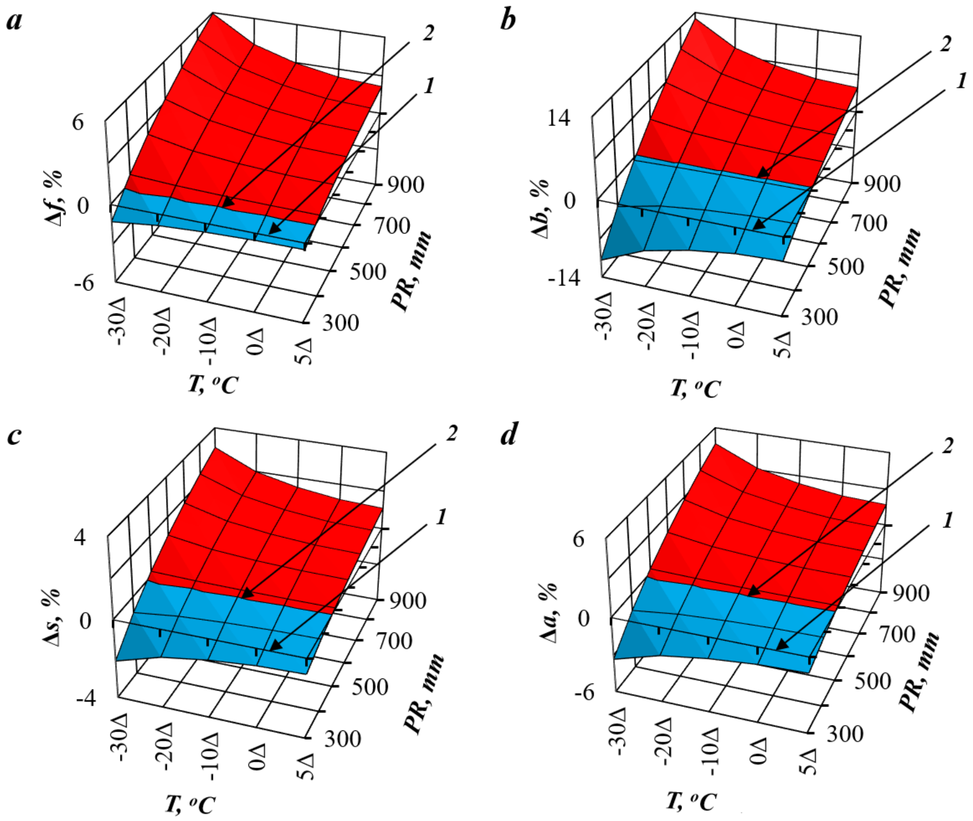

Figure 3. *Possible changes in the biomass of trees with the increase in January temperature by 1°C due to the expected climate change at different territorial levels of temperature and precipitation. 1 – the plane corresponding to the zero change in biomass at the expected temperature increase by 1°C; 2 – the line of differentiation of positive and negative changes in biomass at the expected temperature increase by 1°C*

Figure 4 shows the change in tree biomass (Δ, %) with the decrease in annual precipitation by 100 mm in different climatic zones. At the same time, it is assumed that the January temperature changes only geographically, and precipitation as a result of climate change decreases by 100 mm at different territorial precipitation levels, designated as -400Δ...-900Δ. A general transcontinental pattern has been established for the biomass of branches, stem, and aboveground: in warm climatic zones, a decrease in precipitation by 100 mm at a constant average January temperature causes a decrease in the biomass of stems and aboveground (blue area of surfaces), and in cold climatic zones – its increase (red area of surfaces) (*Figure 4b,c,d*). For foliage biomass, the entire 3D surface is represented by the red zone (*Figure 4a*), which means that when precipitation decreases by 100 mm in all climatic zones, the foliage biomass increases. But during the transition from cold to warm climatic conditions, the value of this increase decreases, and in the warmest zones (January temperature is 5°C), this reduction in the increment of biomass approaches zero, but does not go to "minus". Thus, the patterns of changes in the biomass of foliage with shifts in temperature and precipitation are somewhat different from the changes in the biomass of other components. The reason may be a more pronounced residual variance in the foliage biomass model due to the fact that interspecific variation in foliage biomass is due not only to climatic factors, but also to the environmental "noise" unaccounted.

