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Forest stand biomass of *Picea* spp.: an additive model that may be related to climate and civilisational changes

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Abstract. Since ancient times, climate change has largely determined the fate of human civilisation, which was related mainly to changes in the structure and habitats of forest cover. In the context of current climate change, one must know the capabilities of forests to stabilise the climate by increasing biomass and carbon-depositing abilities. For this purpose, the authors compiled a database of harvest biomass (t/ha) in 900 spruce (*Picea* spp.) sample plots in the Eurasian area and used the methodology of multivariate regression analysis. The first attempt at modelling changes in the biomass additive component composition has been completed, according to the Trans-Eurasian hydrothermal gradients. It is found that the biomass of all components increases with the increase in the mean January temperature, regardless of mean annual precipitation. In warm zonal belts with increasing precipitation, the biomass of most of the components increases. In the process of transitioning from a warm zone to a cold one, the dependence of all biomass components upon precipitation is levelled, and at a mean January temperature of -30°C it becomes a weak negative trend. With an increase in temperature of 1°C in different ecoregions characterised by different values of temperature and precipitation, there is a general pattern of decrease in all biomass components. With an increase in precipitation of 100 mm in different ecoregions characterised by different values of temperature and precipitation, most of the components of biomass increase in warm zonal belts, and decrease in cold ones. The development of such models for the main forest-forming species of Eurasia will make it possible to predict changes in the productivity of the forest cover of Eurasia due to climate change.

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1. Introduction

In recent decades climate change and the possibility of mitigating its consequences for humanity have been recognised as one of the leading problems (Toman et al., 1996). Since ancient times, climate change has largely determined the fate of human civilisation (Behrensmeyer, 2006; Miles-Novelo and Anderson, 2019), the great migrations of peoples (Laczko and Aghazarm, 2009), and changes in the structure and habitats of biota and their main terrestrial component – forest cover (Emanuel et al., 1985; Halofsky et al., 2018; Kosanic et al., 2018). Although it is believed that ancient civilisations died out largely as a result of forest harvesting, “still in no way and by no human device could the wood be exhausted” (Radkau, 2008: 133), and the desertification of once-forested areas of ancient civilisations was the result of climate change.

Nikolay Danilevskiy noted that unlike steppe nomadism, which “indulges in laziness”, the forest promoted the settled lifestyle of the Slavs, a development of primary culture, and hence had a “strong cultural and tribal power”. The forest also had another influence, “forest with its mystic grounds and shade brings a poetic spirit to the people living in it”. He believed that this distinctive culture could originate without any outside influence other than in forest country (Usoltsev, 2019: 9). Thus, forests play an important role both in the history of civilisation and in its future, and therefore any changes in the areas, structure, biological diversity and biological productivity of forests under the influence of climate should be in the focus of world scientists.

One of the most important ecological properties of forest cover is its biomass. However, R. A. Houghton et al. (2009: 9) believe that:

“Our knowledge of distribution and amount of terrestrial biomass is based almost entirely on ground measurements over an extremely small and possibly biased sample, with many regions still unmeasured. Our understanding of change in terrestrial biomass is even more rudimentary, although changes in land use, largely tropical deforestation, are estimated to have reduced biomass, globally”.

In the context of climate change, this state of our knowledge seems to be even more depressing.

Temperature and precipitation are the most informative climatic factors that determine not only the radial annual growth of tree stems, but also the biological productivity of forest stands (DeLucia et al., 2000; Ni et al., 2001; Stegen et al., 2011; D’Aprile et al., 2015; Fang et al., 2016). Analysis of the results of such studies revealed significant contradictions and uncertainties about the assessment of these indices’ dependence on temperature and precipitation using both empirical and functional models (Eggers et al., 2008; Shuman, Shugart, 2009; Poudel et al., 2011; Han et al., 2018). Contradictory results were obtained even within a single region, while the influence of the same climatic factors on the biological production of stands of certain tree species (genera) in the Trans-Eurasian climatic gradients of temperature and precipitation is still unknown, since the available information is fragmentary and contradictory (Strömngren, Linder, 2002; Wilmking et al., 2004; Stegen et al., 2011; Fu et al., 2017), and is obtained in narrow temperature and precipitation ranges shifted in magnitude in different ecoregions.

Moreover, numerous studies of stochastic relationships of biological productivity of stands with temperature and precipitation were carried out for

indices, depersonalised by age and morphology of stands, and even without considering the species composition (Lieth, 1974; Anderson et al., 2006; Keeling, Phillips, 2007; Huston, Wolverton, 2009). However, it is known that the adaptive capacity of forests is species-specific (Spathelf et al., 2018), and it is not correct to identify global patterns of changes in their biological productivity without stratification by species composition. Spruce is one of the most common and socially significant species in Eurasia, and this report is dedicated to this tree species.

The genus *Picea* spp. includes about 45 species, but a relatively intensive hybridisation complicates even their simple description. Usually Meyer's classification scheme was applied, which splits the genus into three sections – *Morinda*, *Casicta* and *Omorica* (Bobrov, 1978). Common spruce (*P. abies* [L.] Karst.), Siberian spruce (*P. obovata* Ldb.), Caucasian spruce (*P. orientalis* [L.] Link), Schrenk's spruce (*P. schrenkiana* F. et M.) and Jezo spruce (*P. jezoensis* [Siebold and Zucc.] Carrière) are the most widely distributed in Eurasia. The common spruce area is fragmented and set before with three local areas – Alpine, Carpathian and Baltic – that independently developed in the postglacial time (Il'inskiy, 1937). The distribution of common spruce to the south of Western Europe and almost to the Arctic Ocean shows that its climate adaptation has a wide range. It is frost-resistant but sensitive to high temperatures and air aridity. Its lateral root system conditions signify a soil moisture dependence. Common spruce is characterised by high shade tolerance; needle longevity reaches from 5 to 7 years in the middle taiga subzone and up to 12–18 years in the Khibiny forest tundra. If common spruce reaches up to 50 metres in height and 2 metres in diameter in Western Europe, then eastward its height unsurprisingly gets shorter and in the European part of Russia it is already only 30 metres tall (Sukachev, 1938). By biological characteristics it resembles the Siberian spruce.

