CLIMATICALLY DETERMINED SPATIAL AND TEMPORAL CHANGES IN THE BIOMASS OF *Betula* spp. OF EURASIA IN THE CONTEXT OF THE LAW OF THE LIMITING FACTOR

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Abstract

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Forest ecosystems play an essential role in climate stabilization, and the study of their capabilities in this aspect is of paramount importance. How climate changes affect the biomass of trees and stands in transcontinental gradients is unknown today? The objective of this study was (a) to verify the operation of the law of the limiting factor at the transcontinental level when modeling changes in the biomass of trees and stands of the genus *Betula* spp. of Eurasia in relation to geographically determined indicators of temperatures and precipitation, and (b) to show the possibility of using the constructed climate-conditioned models of tree and stand biomass in predicting temporal changes in tree and stand biomass based on the principle of space-for-time substitution. As a result of the implementation of the principles of the limiting factor and space-for-time substitution, a common pattern has been established on tree and stand levels: 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 moisture-deficient zones, it decreases; in warm climatic zones, a decrease in precipitation by 100 mm at a constant average January temperature causes a decrease in aboveground biomass, and in cold climatic zones, it increases.

Key words: biomass of trees and stands, database, regression analysis, the principle of space-for-time substitution, the law of the limiting factor, transcontinental level, temperature and precipitation.

Introduction

Since ancient times, the climate change has largely determined the fate of human civilization (Behrensmeyer, 2006; Miles-Novelo, Anderson, 2019), the great migration of people (Laczko, Aghazarm, 2009) and changes in structure and habitat, biota and basic ground component of the forest cover (Halofsky et al., 2018; Kosanic et al., 2018). Although it is believed that ancient civilizations died out mainly as a result of deforestation, there is opinion that the desertification of once forested areas of ancient civilizations was the result of climate change (Radkau, 2008).

Recently, a group of 11,258 scientists from 153 countries stated that the planet Earth is facing a climate emergency, and international efforts are needed to prevent an increase in average annual temperature and CO_2 emissions (Ripple et al., 2020). As climate change poses huge challenges for biota in general, there is a growing understanding of the role of forests in mitigating and adapting to climate change (Matala et al., 2006). Although forest biomass is an important part of sustainable development and the main driving force of successional changes in forests (Lohbeck et al., 2015), nevertheless, the rate of restoration of their biomass significantly exceeds the rate of restoration of biodiversity (Martin et al., 2013). This means a decrease in the stability of the biosphere and its gradual degradation. Therefore, the elimination of uncertainties related to the assessment and monitoring of biological productivity of forests and biodiversity in the context of climate change is of paramount importance.
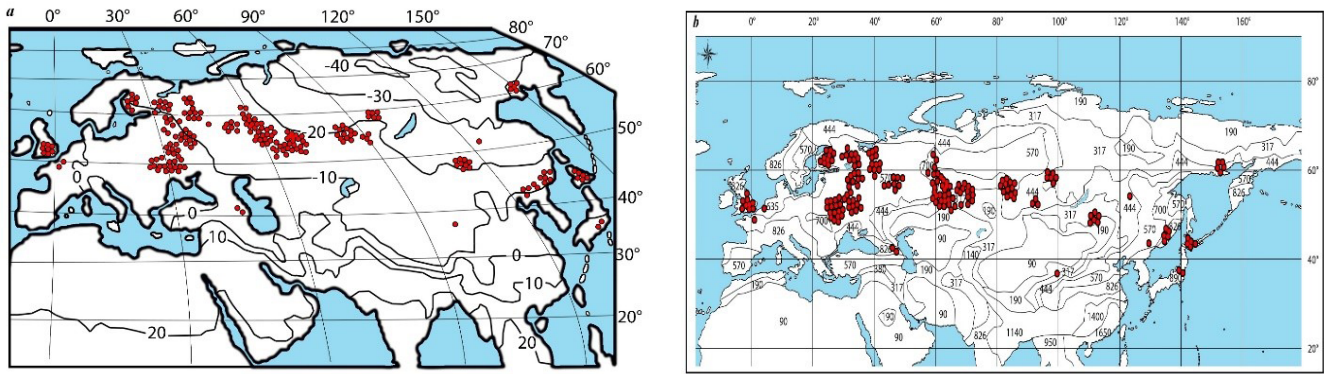
Fig. 1. Distribution of sample plots, where 755 trees for *Betula* biomass have been harvested, on the map of the mean January temperature, °C (https://store.mapsofworld.com/image/cache/data/map_2014/currents-and-temperature-jan-enlarge-900×700.jpg) (a), and on the map of the average annual precipitation, mm (https://www.eldoradoweather.com/climate/world-maps/world-annual-precip-map.html) (b) (World Weather Maps, 2007).