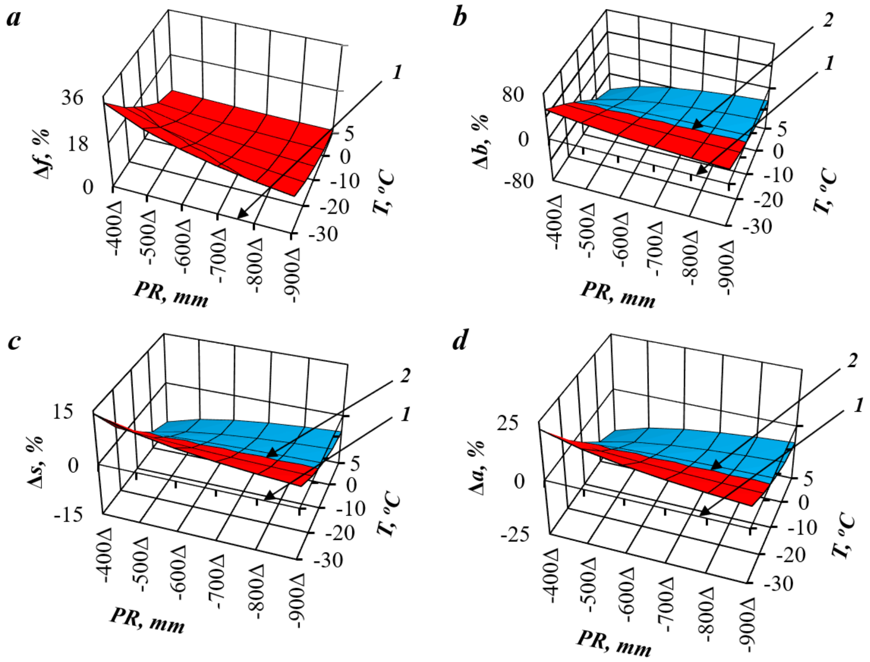

Figure 4. *Possible changes in the biomass of trees with a decrease in precipitation due to the expected climate change at different territorial levels of temperature and precipitation. 1 – the plane corresponding to the zero change in biomass with the expected decrease in precipitation by 100 mm; 2 – the line of differentiation of positive (red) and negative (blue) changes in biomass with the expected decrease in precipitation by 100 mm*

Thus, both the lack of heat and moisture, and their excess, are manifested as factors limiting the biomass of trees of the genus *Betula* sp. at the transcontinental level.

Today, the results of modeling the responses of forest biomass to global changes in temperature and precipitation are contradictory and characterized by uncertainty in the forecasts of climate-driven dynamics of forest cover (Marcolla et al., 2020). One of the most significant is the contradiction of two possible scenarios. On the one hand, an increase in primary production due to the potential enrichment of the atmosphere with CO_2 and its reclamation effect on vegetation. On the other hand, its decrease due to loss of stability with a sharp reduction in the adaptive time lag (Santini et al., 2014; Sperry et al., 2019; Berdugo et al., 2020). The largest reserves of biomass in the zone of moderately moist forests, depersonalized by species composition and morphological structure of stands, were found at moderately low temperatures and moderately abundant precipitation (Keith et al., 2009). Positive dependences of aboveground biomass on average annual precipitation have been established for the total American continent from Canada in the north to the south of Chile. With the average annual temperature, the relationship of this indicator in humid tropical forests is positive, and in forests of excessive moisture is negative, but statistically insignificant. In general, climatic indicators explain the weak, and in many cases statistically insignificant share of the variability of the biomass of stands (Stegen et al., 2011). In some habitats, elevated temperatures can lead to stress from water deficiency and, consequently, to a decrease in biomass (Wilmking et al., 2004).