In the development of trivial empirical models, the additivity of component composition is not provided, according to which the total biomass of components (stems, branches, needles, roots) obtained by component equations would be equal to the value of biomass obtained by the common equation (Dong et al., 2015). According to Sanquetta et al.

(2015), independent (without additivity) fitting of coefficients for biomass components and total biomass is not satisfactory, but this is not observed when simultaneous fitting is used accounting the additivity principle, which results in more effective estimators. The influence of climatic changes on the biomass of a tree species in the format of additive models in accordance with transcontinental hydrothermal gradients has not been studied at all.

Hence, the purpose of this study is to develop a model of changes in the additive component composition of the *Picea* spp. stand biomass on the Trans-Eurasian gradients of the mean January temperature and mean annual precipitation. The database compiled by Usoltsev (2013) makes it possible to perform the analysis of biological productivity (potentially for both biomass and carbon) at the trans-continental level. The ranges of variation of mean temperatures and precipitation in Eurasia (which covers a lot of natural biomes) are large, and using multiple regression analysis, it seems promising to relate the biomass structure of spruce stands described by an additive system of equations to two hydrothermal indices – mean January temperature and mean annual precipitation across Eurasia.

2. Materials and methods

The database on biomass of forest-forming species of Eurasia (Usoltsev, 2013) was used in the modelling process. The data are taken from it in the amount of 900 sample plots with the tree harvesting and biomass estimated for the *Picea* spp. forest stands (Fig. 1 and 2). Data on 10 species of the genus *Picea* spp. obtained from 200 published sources in 24 countries (See: Usoltsev et al., 2019). Sample trees were usually taken on each of the sample plots in 5 to 10 copies, and then samples were taken from each biomass component to determine the dry matter content (and, for wood and bark of stems, also to determine the basic density) and after drying the samples at the temperature of 80–100°C the results were recalculated for the whole tree. The quantity of each biomass component per 1 ha was determined by regression method. Not all biomass components are equally presented in the database: if the mass of stems above bark, branches

and needles is determined on all 900 plots, the mass of the stem bark is determined on 400 plots and the mass of roots on 520. Nevertheless, some sampling procedures for estimating biomass of tree components differed between the studies, since they were performed by representatives of different scientific fields in forestry. But these small methodological differences do not play the determining role in the level of accuracy of biomass estimates, because there is only one definite variant of biomass component structure corresponding to a given structure of taxonomic parameters (morphological structure) of a tree stand (Usoltsev, 2007).

Each sample plot on which the biomass determination was performed is positioned relative to the isolines of the mean January temperature (Fig. 1) and relative to isolines of mean annual precipitation (Fig. 2). The matrix of harvest data is then compiled in which values of the biomass component and morphological indices of forest stands are conjugated with the corresponding values of mean January temperature and precipitation. This matrix is then included in the regression analysis procedure.

According to the structure of the disaggregation three-step additive biomass model (Tang et al., 2000; Dong et al., 2015), the total biomass estimated from the initial equation is divided into its components according to the scheme presented in Fig. 3 and Table 1. We used a schematic map of the contours of the mean January temperature (stage of

deep winter dormancy in forest trees), rather than the mean annual temperature, as warming is most pronounced in the cold half of the year (Golubyatnikov, Denisenko, 2009; Laing, Binyamin, 2013; Felton et al., 2016). In his time, F. Schwarz (1899) showed that, for the growth of trees, air temperature from January to March is twice as decisive as precipitation from May to June. Furthermore, to ensure the maximum stability of the model, each of the selected factors (independent variables) should be presented in the maximum range of its variation (Usoltsev, 2004). In our example, mean January temperatures range from -40°C in the forest-tundra of North-Eastern Siberia to $+15^{\circ}\text{C}$ in the subtropics of Nepal, and mean annual precipitation from 190 mm in the permafrost regions of North-Eastern Siberia and the steppe zone of Eurasia to 1,140 mm in the territory of Nepal.

3. Results

Calculated initial regression equations

$$\ln P_i = a_{0i} + a_{1i}(\ln A) + a_{2i}(\ln V) + a_{3i}(\ln N) + a_{4i}[\ln(Tm + 40)] + a_{5i}(\ln PRm) + a_{6i}[\ln(Tm + 40)] \cdot (\ln PRm), \quad (1)$$

where:

P_i – mass of the i -th fraction, t / ha;

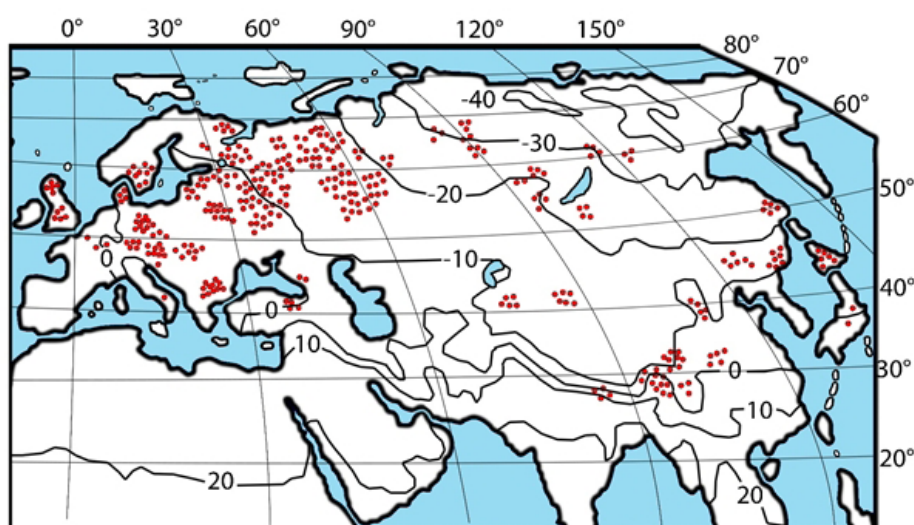


Fig. 1. Distribution of biomass harvest data of 900 *Picea* spp. sample plots on the map of the mean January temperature, $^{\circ}\text{C}$. (World Weather Maps, 2007). <https://www.mapsofworld.com/world-maps/currents-and-temperature-jan-enlarge-map.html>