To estimate biomass and carbon stocks in forests, allometric equations are being developed at the level of trees and stands based on the data obtained from sample plots. The problem of using allometric models in the assessment of biomass and carbon deposited by it is extremely relevant, which is confirmed by the organization of a special conference in 2013 within the framework of the UN-REDD program (Cifuentes-Jara, Henry, 2013). Allometry has a good biological basis (Huxley, 1932; Kofman, 1986) but does not always agree well with empirical data (Fischer et al., 2019). When calculating allometric models of tree biomass, there is always a residual variance, and their use in local conditions gives systematic errors in the range from +316 to -92% (Usoltsev et al., 2017) and from +155 to +239% (Wang et al., 2002), due, in particular, to climatic factors (Wirth et al., 2004; Vasseur et al., 2018; Rudgers et al., 2019).

In the proposed allometric models sensitive to climate change (Wirth et al., 2004; Vasseur et al., 2018; Rudgers et al., 2019; He et al., 2021), the prediction of changes in the biomass of trees and stands during climatic shifts is based on the principle of space-for-time substitution. It means using modern patterns observed in spatial gradients to understand and model the same patterns and processes in time gradients that are currently cannot observable (Pickett, 1989; Blois et al., 2013).

It is known that the production of plant biomass is limited by a factor that is in minimum or excess relative to its needs according to the principle of limiting factor (Liebig, 1840; Shelford, 1913; Molchanov, 1971; Rosenberg et al., 2016). 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. The change of the limiting factor occurs in the subzone of the middle taiga (Fonti, 2020).

The aim of this study was to test two working hypotheses:
- whether the effect of the law of the limiting factor is manifested at the transcontinental level when modeling changes in the biomass of trees and stands on the territory of Eurasia in relation to geographically determined indicators of temperatures and precipitation on the example of the genus *Betula* spp.;
- to show whether the constructed climate-conditioned models of biomass of trees and stands, sensitive to temperature

and precipitation in territorial gradients, can be used to predict changes in biomass in temporal gradients based on the principle of space-for-time substitution.

Material and methods

Study site

755 trees (Fig. 1) and 540 stands (Fig. 2) of the genus *Betula* spp. were selected from the compiled biomass databases of 15,300 model trees (Usoltsev, 2020) and 7,500 forest stands (Usoltsev, 2010) (Table 1). Data on the biomass of trees and stands were obtained within the ranges of different species of the genus *Betula*, but their representation in Eurasia varies significantly. Data on biomass and dendrometric characteristics were plotted on the maps of average January temperature (Fig. 1) and average annual precipitation (Fig. 2), taken from World Weather Maps (2007). The use of winter temperature maps instead of the annual average was justified earlier (Usoltsev et al., 2019).