We cannot compare the results obtained by us with the available results of biomass forecasting based on simulation models. According to their forecasts, changes in the carbon pool by the end of this century range from -106 to +201 Pg (billion tons). Various scenarios of the Dynamic Global Vegetation Model (LPJ-DGVM) show significant uncertainty about the future carbon storage in terrestrial biota. Thus, even the sign of a change in the carbon pool on the planet is reliably unknown, and we do not fully know whether the biota of the planet is a source or storage of carbon (Schaphoff et al., 2006).

Our results on changes in aboveground tree biomass in two climatic gradients confirm the patterns previously established by Russian researchers at the local and regional levels. A similar pattern was observed earlier at the local level in the swamp forests of the Tomsk region in Siberia, when at maximum amounts of temperatures above 10 °C, equal to 2200 °C, with an increase in precipitation from 400 to 600 mm, the radial growth of stems increases by 30-50%, and at minimum amounts of temperatures (1600 °C) with an increase in precipitation in the same range, the radial growth decreases by 4-9%. Accordingly, at a precipitation level of 400 mm with an increase in the sum of temperatures from 1600 to 2200 °C, the radial growth decreases by 14-20%, and at a precipitation level of 600 mm in the same temperature range, it increases by 14-33% (Glebov and Litvinenko, 1976). According to the results obtained by Molchanov (1976), in the conditions of the North of Eurasia, the air temperature has the greatest influence on the growth of the annual ring, and in the conditions of the southern forest-steppe, precipitation plays the dominant role. A similar propeller-like pattern, sensitive to climate change, was previously identified for the biomass of pine stands (Usoltsev et al., 2019).

These patterns correspond to Liebig's principle of limiting factors (Liebig, 1840). However, Liebig's law of a limiting factor works well in stationary conditions. With rapid changes in limiting factors (for example, air temperature or precipitation), forest ecosystems are in a transitional (non-stationary) state, in which some factors that have not yet been significant may come to the fore, and the final result may be determined by other limiting factors (Odum, 1971).

We used the existing changes in the tree biomass in the territorial climate gradients to predict its possible changes in the assumed temporal gradients of temperature and precipitation. However, the fundamental assumption that the spatial relationship between climate and biomass can be used to predict the temporal trajectories of biological productivity in a changing climate remains largely untested (Veloz et al., 2012). The success of applying the theory of space-for-time substitution in plant ecology depends on the extent to which the ecological conditions that determine the properties of plants in territorial gradients correspond to the future ecological conditions that determine the properties of plants in the temporal gradient (Bjorkman et al., 2018; Bergstrom et al., 2021). Nevertheless, when there is no other way to study ecosystem processes in perspective, the method of spatial-for-time substitution is still quite an acceptable alternative.

Conclusion

On the basis of the database on the aboveground biomass of 1,717 *Betula* spp. trees growing on the territory of Eurasia, formed by the authors, a regression model was developed that includes both denrometric indicators of trees and territorial long-term data on temperature and precipitation as independent variables. The obtained trans-Eurasian regularities are used to predict changes in biomass due to climate shifts based on the theory of space-for-time substitution. The regularities of the Eurasian scale are obtained: in sufficiently moisture-rich climatic zones, an increase in temperature by 1°C with a constant amount of precipitation causes an increase in aboveground biomass, and in water-deficient zones its decrease; in warm climatic zones, a decrease in precipitation by 100 mm with a constant average January temperature causes a decrease in aboveground biomass, and in cold climatic zones its increase.

REFERENCES

[1] Baskerville, G. L. (1972): Use of logarithmic regression in the estimation of plant biomass. – Canadian Journal of Forest Research 2: 49-53.

[2] Berdugo, M., Delgado-Baquerizo, M., Soliveres, S., Hernández-Clemente, R., Zhao, Y., Gaitán, J. J., Gross, N., Saiz, H., Maire, V., Lehman, A., Rillig, M. C., Solé, R. V., Maestre, F. T. (2020): Global ecosystem thresholds driven by aridity. – Science 367(6479): 787-790.