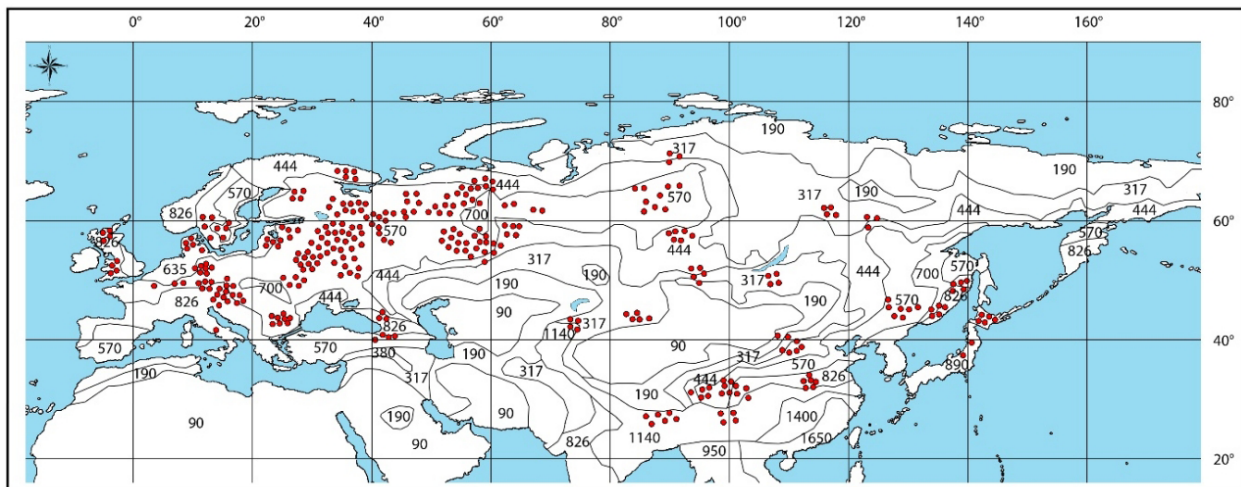


Fig. 2. Distribution of biomass harvest data of 900 *Picea* spp. sample plots on the map of the mean annual precipitation, mm sample trees on the map of the mean annual precipitation, mm. (World Weather Maps, 2007): (<https://eldoradoweather.com/climate/world-maps/world-annual-precip-map.html>)

- A – the age of the stand, years;
 V – wood supply, m^3 / ha ;
 N – stand density, thousand ind./ha;
 i – phytomass fraction index: total (t), aboveground (a), roots (r), crowns (c), stem above bark (s), foliage (f), branches (b), stem wood (w) and stem bark (bk);
 Tm – average January temperature, $^{\circ}\text{C}$;
 PRm – average annual rainfall, mm.

Since the mean January temperature in the northern limit of Eurasia has negative values, the corresponding independent variable is modified to the form $(Tm + 40)$ which may be subjected to logarithmic procedure.

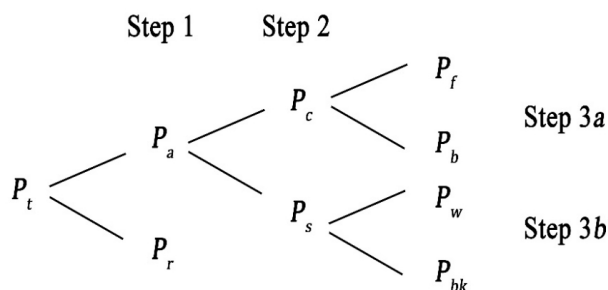


Fig. 3. The pattern of disaggregating three-step proportional weighting additive model. Designation: P_t , P_r , P_a , P_c , P_s , P_f , P_b , P_w and P_{bk} are forest stand biomass respectively: total, underground (roots), aboveground, crown (foliage and branches), stems above bark (wood and bark), foliage, branches, stem wood and stem bark correspondingly, t per ha

The coefficients of Eq. (1) are calculated using the Statgraphics software for multiple regression analysis and their characteristics are obtained. Equations after correcting on logarithmic transformation by G. L. Baskerville (1972) and anti-log transforming are given in Table 2. They are characterised by a significance level of not lower than 0.05. The equations are adequate to the harvest data presented in the above-mentioned database. The equations obtained are modified to the additive form according to the above-mentioned algorithm (Fig. 3 and Table 1), and the final form of the transcontinental additive model of component composition of *Picea* spp. biomass is shown in Table 3.

For comparison of the adequacy of the initial (see Table 2) and additive (see Table 3) equations, those and others are tabulated on the experimental mass-forming indices, and the predicted biomass values obtained are compared with the observed ones according to $adjR^2$ (Table 4). The results of the comparison shown in Table 4 indicate that the adequacy indices of the two systems of equations are close to each other. The ratio of harvest biomass data and values obtained by the calculation of initial and additive models of *Picea* spp. biomass (Fig. 4) show the degree of correlation of these values and the absence of visible differences in the structure of residual dispersions obtained from the two models.