Data analysis

The empirical material of the databases was obtained by representatives of different fields of forest sciences with different target settings and corresponding methodological specifics. A part of this material was obtained during the implementation of the International Biological Program in the 1960s to 1970s using a unified methodology. However, a significant part of the data was obtained in the course of initiative spontaneous research, and their number is unevenly distributed across regions. This unevenness is partly caused by natural features due to the specifics of the habitats of various tree species and partly by purely random factors associated with the presence or absence of relevant research teams in specific regions. The largest part of the actual data on the biomass of trees and stands is confined to the regions with the highest population density, and the areas of the north of the boreal zone, and especially the sparsely populated areas of the north–east of Russia, are represented in databases by rare studies.
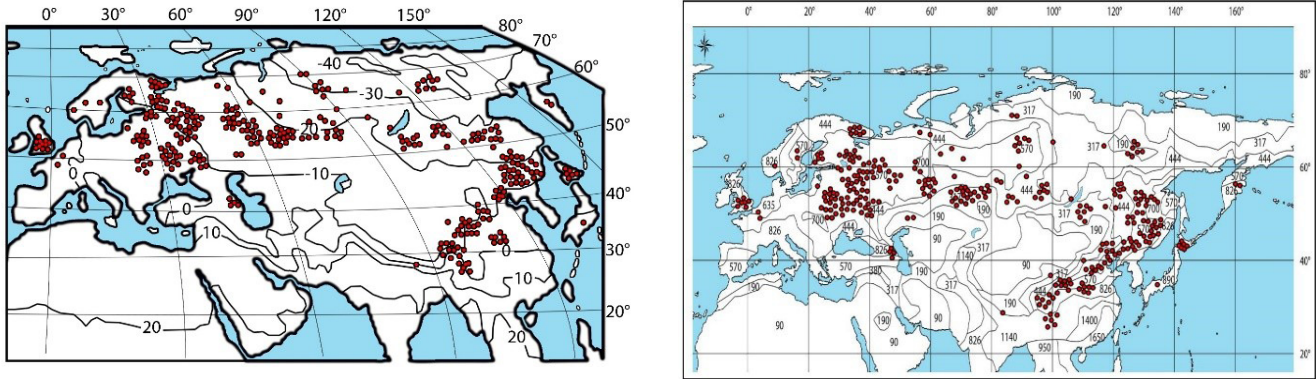
Fig. 2. Distribution of sample plots, where 540 stands for *Betula* biomass have been harvested, on the map of the mean January temperature, °C (https://store.mapsofworld.com/image/cache/data/map_2014/currents-and-temperature-jan-enlarge-900×700.jpg) (a), and on the map of the average annual precipitation, mm (https://www.eldoradoweather.com/climate/world-maps/world-annual-precip-map.html) (b) (World Weather Maps, 2007).

Table 1. Statistical characteristics of database *Betula* single-tree and stands samples in Eurasia.

Statistic designation [a]	Tree indices analyzed [b]					Stand indices analyzed [c]			
	H	D	*pbas*	*Dcr*	P_{tree}	A	V	N	P_{stand}
Mean	15.6	13.3	504.7	2.9	117.3	44	167.8	16.1	104.2
Min	1.5	0.2	297.7	0.3	0.03	2	0.3	0.08	0.3
Max	27.8	51.5	882.8	13.4	1279.1	240	500.0	2163.0	280.2
SD	6.4	8.5	54.9	1.9	159.7	27.8	103.6	113.7	61.5
CV.%	40.7	63.6	10.9	64.7	136.1	63.7	61.7	705.7	59.0
N	747	754	755	755	755	540	534	516	513

Notes: [a] – Mean is mean value; min is minimum value; max is maximum value; SD is standard deviation; CV is coefficient of variation; n is number of observations.

[b] – H is tree height (m); D is stem diameter at breast height (cm); *Dcr* is crown width (m); *pbas* – wood basic density, kg/m³; P_{tree} is aboveground biomass in dry weight (kg).

[c] – A is stand age (years); V is stem volume, m³/ha; N is tree number (1000 individuals per ha); P_{stand} is aboveground stand biomass in dry weight (t per ha).