[3] Bergstrom, D. M., Wienecke, B. C., van den Hoff, J., Hughes, L., Lindenmayer, D. B., Ainsworth, T. D., Baker, C. M., Bland, L., Bowman, D. M. J. S., Brooks, S. T., Canadell, J. G., Constable, A. J., Dafforn, K. A., Depledge, M. H., Dickson, C. R., Duke, N. C., Helmstedt, K. J., Holz, A., Johnson, C. R., McGeoch, M. A., Melbourne-Thomas, J., Morgain, R., Nicholson, E., Prober, S. M., Raymond, B., Ritchie, E. G., Robinson, S. A., Ruthrof, K. X., Setterfield, S. A., Sgrò, C. M., Stark, J. S., Travers, T., Trebilco, R., Ward, D. F. L., Wardle, G. M., Williams, K. J., Zylstra, P. J., Shaw, J. D. (2021): Combating ecosystem collapse from the tropics to the Antarctic. – Global Change Biology 27: 1-12.

[4] Bijak, S. (2010): Tree-ring chronology of silver fir and ist dependence on climate of the Kaszubskie Lakeland (Northern Poland). – Geochronometria 35: 91-94.

[5] Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Georges, D., Goetz, S. J., Guay, K. C., Henry, G. H. R., RisLambers, J. H., Hollister, R. D., Karger, D. N., Kattge, J., Manning, P., Prevéy, J. S., Rixen, C., Schaepman-Strub, G., Thomas, H. J. D., Vellend, M., Wilmking, M., Wipf, S., Carbognani, M., Hermanutz, L., Lévesque, E.,

Molau, U., Petraglia, A., Soudzilovskaia, N. A., Spasojevic, M. J., Tomaselli, M., Vowles, T., Alatalo, J. M., Alexander, H. D., Anadon-Rosell, A., Angers-Blondin, S., Beest, M., Berner, L., Björk, R. G., Buchwal, A., Buras, A., Christie, K., Cooper, E. J., Dullinger, S., Elberling, B., Eskelinen, A., Frei, E. R., Grau, O., Grogan, P., Hallinger, M., Harper, K. A., Heijmans, M. M. P. D., Hudson, J., Hülber, K., Iturrate-Garcia, M., Iversen, C. M., Jaroszynska, F., Johnstone, J. F., Jørgensen, R. H., Kaarlejärvi, E., Klady, R., Kuleza, S., Kulonen, A., Lamarque, L. J., Lantz, T., Little, C. J., Speed, J. D. M., Michelsen, A., Milbau, A., Nabe-Nielsen, J., Nielsen, S. S., Ninot, J. M., Oberbauer, S. F., Olofsson, J., Onipchenko, V. G., Rumpf, S. B., Semenchuk, P., Shetti, R., Collier, L. S., Street, L. E., Suding, K. N., Tape, K. D., Trant, A., Treier, U. A., Tremblay, J.-P., Tremblay, M., Venn, S., Weijers, S., Zamin, T., Boulanger-Lapointe, N., Gould, W. A., Hik, D. S., Hofgaard, A., Jónsdóttir, I. S., Jorgenson, J., Klein, J., Magnusson, B., Tweedie, C., Wookey, P. A., Bahn, M., Blonder, B., van Bodegom, P. M., Bond-Lamberty, B., Campetella, G., Cerabolini, B. E. L., Chapin III, F. S., Cornwell, W. K., Craine, J., Dainese, M., de Vries, F. T., Díaz, S., Enquist, B. J., Green, W., Milla, R., Niinemets, Ü., Onoda, Y., Ordoñez, J. C., Ozinga, W. A., Penuelas, J., Poorter, H., Poschlod, P., Reich, P. B., Sandel, B., Schamp, B., Sheremetev, S., Weiher, E. (2018): Plant functional trait change across a warming tundra biome. – Nature 562: 57-80.

[6] Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Jackson, S. T., Ferrier, S. (2013): Space can substitute for time in predicting climate-change effects on biodiversity. – Proceedings of the National Academy of Sciences USA 110: 9374-9379.

[7] Bloom, A. J., Chapin III, F. S., Mooney, H. A. (1985): Resource limitation in plants - An economic analogy. – Annual Review of Ecological Systems 16: 363-392.