The problem of transforming the model (1) into a tabular variant is that we can specify only the in-

Table 1. The structure of the three-step additive model sold under proportional weighting supposed by Dong et al. (2015). Symbols here and further as per Fig. 3 and Eq. (1)

Step 1	$P_a = \frac{1}{1 + \frac{a_r D^{b_r} H^{c_r}}{a_a D^{b_a} H^{c_a}}} \times P_t$	$P_r = \frac{1}{1 + \frac{a_a D^{b_a} H^{c_a}}{a_r D^{b_r} H^{c_r}}} \times P_t$
Step 2	$P_c = \frac{1}{1 + \frac{a_s D^{b_s} H^{c_s}}{a_c D^{b_c} H^{c_c}}} \times P_a$	$P_s = \frac{1}{1 + \frac{a_c D^{b_c} H^{c_c}}{a_s D^{b_s} H^{c_s}}} \times P_a$
Step 3a	$P_f = \frac{1}{1 + \frac{a_b D^{b_b} H^{c_b}}{a_f D^{b_f} H^{c_f}}} \times P_c$	$P_b = \frac{1}{1 + \frac{a_f D^{b_f} H^{c_f}}{a_b D^{b_b} H^{c_b}}} \times P_c$
Step 3b	$P_w = \frac{1}{1 + \frac{a_{bk} D^{b_{bk}} H^{c_{bk}}}{a_w D^{b_w} H^{c_w}}} \times P_s$	$P_{bk} = \frac{1}{1 + \frac{a_w D^{b_w} H^{c_w}}{a_{bk} D^{b_{bk}} H^{c_{bk}}}} \times P_s$

dicators of the stand age, as well as temperature and precipitation, while the values of stem volume and tree density can be entered into the table in the form of calculated values obtained by a system of auxiliary recursive equations having the general form:

$$N = f [A, 1/A, (Tm+40), PRm], \quad (2)$$

$$V = f [1/A, N, (Tm+40), PRm]. \quad (3)$$

The results of calculating (2) and (3) are given in Table 5.

The results of tabulating the equations in the sequence (2), (3) and (1) represent a rather cumbersome table. We took from it the component biomass for the age of 100 years and built graphs of their dependence on temperature and precipitation (Fig. 5).

The obtained additive models of spruce stand biomass make it possible to establish quantitative changes in the biomass structure due to climatic changes, in particular, mean January temperature and mean annual precipitation. Let us pay attention to the fact that in Fig. 5 both temperature and precipitation trends of biomass have positive dependences. The exception is the foliage biomass, which during the transition from the regions of insufficient moisture ($PRm = 300$ mm) to the regions of increased moisture ($PRm = 900$ mm) in the warm zone ($Tm = +10^\circ\text{C}$) does not increase, but decreases.

Figure 6 shows the change (Δ , %) in the *Picea* spp. forest biomass with an increase in temperature of 1°C in different ecoregions characterised by different values of temperature and precipitation. It is assumed that climate change does not affect precipitation, which changes only geographically (by ecoregions), while as a result of the expected climate change the temperature increases by 1°C at different territorial (zonal) temperature levels, designated as $-30\Delta \dots +10\Delta$. Thus, Fig. 6 shows the common pattern of the increase (the location of the increment surface above the zero plane) in both the total biomass and all its components, including the roots, of spruce stands with a temperature increase of 1°C in all the temperature zones of Eurasia and in all the regions with different precipitation levels.

Figure 7 shows the change (Δ , %) in the *Picea* spp. forest biomass with an increase in precipitation of 100 mm in different ecoregions. It is assumed that January temperature changes only geographically, while as a result of the expected climate change the precipitation increases by 100 mm at different territorial precipitation levels designated as $300\Delta \dots 800\Delta$. In warm zones ($0^\circ\text{C} \dots 10^\circ\text{C}$), with an increase in precipitation of 100 mm, biomass total, aboveground, stems and roots increase (the location of the increment surface above the zero plane), and in cold ones ($-20^\circ\text{C} \dots -30^\circ\text{C}$) they decrease (the location of the increment surface under the zero plane). Biomass components of the crown respond ambiguously to changes in precipita-

Table 2. Characteristics of initial model (1) after its anti-log transforming

Biomass components		The initial model characteristics			
P_t	1.6868	$A^{-0.0631}$	$V^{0.8917}$	$N^{0.0303}$	
Step 1					
P_a	1.84E-01	$A^{-0.0528}$	$V^{0.8846}$	$N^{0.0456}$	
P_r	7.34E+01	$A^{0.0144}$	$V^{0.8453}$	$N^{0.0528}$	
Step 2					
P_c	1.37E-05	$A^{-0.2301}$	$V^{0.7464}$	$N^{0.2057}$	
P_s	2.98E-01	$A^{0.0435}$	$V^{0.9822}$	$N^{0.0235}$	
Step 3a					
P_f	1.83E-10	$A^{-0.2702}$	$V^{0.6718}$	$N^{0.2592}$	
P_b	1.84E-04	$A^{-0.1596}$	$V^{0.8371}$	$N^{0.2046}$	
Step 3b					
P_w	7.05E-02	$A^{0.0950}$	$V^{0.9731}$	$N^{-0.0138}$	
P_{bk}	3.11E-01	$A^{0.1663}$	$V^{0.7954}$	$N^{0.1152}$	

Continuation of Table 2

Biomass components		The initial model characteristics			adjR ^{2*}	SE*
P_t	($Tm+40$) ^{0.4910}	($Tm+40$) ^{-0.0924 ln(PRm)}	$PRm^{0.0487}$		0.974	1.25
Step 1						
P_a	($Tm+40$) ^{0.8254}	($Tm+40$) ^{-0.1201 ln(PRm)}	$PRm^{0.2744}$		0.974	1.21
P_r	($Tm+40$) ^{-0.7995}	($Tm+40$) ^{0.0772 ln(PRm)}	$PRm^{-0.6934}$		0.913	1.49
Step 2						
P_c	($Tm+40$) ^{3.9073}	($Tm+40$) ^{-0.6237 ln(PRm)}	$PRm^{1.8394}$		0.812	1.50
P_s	($Tm+40$) ^{0.3354}	($Tm+40$) ^{-0.0491 ln(PRm)}	$PRm^{0.0240}$		0.986	1.17
Step 3a						
P_f	($Tm+40$) ^{6.6083}	($Tm+40$) ^{-1.0477 ln(PRm)}	$PRm^{3.5374}$		0.700	1.63
P_b	($Tm+40$) ^{2.8783}	($Tm+40$) ^{-0.4661 ln(PRm)}	$PRm^{1.2422}$		0.817	1.60
Step 3b						
P_w	($Tm+40$) ^{0.3654}	($Tm+40$) ^{-0.0489 ln(PRm)}	$PRm^{0.1941}$		0.989	1.16
P_{bk}	($Tm+40$) ^{-0.6774}	($Tm+40$) ^{0.0880 ln(PRm)}	$PRm^{-0.1867}$		0.934	1.36