The lack of a unified methodology affected the qualitative level of data on the biological productivity of forests. It is very difficult to take into account possible overestimations and underestimations of biomass estimates in numerous "gray" Soviet and Russian publications that make up most of the Eurasian database. The danger of such distortions and errors in the databases is obvious. Having calculated the biomass model, which includes the indicators of the taxation of a tree or stand as independent variables, we obtain a residual variance, which is explained by both climatic variables and trivial errors in calculations and other uncertainties. These errors and uncertainties can distort the contribution of climate variables to the explanation of biomass variability "exactly the opposite." This refers to a situation where the predominant share of the explained residual variance falls not on climate variables but on the mentioned uncertainties and errors. In such cases, the ecologically determined positive impact of the climate variable on biomass is "suppressed" by the influence of the mentioned uncertainties and errors, and the dependence can change from a positive sign to a negative one.

In connection with the above, the effectiveness of the results of the analysis and synthesis of existing databases on forest biomass may be significantly limited by their qualitative level, especially when we try to obtain generalizing patterns (Utkin, 2004). Nevertheless, we have made such an attempt.

Methodology

In accordance with the objectives of the study, data analysis and model building are performed at two levels: both individual trees and stands. Two types of models are planned to be built at the tree level: models designed for lidar air sensing and for ground-based taxation. Accordingly, when targeting lidar biomass estimation, crown width and tree height are included in the model as independent variables, and when targeting ground taxation, stem diameter at breast height and tree height are included in the model. It is currently unknown to what extent the models of these two sublevels for *Betula* trees can be sensitive to changes in climatic variables. However, it was found that the contribution of
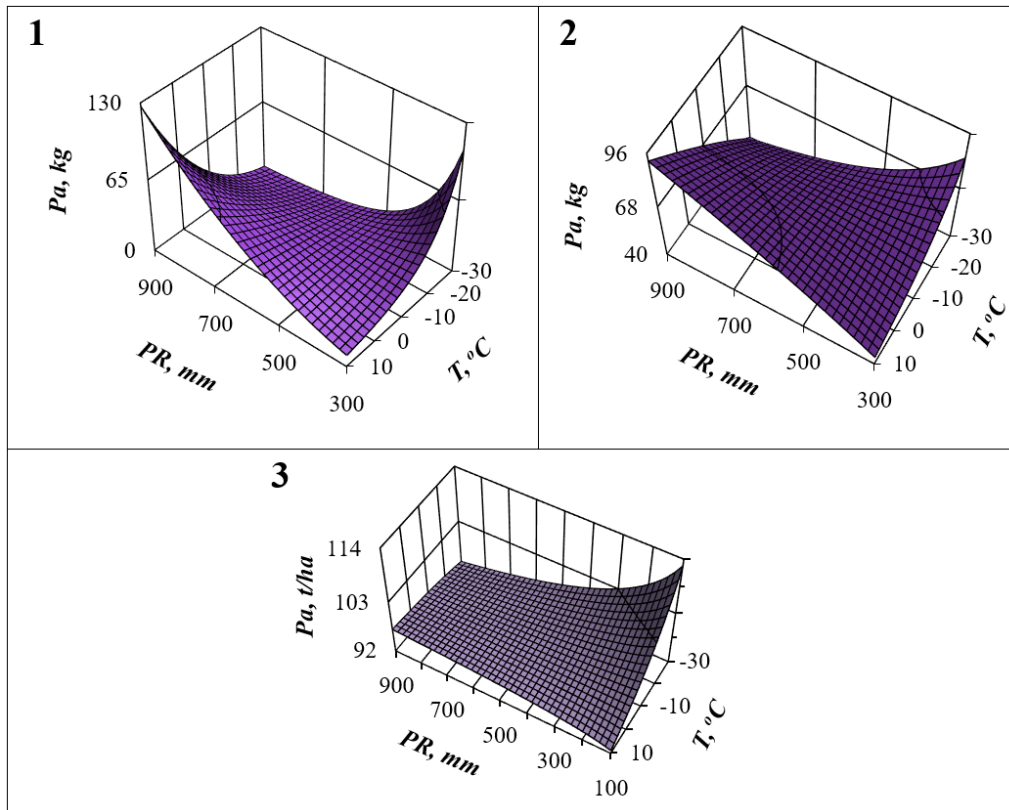
Fig. 3. Changes in aboveground biomass due to the average January temperature (*T*, °C) and average annual precipitation (*PR*, mm): 1 – according to the tree-level model (1) designed for estimating biomass by means of LIDAR sensing; 2 – according to the tree-level model (2) designed to estimate biomass by ground-based taxation; 3 – according to the stand-level model (3) designed to assess aboveground biomass.

climatic variables to the explanation of the variability of the biomass of *Quercus* spp. trees varies from 11 to 28% depending on the structure of the model, namely, on the number and combination of dendrometric (morphological) variables (Usoltsev et al., 2020). At the level of stands, it is also planned to build a model of their biomass.