[8] Burian, K. (1970): Produktion und Strahlungsnutzung bei Helianthus annuus, Zea mays und Phaseolus vulgaris während der gesamten Vegetationszeit. – Sitzungsberichte der Akademie der Wissenschaften mathematisch-naturwissenschaftliche Klasse 178: 1-35.

[9] Cárdenas-Pérez, S., Rajabi Dehnav, A., Leszczynski, K., Lubinska-Mielinska, S., Ludwiczak, A., Piernik, A. (2022): *Salicornia europaea* L. functional traits indicate its optimum growth. – Plants 11: 1051.

[10] DeLeo, V. L., Menge, D. N. L., Hanks, E. M., Juenger, T. E., Lasky, J. R. (2020): Effects of two centuries of global environmental variation on phenology and physiology of Arabidopsis thaliana. – Global Change Biology 26: 523-538.

[11] Devi, N. M., Kukarskih, V. V., Galimova, A. A., Mazepa, V. S., Grigoriev, A. A. (2020): Climate change evidence in tree growth and stand productivity at the upper treeline ecotone in the Polar Ural. – Forest Ecosystems 7: 7.

[12] Falster, D. S., Duursma, R. A., Ishihara, M. I., Barneche, D. R., FitzJohn, R. G., Vårhammar, A., Aiba, M., Ando, M., Anten, N., Aspinwall, M. J., Baltzer, J. L., Baraloto, C., Battaglia, M., Battles, J. J., Bond-Lamberty, B., van Breugel, M., Camac, J., Claveau, Y., Coll, L., Dannoura, M., Delagrange, S., Domec, J.-C., Fatemi, F., Feng, W., Gargaglione, V., Goto, Y., Hagihara, A., Hall, J. S., Hamilton, S., Harja, D., Hiura, T., Holdaway, R., Hutley, L. S., Ichie, T., Jokela, E. J., Kantola, A., Kelly, J. W. G., Kenzo, T., King, D., Kloeppel, B. D., Kohyama, T., Komiyama, A., Laclau, J.-P., Lusk, C. H., Maguire, D. A., le Maire, G., Mäkelä, A., Markesteijn, L., Marshall, J., McCulloh, K., Miyata, I., Mokany, K., Mori, S., Myster, R. W., Nagano, M., Naidu, S. L., Nouvellon, Y., O'Grady, A. P., O'Hara, K. L., Ohtsuka, T., Osada, N., Osunkoya, O. O., Peri, P. L., Petritan, A. M., Poorter, L., Portsmuth, A., Potvin, C., Ransijn, J., Reid, D., Ribeiro, S. C., Roberts, S. D., Rodríguez, R., Saldaña-Acosta, A., Santa-Regina, I., Sasa, K., Selaya, N. G., Sillett, S. C., Sterck, F., Takagi, K., Tange, T., Tanouchi, H., Tissue, D., Umehara, T., Utsugi, H., Vadeboncoeur, M. A., Valladares, F., Vanninen, P., Wang, J. R., Wenk, E., Williams, R., Ximenes, F., de Aquino Yamaba, A., Yamada, T., Yamakura, T., Yanai, R. D., York, R. A. (2015): BAAD: a Biomass And Allometry Database for woody plants. – Ecology 96: 1445-1445.

[13] Fitzpatrick, M. C., Sanders, N. J., Ferrier, S., Longino, J. T., Weiser, M. D., Dunn, R. R. (2011): Forecasting the future of biodiversity: a test of single- and multi-species models for ants in North America. – Ecography 34: 836-847.

[14] Fonti, M. V. (2020): Climatic signal in the parameters of annual rings (wood density, anatomical structure and isotopic composition) of coniferous and deciduous tree species in various natural and climatic zones of Eurasia. – Diss. Doct. Biol. Sci.: 03.02.08. Krasnoyarsk, Siberian Federal University, 45p. (In Russian). (https://research.sfu-kras.ru/sites/research.sfu-kras.ru/files/Avtoreferat_Fonti.pdf).