* $adjR^2$ – coefficient of determination adjusted for the number of parameters; SE – equation standard error

Table 3. Final three-step additive model of *Picea* forest biomass

Step 1	$Pt = 1.6868 A^{-0.0631} V^{0.8917} N^{0.0303} (Tm+40)^{0.4910} PRm^{0.0487} (Tm+40)^{-0.0924(\ln PRm)}$
	$Pa = \frac{1}{1+4.00E+02 A^{0.0672} V^{-0.0393} N^{0.0072} (Tm+40)^{-1.6249} PRm^{-0.9679} (Tm+40)^{0.1973(\ln PRm)}} \times Pt$
	$Pr = \frac{1}{1+2.50E-03 A^{-0.0672} V^{0.0393} N^{-0.0072} (Tm+40)^{1.6249} PRm^{0.9679} (Tm+40)^{-0.1973(\ln PRm)}} \times Pt$
Step 2	$Pc = \frac{1}{1+2.18E+04 A^{0.2737} V^{0.2358} N^{-0.1822} (Tm+40)^{-3.5683} PRm^{-1.8154} (Tm+40)^{0.5745(\ln PRm)}} \times Pa$
	$Ps = \frac{1}{1+4.59E-05 A^{-0.2737} V^{-0.2358} N^{0.1822} (Tm+40)^{3.5683} PRm^{1.8154} (Tm+40)^{-0.5745(\ln PRm)}} \times Pa$
Step 3a	$Pf = \frac{1}{1+1.00E+06 A^{0.1107} V^{0.1653} N^{-0.0546} (Tm+40)^{-3.7300} PRm^{-2.2952} (Tm+40)^{0.5817(\ln PRm)}} \times Pc$
	$Pb = \frac{1}{1+9.96E-07 A^{-0.1107} V^{-0.1653} N^{0.0546} (Tm+40)^{3.7300} PRm^{2.2952} (Tm+40)^{-0.5817(\ln PRm)}} \times Pc$
Step 3b	$Pw = \frac{1}{1+4.4055 A^{0.0713} V^{-0.1776} N^{0.1290} (Tm+40)^{-1.0428} PRm^{-0.3808} (Tm+40)^{0.1369(\ln PRm)}} \times Ps$
	$Pbk = \frac{1}{1+2.27E-01 A^{-0.0713} V^{0.1776} N^{-0.1290} (Tm+40)^{1.0428} PRm^{0.3808} (Tm+40)^{-0.1369(\ln PRm)}} \times Ps$

Table 4. Comparison of coefficients of determination of the initial and additive equations of *Picea* spp. forest biomass

Biomass components								
Pt	Pa	Pr	Ps	Pw	Pbk	Pc	Pb	Pf
Initial equations								
0.883	0.898	0.595	0.912	0.956	0.533	0.410	0.363	0.249
Additive equations								
0.883	0.899	0.595	0.919	0.947	0.541	0.448	0.443	0.349

tion. Foliage biomass decreases in cold zones (-10°C ... -30°C), but branch biomass increases, regardless of regional levels of current precipitation. In warm zones (0°C ... 10°C), the foliage and branch biomass remain unchanged with an increase in precipitation of 100 mm at the current levels of precipitation in all the ecoregions (all the increment surface is under the zero plane). A more accurate geographical localisation of these dependences is not yet possible, as will be discussed below.

4. Discussion

As we can see on these graphs (Fig. 5), all the *Picea* spp. biomass components, with some exceptions for foliage, change in one general scheme, but in differ-

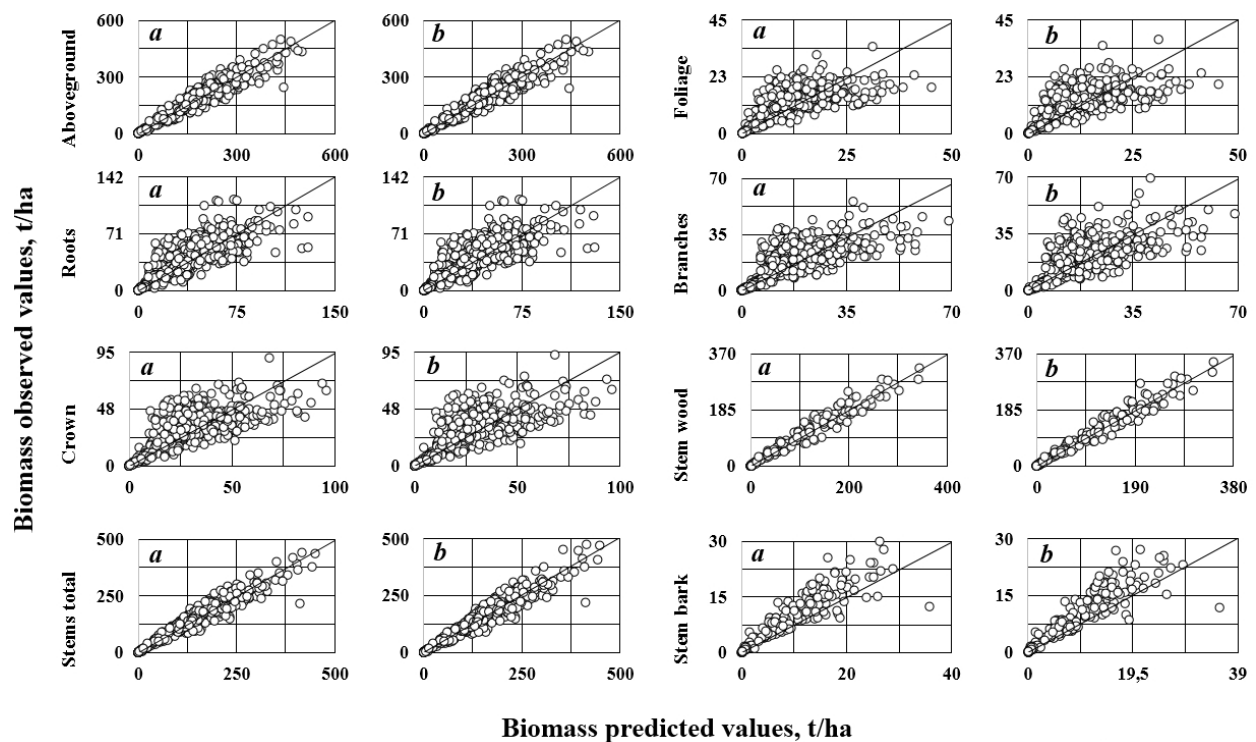
ent ratios. The biomass of all components increases with the increase in the mean January temperature from -30°C to $+10^{\circ}\text{C}$, regardless of precipitation. In warm zonal belts ($Tm = +10^{\circ}\text{C}$) with precipitation increasing from 300 to 900 mm the biomass of all components increases, except for the foliage biomass, but the latter decreases under the same conditions. With the transition from warm zones ($Tm = +10^{\circ}\text{C}$) to cold ($Tm = -30^{\circ}\text{C}$), the dependence upon precipitation of the biomass of all components except for foliage is levelled, i.e. it becomes less pronounced, and at the temperature Tm equal to -30°C acquires a weak negative trend.