Data on the biomass of trees and stands, the characteristics of which are given in Tables 1 and 2, were processed by multiple regression analysis. In order to reduce the volume of the article, model constructions are given here only for aboveground biomass, bearing in mind that the patterns are basically identical separately for each component (stems, foliage and branches). The justification of the model structure was given earlier (Usoltsev et al., 2019, 2020).

Regression models sensitive to climate change are calculated at the above three levels:

(1) at the level of individual trees in orientation to lidar assessment of biomass

$\ln P_{tree}$ = 102.229 + 0.8272 (lnDcr) + 2.6933 (ln$H$) − 29.5951 [ln(T+50)] − 17.4363(lnPR) + 4.8155 [ln(T+50)]·(lnPR);
adjR^2 = 0.950;
SE = 0.39

(2) at the level of individual trees in orientation to the traditional terrestrial assessment of biomass

$\ln P_{tree}$ = 21.4126 + 1.0065 (ln$D$) + 0.7590 (ln$H$) + 0.2500 (ln$D$)(ln$H$) + 0,5117 [ln(*pbas*)] − 7.5780 [ln(T+50)] − 4.3674 (lnPR) + 1. 2279 [ln(T+50)]·(lnPR);
adjR^2 = 0.990;
SE = 0.18.

(3) at the level of stands in orientation to the traditional terrestrial assessment of biomass

$\ln P_{stand}$ = 2.3087 − 0.0252 (ln$A$) + 0.9339 (ln$V$) + 0.0183 (ln$N$) − 0.0128 (ln$A$)(ln$N$) − 0.60557 [ln(T+50)] − 0.3598 (lnPR) + 0.0929 [ln(T+50)]·(lnPR);
adjR^2 = 0.975;
SE = 0.12

In (1)-(3), *T* is the average January temperature in °C; *PR* is the average annual precipitation in mm; [ln(T+50)]·(lnPR) is the combined variable that characterizes the combined effect of temperature and precipitation. The abbreviation adjR^2 is a coefficient of determination adjusted for the number of parameters; SE – equation standard error.