[15] Forrester, D. I., Tachauer, I. H. H., Annighoefer, P., Barbeito, I., Pretzsch, H., Ruiz-Peinado, R., Stark, H., Vacchiano, G., Zlatanov, T., Chakraborty, T., Saha, S., Sileshi, G. W. (2017): Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. – Forest Ecology and Management 396: 160-175.

[16] Frauendorf, T. C., MacKenzie, R. A., Tingley III, R. W., Infante, D. M., El-Sabaawi, R. W. (2020): Using a space-for-time substitution approach to predict the effects of climate change on nutrient cycling in tropical island stream ecosystems. – Limnology and Oceanography 65: 3114-3127.

[17] Fu, L., Sun, W., Wang, G. (2017): A climate-sensitive aboveground biomass model for three larch species in northeastern and northern China. – Trees 31: 557-573.

[18] Glebov, F. Z., Litvinenko, V. I. (1976): The dynamics of tree ring width in relation to meteorological indices in different types of wetland forests. – Lesovedenie (Soviet Forest Science) 4: 56-62.

[19] Grimm, G. W., Renner, S. S. (2013): Harvesting Betulaceae sequences from Gen-Bank to generate a new chronogram for the family. – Botanical Journal of the Linnean Society 172: 465-477.

[20] Hynynen, J., Niemistö, P., Viherä-Aarnio, A., Brunner, A., Hein, S., Velling, P. (2009): Silviculture of birch (Betula pendula Roth and Betula pubescens Ehrh.) in northern Europe. – Forestry: An International Journal of Forest Research 83: 103-119.

[21] Johnson, E. A., Miyanishi, K. (2008): Testing the assumptions of chronosequences in succession. – Ecology Letters 11: 419-431.

[22] Keith, H., Mackey, B. G., Lindenmayer, D. B. (2009): Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. – Proceedings of the National Academy of Sciences of the United States of America 106(28): 635-640.

[23] Kosanic, A., Anderson, K., Harrison, S., Turkington, T., Bennie, J. (2018): Changes in the geographical distribution of plant species and climatic variables on the West Cornwall Peninsula (South West UK). – PLoS ONE 13: e0191021.

[24] Laughlin, D. C., Mommer, L., Sabatini, F. M., Bruelheide, H., Kuyper, T. W., McCormack, M. L., Bergmann, J., Freschet, G. T., Guerrero-Ramírez, N. R., Iversen, C. M., Kattge, J., Meier, I. C., Poorter, H., Roumet, C., Semchenko, M., Sweeney, C. J., Valverde-Barrantes, O. J., van der Plas, F., van Ruijven, J., York, L. M., Aubin, I., Burge, O. R., Byun, C., Ćušterevska, R., Dengler, J., Forey, E., Guerin, G. R., Hérault, B., Jackson, R. B., Karger, D. N., Lenoir, J., Lysenko, T., Meir, P., Niinemets, Ü., Ozinga, W. A., Peñuelas, J., Reich, P. B., Schmidt, M., Schrodt, F., Velázquez, E., Weigelt, A. (2021): Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs. – Nature Ecology & Evolution 5(8): 1123-1134.

[25] Lei, X., Yu, L., Hong, L. (2016): Climate-sensitive integrated stand growth model (CS-ISGM) of Changbai larch (Larix olgensis) plantations. – Forest Ecology and Management 376: 265-275.

[26] Liebig, J. (1840): Die organische Chemie in ihrer Anwendung auf Agricultur und Physiologie. – Braunschweig: Verlag Vieweg. Deutsches Textarchiv, available at: http://www.deutschestextarchiv.de/liebig_agricultur_1840. Accessed on 26.11.2019.

[27] Liepa, I. Y. (1980): Dynamics of wood stock: Forecast and ecology. – Riga, Zinatne, 170p. (In Russian).

[28] Lieth, H. (1975): Modeling the primary productivity of the world. – In: Lieth, H., Whittaker, R. H. (eds.) Primary productivity of the biosphere. New York, Springer-Verlag, pp. 237-263.