Almost full compliance with our data, though obtained for the other production index (NPP), can be seen in the graph presented by T. Luo; according to his results of modelling 167 spruce–fir forest stands, represented throughout China by species

Table 5. Characteristics of the recursive system of auxiliary equations for mass-forming indices of spruce stands

Mass-forming indices		Auxiliary equation characteristics			
$\ln N$	-6.9760	-1.1359 $\ln A$	-9.0578 (1/A)	-	3.9808 $\ln(Tm+40)$
$\ln V$	26.6476	0.4128 $\ln N$	-55.2965 (1/A)	-0.0821 ($\ln N$)($\ln A$)	-6.4361 $\ln(Tm+40)$

Mass-forming indices	Auxiliary equation characteristics		adjR ²	SE
$\ln N$	2.4072 $\ln PRm$	-0.7650 [$\ln(Tm+40)$] $\ln(PRm)$	0.567	0.59
$\ln V$	-4.2439 $\ln PRm$	1.3318 [$\ln(Tm+40)$] $\ln(PRm)$	0.779	0.64



of *Picea wilsonii* Masters, *P. jezoensis* (Siebold and Zucc.), and *P. koraiensis* Nakai in dependence of temperature and precipitation. There is only some difference from the obtained regularity for biomass in the regularity of the reduction of NPP in the cold zone ($Tm = -4^{\circ}\text{C}$) as precipitation increases from 400 to 1400 mm: it occurs in China more intensively than in our Eurasian gradient.

There are more significant differences in our regularities for the dark-conifer genus *Picea* spp. when compared to the same Trans-Eurasian patterns obtained for the two-needled subgenus *Pinus* L. where the pine models manifested propeller-shaped surfaces (Usoltsev et al., 2018). If the decrease in the

spruce stand biomass on the moisture-poor ecoregions ($PRm = 300$ mm) occurs less intensively compared to moisture-rich ($PRm = 900$ mm) ones as the transition from warm ($Tm = +10^{\circ}\text{C}$) to cold ($Tm = -30^{\circ}\text{C}$) zones, then the pine stand biomass in such moisture-poor ecoregions in the same temperature gradient significantly increases. A possible reason is that the ecoregions where pine grows are represented by a steppe zone where spruce cannot grow. Some sample plots with estimations of spruce biomass fall on the pole of continentality in Yakutia in the permafrost region, where precipitation, as in the steppe zone, is about 300 mm.