Since the average temperature of January in high latitudes has a negative value, for its logarithmic transformation in the models (1)-(3), it is modified to the form (T+50). Regression coefficients for all the biomass components in models (1)-(3) are significant at the level of p < 0.001. Models (1)-(3) are valid within the rang-
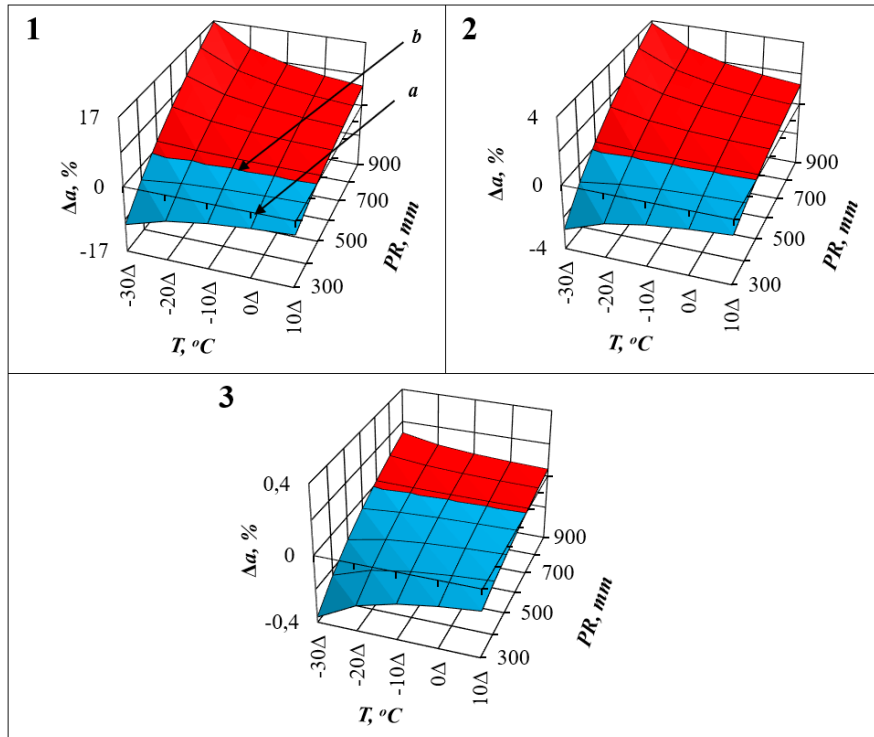
Fig. 4. The change in the biomass of trees and stands with an increase in temperature by 1 ° C due to the expected climate change at different territorial levels of temperatures and precipitation. Here and further: the numbers from 1 to 3 correspond to the model numbers (1)-(3) and the numbers shown in Fig. 3; (a) the plane corresponding to the zero change in biomass with an expected temperature increase of 1 ° C; (b) the line of demarcation of positive and negative changes in biomass with an expected temperature increase of 1 ° C.
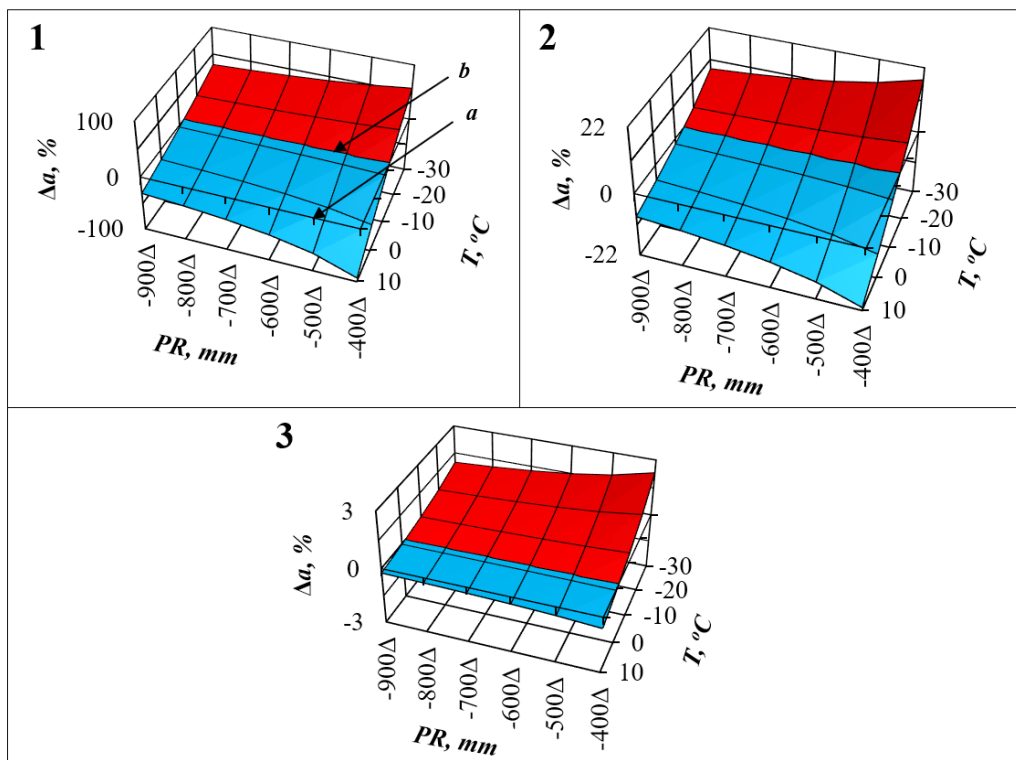

Fig. 5. Changes in the biomass of trees and stands with a decrease in precipitation by 100 mm due to the expected climate change at different territorial levels of temperatures and precipitation.

es of independent variables shown in Table 1. When calculating models (1)-(3), a correction for the logarithmic transformation was applied (Sprugel, 1983; Wood, 1986).