[29] Marcolla, B., Migliavacca, M., Rödenbeck, C., Cescatti, A. (2020): Patterns and trends of the dominant environmental controls of net biome productivity. – Biogeosciences 17: 2365-2379.

[30] Mohan, J. E., Cox, R. M., Iverson, L. R. (2009): Composition and carbon dynamics of forests in northeastern North America in a future, warmer world. – Canadian Journal of Forest Research 39: 213-230.

[31] Molchanov, A. A. (1976): Dendro-climatic fundamentals of weather forecasts. – Moscow, Russia, “Nauka” Publishing House, 168 p.

[32] Morley, J. W., Batt, R. D., Pinsky, M. L. (2016): Marine assemblages respond rapidly to winter climate variability. – Global Change Biology 23: 2590-2601.

[33] Mugasha, W. A., Eid, T., Bollandsås, O. M., Malimbwi, R. E., Chamshama, S. A. O., Zahabu, E., Katani, J. Z. (2012): Allometric models for prediction of aboveground biomass of single trees in miombo woodlands in Tanzania. – Proceedings of the first Climate Change Impacts, Mitigation and Adaptation Programme Scientific Conference, pp. 8-17.

[34] Niu, S., Wang, S., Wang, J., Xia, J., Yu, G. (2020): Integrative ecology in the era of big data. From observation to prediction. – Science China Earth Sciences 63: 1-14.

[35] Odum, E. P. (1971): Fundamentals of ecology. – London, Philadelphia, Toronto, W.B. Saunders Company, 574p.

[36] Paul, K. I., Roxburgh, S. H., Chave, J., England, J. R., Zerihun, A., Specht, A., Lewis, T., Bennett, L. T., Baker, T. G., Adams, M. A., Huxtable, D., Montagu, K. D., Falster, D. S., Feller, M., Sochacki, S., Ritson, P., Bastin, G., Bartle, J., Wildy, D., Hobbs, T., Larmour, J., Waterworth, R., Stewart, H. T. L., Jonson, J., Forrester, D. I., Applegate, G., Mendham, D., Bradford, M., O'Grady, A., Green, D., Sudmeyer, R., Rance, S. J., Turner, J., Barton, C., Wenk, E. H., Grove, T., Attiwill, P. M., Pinkard, E., Butler, D., Brooksbank, K., Spencer, B., Snowdon, P., O'Brien, N., Battaglia, M., Cameron, D. M., Hamilton, S., McAuthur, G., Sinclair, J. (2016): Testing the generality of above-ground biomass allometry across plant functional types at the continent scale. – Global Change Biology 22(6): 2106-2124.

[37] Pickett, S. (1989): Space-for-time substitution as an alternative to long-term studies. – In: Likens, G. E. (ed.) Long-term studies in ecology: Approaches and alternatives. New York, Springer, pp. 110-135.

[38] Qiu, Q., Yun, Q., Zuo, Sh., Yan, J., Hua, L., Ren, Y., Tang, J., Li, Y., Chen, Q. (2018): Variations in the biomass of Eucalyptus plantations at a regional scale in Southern China. – Journal of Forestry Research 29(5): 1263-1276.

[39] Reich, P. B., Luo, Y., Bradford, J. B., Poorter, H., Perry, C. H., Oleksyn, J. (2014): Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. – Proceedings of the National Academy of Sciences of the United States of America 111: 13721-13726.

[40] Russell, M. B., Domke, G. M., Woodall, C. W., D’Amato, A. W. (2015): Comparisons of allometric and climate-derived estimates of tree coarse root carbon stocks in forests of the United States. – Carbon Balance and Management 10: 20.

[41] Santini, M., Collalti, A., Valentini, R. (2014): Climate change impacts on vegetation and water cycle in the Euro-Mediterranean region, studied by a likelihood approach. – Regional Environmental Change 14(4): 1405-1418.

[42] Sato, H., Kobayashi, H., Delbart, N. (2010): Simulation study of the vegetation structure and function in eastern Siberian larch forests using the individual-based vegetation model SEIB-DGVM. – Forest Ecology and Management 259: 301-311.