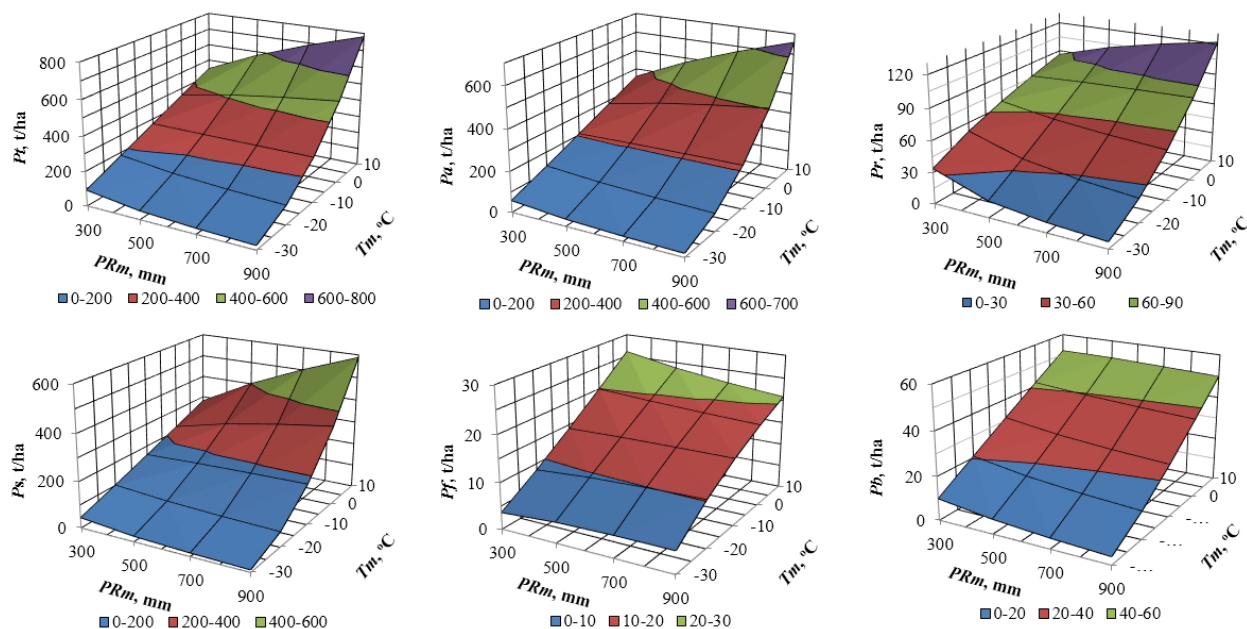


Fig. 5. Dependence of *Picea* spp. biomass on mean January temperatures (T_m) and annual precipitation (PR_m). Designation: P_t , P_s , P_a , P_f , P_r , and P_b – respectively, total biomass, stems, aboveground, foliage, roots and branches, t/ha

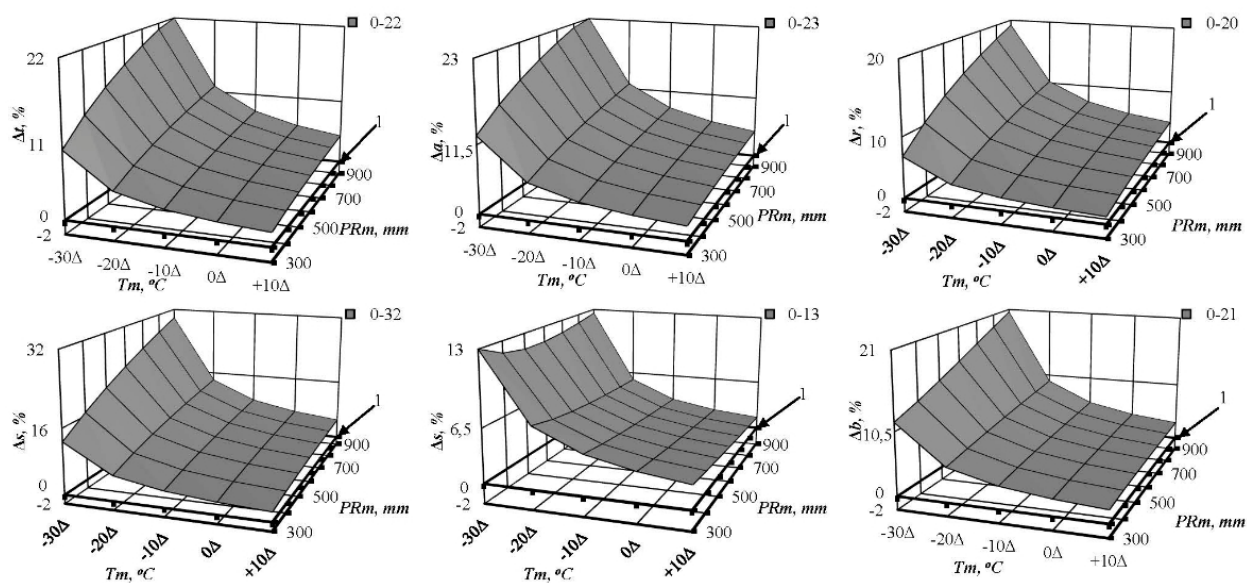


Fig. 6. Changes in *Picea* spp. stand biomass with a temperature increase of 1°C due to the expected climate change at different territorial levels of temperature and precipitation. T_m – mean January temperature, °C; PR_m – mean annual precipitation, mm. On the axes of ordinates the biomass components consistently marked, changing with increasing temperature by 1°C (%): total Δt , aboveground Δa , roots Δr , stems Δs , foliage Δf and branches Δb . 1 – the plane corresponding to zero change in biomass at the expected temperature increase of 1°C

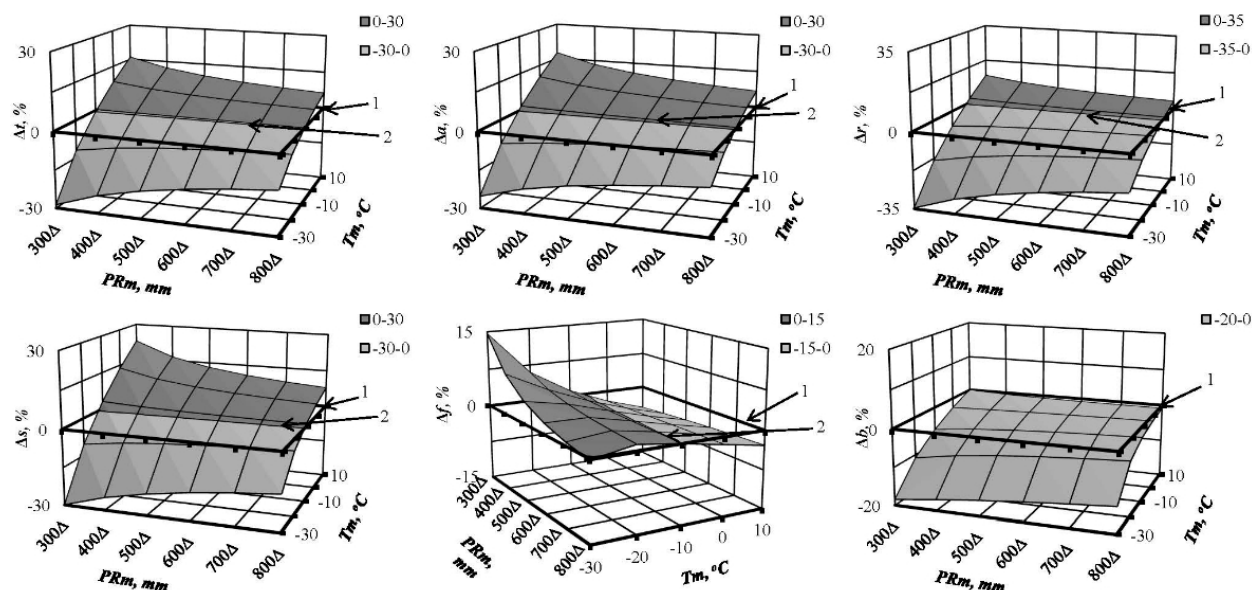


Fig. 7. Changes in *Picea* spp. stand biomass with a precipitation increase of 100 mm due to the expected climate change at different territorial levels of temperature and precipitation. On the axes of ordinates the biomass components consistently marked, changing with increasing precipitation by 100 mm (%): total Δt , aboveground Δa , roots Δr , stems Δs , foliage Δf and branches Δb . 1 – the plane corresponding to zero change of biomass at the expected precipitation increase by 100 mm; 2 – the line of differing of positive and negative changes in biomass (Δ ,%) with an expected increase in precipitation of 100 mm