Results

The geometric interpretation of models (1)-(3) is presented in the form of 3D images of the biomass of trees and stands depending on temperature and precipitation (Fig. 3). They are obtained by substituting in (1)-(3) the average values of the independent variables given in Table 1. In Figure 3, we can see that the dependences of the aboveground biomass of trees of the same size, as well as of stands of the same morphological structure, on temperature and precipitation are described by three-dimensional propeller-shaped surfaces. At each of the three levels of analysis in cold regions, as precipitation increases, biomass decreases, but as it moves to warm regions, it is characterized by the opposite trend. As the temperature rises in humid regions, the biomass increases but as the transition to dry conditions begins to decrease.

The principle of the limiting factor in the developed models can be interpreted by a combination of signs for climatic variables, namely, the presence of a minus sign for $\ln(T+50)$] and $(\ln PR)$ and a plus sign for the combined variable $[\ln(T+50)]\cdot(\ln PR)$ (see models (1)-(3)). We could see a similar combination of signs for climatic variables in propeller-shaped models of stem radial growth in swamp forests of Western Siberia (Glebov, Litvinenko, 1976), where the law of limiting the factor was shown at local facilities. If other combinations of "minus" and "plus" signs are obtained as a result of regression analysis, this will mean that the effect of the law of the limiting factor for a particular type of trees or stands is not confirmed. Such a deviation from the principle of the limiting factor may be caused by the aforementioned insufficient qualitative level of empirical material as well as its insufficient representation in the territorial gradients of temperature and precipitation.

Let us consider the described patterns from another point of view, realizing the concept of space-for-time substitution and the principle of "What happens if ...?." In other words, what will be the reaction of the biomass of trees and stands if, with the constancy of territorial gradients of temperature and precipitation, we assume an increase in temperature over time by 1 °C and a reduction in annual precipitation by 100 mm. Taking the first derivatives from the two-factor surfaces presented in Fig. 3, we obtained the regularities of biomass changes at given temperature and precipitation increments.

Figure 4 shows the change in the biomass of trees and stands (Δa, %) with an increase in temperature by 1 °C in different climatic zones (territorial gradients), characterized by different values of temperature and precipitation. 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, denoted as − 30Δ + 10Δ. General conclusion: in sufficiently moisture-rich climatic zones, an increase in temperature with a constant amount of precipitation causes an increase in the biomass of trees and stands (red areas of surfaces in Fig. 4), and in areas of moisture deficiency, its decrease is observed (blue areas of surfaces in Fig. 4).

Figure 5 shows the change in the biomass of trees and stands (Δa, %) with a decrease in annual precipitation by 100 mm in different climatic zones. It is assumed that the January temperature

changes only geographically, and the amount of precipitation as a result of climate change decreases by 100 mm at different territorial precipitation levels, designated as -400Δ – 900Δ. General conclusion: in warm climatic zones, a decrease in precipitation by 100 mm at a constant average temperature in January causes a decrease in aboveground biomass (blue area of surfaces), and in cold climatic zones, it increases (red area of surfaces) (Fig. 5).

Discussion

In the rare available publications devoted to modeling forest biomass under the influence of simultaneous action of temperatures and precipitation, the contribution of these variables to the explanation of biomass variability is either insignificant or zero (Stegen et al., 2011). This is mainly due to the local or regional level of models that is limited, for example, with the territory of Western Europe (Forrester et al., 2017). In such cases, the range of climatic variables is too narrow to be statistically significant against the background of varying structural variables (taxation indices) of trees and stands. Therefore, the authors limited themselves only to stating the fact of replacing one limiting factor with another (Kira, Shidei, 1967; Fonti, 2020). The availability of above-mentioned databases on the biological productivity of trees and stands of forest-forming species growing on the territory of Eurasia in wide ranges of temperatures and precipitation made possible to analyze the change in these indicators of bioproductivity due to temperature and precipitation simultaneously.