[43] Schaphoff, S., Lucht, W., Gerten, D., Sitch, S., Cramer, W., Prentice, I. C. (2006): Terrestrial biosphere carbon storage under alternative climate projections. – Climatic Change 74(1-3): 97-122.

[44] Schepaschenko, D., Shvidenko, A., Usoltsev, V. A., Lakyda, P., Luo, Y., Vasylyshyn, R., Lakyda, I., Myklush, Y., See, L., McCallum, I., Fritz, S., Kraxner, F., Obersteiner, M. (2017): A dataset of forest biomass structure for Eurasia. – Scientific Data 4: 1-11. Article 170070.

[45] Shuman, J. K., Shugart, H. H., O'Halloran, T. L. (2011): Sensitivity of Siberian larch forests to climate change. – Global Change Biology 2: 2370-2384.

[46] Sperry, J. S., Venturas, M. D., Todd, H. N., Trugman, A. T., Anderegg, W. R. L., Wang, Y., Tai, X. (2019): The impact of rising CO_2 and acclimation on the response of US forests to global warming. – Proceedings of the National Academy of Sciences of the United States of America 116(51): 25734-25744.

[47] Stegen, J. C., Swenson, N. G., Enquist, B. J., White, E. P., Phillips, O. L., Jorgensen, P. M., Weiser, M. D., Mendoza, A. M., Vargas, P. N. (2011): Variation in above-ground forest biomass across broad climatic gradients. – Global Ecology and Biogeography 20(5): 744-754.

[48] Tolmachev, A. I. (1962): Fundamentals of Plant Habitat Theory: Introduction to Plant Community Chorology. – Leningrad, State University Publishing, 100p. (In Russian).

[49] Toromani, E., Bojaxhi, F. (2010): Growth response of silver fir and Bosnian pine from Kosovo. – South-East Europian Forestry 1: 20-28.

[50] Tranquillini, W. (1955): Die Bedeutung des Lichtes und der Temperatur für die Kohlensäureassimilation von Pinus cembra - Jungwuchs an einem hochalpinen Standort. – Planta 46(2): 154-178.

[51] Usoltsev, V. A. (2020): Single-tree biomass data for remote sensing and ground measuring of Eurasian forests: digital version. – The second edition, enlarged, Yekaterinburg, Ural State Forest Engineering University; Botanical Garden of Ural Branch of RAS. CD-ROM. Retrieved from: https://elar.usfeu.ru/bitstream/123456789/9647/2/Base1_v2_ob.pdf.

[52] Usoltsev, V. A., Shobairi, S. O. R., Tsepordey, I. S., Chasovskikh, V. P. (2019): Modelling forest stand biomass and net primary production with the focus on additive models sensitive to climate variables for two-needled pines in Eurasia. – Journal of Climate Change 5(1): 41-49.

[53] Veloz, S., Williams, J. W., Blois, J. L., He, F., Otto-Bliesner, B., Liu, Z. (2012): No-analog climates and shifting realized niches during the late Quaternary: Implications for 21st-century predictions by species distribution models. – Global Change Biology 18: 1698-1713.

[54] Wilmking, M., Juday, G. P., Barber, V. A., Zald, H. S. (2004): Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. – Global Change Biology 10: 1724-1736.

[55] World Weather Maps (2007): Retrieved from: https://www.mapsofworld.com/referrals/weather.

[56] Zeng, W. S., Duo, H. R., Lei, X. D., Chen, X. Y., Wang, X. J., Pu, Y., Zou, W. (2017): Individual tree biomass equations and growth models sensitive to climate variables for Larix spp. in China. – European Journal of Forest Research 136: 233-249.

[57] Zeng, W. S., Chen, X. Y., Pu, Y., Yang, X. Y. (2018): Comparison of different methods for estimating forest biomass and carbon storage based on National Forest Inventory data. – Forest Research 31: 66-71.

[58] Zubairov, B., Heußner, K.-U., Schröder, H. (2018): Searching for the best correlation between climate and tree rings in the Trans-Ili Alatau, Kazakhstan. – Dendrobiology 79: 119-130.