However, this trend does not correspond to the results obtained by other scientists. For example, at the local level in the marsh forests of the Siberia, at the maximum amounts of temperature sums above 10°C (2200°C) there is an increase in the radial growth of stems by 30–50% with an increase in precipitation from 400 to 600 mm, and at the minimum amounts of temperature sums (1600°C) the radial growth is reduced by 4–9% with an increase in precipitation in the same range. Correspondingly, at the level of precipitation of 400 mm the radial growth is reduced by 14–20% with an increase in the sum of temperatures from 1600 to 2200°C, and it increases by 14–33% in the same temperature range at the level of precipitation of 600 mm (Glebov, Litvinenko, 1976). According to the results obtained by A. A. Molchanov (1976), in the North of Eurasia the greatest influence on the growth of the annual tree ring comes from air temperature, and in the conditions of the southern forest-steppe the dominant role is played by precipitation.

The third type of the investigated regularity was shown by the example of fir (*Abies* spp.) stands of

Eurasia: our modelling suggested that the biomass of all components grows as precipitation total increases from 300 to 900 mm, as well as due to the increase in the mean January temperature from -30°C to +10°C (Usoltsev et al., 2019a). The finding is consistent with the increase in relative radial increment of boreal forests in Canada if both mean annual temperature and annual precipitation increase (Miao and Li, 2011).

Finally, the fourth type of investigated pattern was detected on the example of larch (*Larix* spp.) forests of Eurasia: the unified regularity to all the biomass components of wood story is the following: increase with raising temperature in the range from -40°C to 0°C at invariable precipitation, but decrease with raising precipitation in the range from 200 to 900 mm at constant temperature (Usoltsev et al., 2019b).

These uncertainties can be explained by differing species-specific hydrothermal optima between the studied species, and by the insufficient representation of empirical biomass data to date.

Of course, the solution to each new problem and the corresponding removal of associated uncertainty generates several new unknowns. In our case, there are at least three uncertainties that have arisen.

1) The patterns shown are hypothetical: they reflect the long-term adaptive responses of forest stands to regional climatic conditions and do not take into account the rapid trends in current environmental changes, which place serious constraints on the ability of forests to adapt to new climatic conditions (Alcamo et al., 2007; Pastore et al., 2019).

2) Since the database used has a lot of “gaps” and does not completely cover the territory of Eurasia, the shown patterns are preliminary. Therefore, today there is no sense in using more advanced climate maps, for example, by Köppen (1918) or Geiger (1954), or the maps taking into account the topography of the territories, but having some shifts in the time of their designing and the time period of establishing our sample plots. As the database will be supplemented and climate maps will be updated, these patterns will be modified.

3) The patterns shown in accordance with the database used are related to fir forests, pure or with slight admixture of other tree species. However, most of the forest area is represented by mixed-tree coenoses. There is a lot of evidence that mixed-tree coenoses are more resistant to stresses caused by abiotic factors and are more productive than pure coenoses (Liang et al., 2016). However, a recent study of net primary production (NPP) of aboveground biomass from forest phytocoenoses in Spain and Canada over a wide range of biodiversity index, mean temperature and moisture conditions (Paquette et al., 2018) led to a paradoxical conclusion. It was found that in pure forest stands (biodiversity index is zero), NPP reacts to temperature rise up to 1–2°C in different climatic zones in different ways: it grew in forests of the temperate zone, remained stable in boreal forests and declined in the Mediterranean forests, but as the biodiversity index increases in different zones, these trends gradually transformed into a unified negative trend common for all zones (Paquette et al., 2018). This result calls into question all previously obtained regularities of changes in biomass and NPP of pure (or almost pure) forest communities in variable climate conditions: in forests with an increased biodiversity

index, previously established patterns can be significantly modified and even reversed.

5. Conclusion

The first attempt was made at modelling changes in the additive component composition of 900 spruce (*Picea* spp.) plots' biomass (t/ha), according to the trans-Eurasian hydrothermal gradients of Eurasia using a database compiled on the structure of harvest biomass. It is found that the biomass of all components increases with an increase in mean January temperature, regardless of mean annual precipitation. In warm zonal belts with increasing precipitation the biomass of all components increases, except for foliage mass, which decreases under the same conditions. In the process of transition from a warm zone to a cold one, the dependence of all biomass components upon precipitation is levelled, and at a mean January temperature of -30°C it becomes a weak negative trend. With an increase in temperature of 1°C in different ecoregions characterised by different values of temperature and precipitation, there is a general pattern of decrease in total biomass, and all its components, including roots. With an increase in precipitation of 100 mm in different ecoregions characterised by different values of temperature and precipitation, in warm zonal belts (0°C ... 10°C) biomass total, aboveground, stems and roots increases, and decreases in cold ones (-20°C ... -30°C). The foliage biomass in cold zones (-10°C ... -30°C) increases regardless of regional levels of current precipitation, and decreases in warm zones (0°C ... 10°C). The branch biomass decreases in all ecoregions. The development of such models for the main forest-forming species of Eurasia will make it possible to predict changes in the productivity of the forest cover of Eurasia due to climate change.

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