The analysis of changes in the biomass of birch trees and stands, performed not in a pair relationship with temperature or precipitation, but in a two-factor relationship with both independent variables, allowed us to establish the presence of a replacement of one limiting factor with another when moving the object of study in territorial gradients of temperature and precipitation. At the same time, the presence of unidirectional influence of climatic factors on birch biomass at the levels of both tree and stand was established. A similar unidirectionality of the influence of climatic factors on the biomass of trees, stands and net primary production of stands was confirmed earlier for the genera *Picea* spp. (Usoltsev et al., 2022a) and *Pinus* sp. (Usoltsev et al., 2022b).

In our study, the regression analysis procedure made it possible to evaluate the contribution of each independent variable to the explanation of the variability of the analyzed variable (Liepa, 1980). The contribution of climatic variables to the explanation of the variability of the biomass of trees and stands in models (1), (2) and (3) was 21, 19 and 7%, and the contribution of structural variables was 79, 81 and 93%, respectively. Since the contribution of climate variables is formed according to the residual principle, i.e., it is extracted from the residual variance formed after evaluating the contribution of structural variables, the contribution of climate variables strongly depends on the structure of the model, in particular, on which structural variables and what combination of them are included in the model as independent variables (Usoltsev et al., 2020).

The established patterns of changes in the biomass of trees and stands, taking into account the expected climatic shifts (Figs 3–5), can be considered as preliminary, since the assumption that spatial relationships between climate and biomass can be used to predict temporal trajectories of biological productiv-

ity in a changing climate remains untested in practice (Veloz et al., 2012). The success of the application of 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 (Bergstrom et al., 2021). Nevertheless, when there is no other way to predict ecosystem processes, the space-for-time substitution method can serve as a completely acceptable alternative. And this alternative is convincingly shown in our work in models of three levels, both for trees and for stands, using the example of the genus *Betula* spp.

Conclusion

In the available publications devoted to the modeling of forest biomass under the influence of the simultaneous action of temperatures and precipitation, the contribution of these variables to the explanation of the variability of biomass was either insignificant or zero due to the narrow range of climatic variables at the level of a particular region. Therefore, it was only stated that one limiting factor was replaced by another, e.g., the limiting factor of temperature in the forest tundra was replaced by the limiting factor of moisture in the forest-steppe in the latitudinal gradient.

The author's database of the tree biomass and stands of the forest-forming species growing on the territory of Eurasia, in wide ranges of temperatures and precipitation, made it possible to develop models of the biomass and stands of the genus *Betula* spp. as the functions of the structural indicators, as well as average January temperatures, average annual precipitation and the combined effect of temperatures and precipitation.

The contributions of independent variables to the explanation of the variability of the biomass of trees and stands in the designed models were established, which ranged from 79 to 93% for structural variables and from 7 to 21% for climatic variables.

Taking into account the combined effect of temperatures and precipitation in the models of tree and stand biomass allowed us to establish a pattern described by a 3D propeller-shaped surface. In cold regions, with increasing precipitation, biomass decreases but as the transition to warm regions is characterized by the opposite trend. With an increase in temperature in humid regions, the biomass increases, but as the transition to dry conditions, it begins to decrease. Thus, in different climatic gradients, the limiting factor may be either a lack or an excess of the active factor.

A similar unidirectionality of the influence of climatic factors on the biomass of trees and stands, as well as the net primary production of stands, was previously shown for the genus *Picea* spp. and subgenus *Pinus* sp. Apparently, the established pattern is common to the main forest-forming genera of Eurasia on the levels of a tree and of a stand. This action is illustrated for the first time in trans-Eurasian climatic gradients, both spatial and temporal, which can be used in the development of strategies for managing the carbon-depositing capacity of forests.

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