



Fir (*Abies* spp.) stand biomass additive model for Eurasia sensitive to winter temperature and annual precipitation

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Abstract

Climate change, especially modified courses of temperature and precipitation, has a significant impact on forest functioning and productivity. Moreover, some alterations in tree biomass allocation (e.g. root to shoot ratio, foliage to wood parts) might be expected in these changing ecological conditions. Therefore, we attempted to model fir stand biomass (t ha^{-1}) along the trans-Eurasian hydrothermal gradients using the data from 272 forest stands. The model outputs suggested that all biomass components, except for the crown mass, change in a common pattern, but in different ratios. Specifically, in the range of mean January temperature and precipitation of -30°C to $+10^{\circ}\text{C}$ and 300 to 900 mm, fir stand biomass increases with both increasing temperature and precipitation. Under an assumed increase of January temperature by 1°C , biomass of roots and of all components of the aboveground biomass of fir stands increased (under the assumption that the precipitation level did not change). Similarly, an assumed increase in precipitation by 100 mm resulted in the increased biomass of roots and of all aboveground components. We conclude that fir seems to be a perspective taxon from the point of its productive properties in the ongoing process of climate change.

Key words: fir forests; stand biomass; regression models; additive biomass equations; hydrothermal indices

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1. Introduction

Since 1850, the amount of greenhouse gases in the atmosphere has doubled, threatening the planet with catastrophic climate change (Fatichi et al. 2019). At the UN climate summit in Paris in December 2015, 196 countries committed to reducing CO_2 emissions and preventing mean global temperature from rising by more than 2°C by the end of the century. Forest ecosystems, as sinks of atmospheric carbon, play an important role in this perspective. The ability of forests to sequester atmospheric carbon and to produce organic matter represents the basis of their functioning (Dylis 1978). The concentration of CO_2 in the atmosphere can be reduced by increasing carbon stock in the vegetative cover by effective forest management. On the other hand, climate change has a significant impact on vegetation productivity, which in turn affects cycling of organic matter and gas exchange

in the biosphere (Golubyatnikov & Denisenko 2009).

Key data describing the quantitative characteristics of world forests are needed for a global quantitative description of natural and social phenomena (including biosphere functions of forest cover), the scientific community therefore needs to respond to the onset of the Big Data Era (Kudyba et al. 2014). In recent years, scientists from a number of countries have created unified global databases of empirical data and have derived general patterns describing fundamental functions of forest cover. To deepen our understanding of global forest ecosystems, the preference for large-scale synthesis of environmental data and modern digital learning methods is becoming increasingly apparent (Crowther et al. 2015; Poorter et al. 2015; Liang et al. 2016; Lockers et al. 2016; Jucker et al. 2017; Bohn & Huth 2017).

Temperature and precipitation are the key climatic factors that determine not only the radial growth of

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tree stems, but also forest stand productivity as a whole (DeLucia et al. 2000; Ni et al. 2001; Stegen et al. 2011; D’Aprile et al. 2015; Fang et al. 2016). Numerous studies of stochastic relationships of stand productivity with temperature and precipitation have been carried out at a regional level without accounting for stand age and morphology, and at a global level with or without taking species composition into account (Lieth 1974; Anderson et al. 2006; Keeling & Phillips 2007; Huston & Wolverton 2009). The analysis of the results from such studies revealed significant contradictions and uncertainties associated with the assessment of the dependence of these indices on temperature and precipitation using either empirical or functional models (Eggers et al. 2008; Shuman & Shugart 2009; Poudel et al. 2011; Han et al. 2018). Contradictory results were obtained even within the same region (Eggers et al. 2008; Shuman & Shugart 2009; Poudel et al. 2011; Han et al. 2018). Moreover, the influence of the climatic factors on biomass production of certain tree species (genera) along Trans-Eurasian climatic gradients of temperature and precipitation is still unknown, since the underlying information is fragmentary or contradictory (Wilmking et al. 2004; Stegen et al. 2011; Fu et al. 2017).

Fir (*Abies* spp.) is a genus comprising about 50 species of evergreen coniferous trees belonging to the *Pinaceae* family. They frequently occur in Eurasia, North and Central America, and North Africa, mainly in the mountainous regions. Under the Eurasian conditions, the most frequent *Abies* species are: *A. alba* Mill., *A. sibirica* L., *A. nephrolepis* Maxim., *A. nordmanniana* Spach., *A. spectabilis* (D. Don.) Mirb., and *A. sachalinensis* (F. Schmidt) Mast., *A. veitchii* Lindl., *A. firma* Sieb. et Zucc. In the European territory, *Abies alba* has been the most frequently studied species of this genus (e.g. Barbu & Barbu 2005; Savill et al. 2016). Recent research has shown that although *Abies alba* is much less significant economically than *Picea abies* L. Karst and *Pinus sylvestris* L. (both are most common coniferous trees), it might just be the species with the best future perspective under the ongoing climate change (Lindner et al. 2008). The latest work (Bosela et al. 2018) has shown that *A. alba* has a great productive potential, which has recently improved due to the reduction of acid deposition in Central Europe.

When constructing and using allometric models of tree biomass the principle of additivity need to be accounted for (Jacobs & Cunia 1980). Additivity of biomass components means that the resulting sum of biomass estimates of individual tree components (stems, branches, foliage, roots) obtained from component equations is equal to the value of the total biomass obtained from a general equation for the whole tree (Young et al. 1964). An analysis performed by Sanquetta et al. (2015) showed that additivity of biomass components is not ensured in 80% of derived models, mainly due to the complexity of statistical analyses and the inaccessibility of adequate modern software (Bi et al. 2004).

The first attempts to implement the principle of additivity were performed in the late 1960s and early 1970s on the examples of linear biomass models (Kurucz 1969; Kozak 1970). They were followed by the transition to additive systems of nonlinear equations, which are more suitable for accurate biomass quantification, but their computational algorithms are much more complex. One of recent developments is a two-step nonlinear seemingly unrelated regression (Parresol 2001; Dong et al. 2016). The statistical accuracy and, accordingly, the complexity of the calculation algorithms, was consistently increasing as such models were developed, and therefore modern software tools were required. All aforementioned additive systems of equations use an “aggregation” method based on the principle “from the particular (i.e. from component equations) to the general”.

Recently, a disaggregation method of proportional weighing based on the principle “from general to particular” was proposed and developed as an alternative to the above-mentioned approach. It has been implemented in two versions: as two-step (Zheng et al. 2015) and three-step (Dong et al. 2015) additive systems of disaggregated equations. The first of them has been applied to above-ground biomass, while the second to total tree biomass, i.e. both aboveground and underground parts.

To date, the influence of climate change on biomass of tree species has not been studied by a systematic application of additive models in accordance to transcontinental hydrothermal gradients. Hence, the purpose of this study was to develop an additive model of biomass estimation of fir stands along the Trans-Eurasian gradients of mean January temperatures and precipitation. The Eurasian database of biomass in trees and individual tree components compiled by Usoltsev (see works: Usoltsev 2010, 2013 for more details) makes it possible to perform an analysis of biological productivity (eventually for both biomass and carbon) at a trans-continental level. The variation range of mean temperatures and precipitation in Eurasia is large and covers a spectrum of natural ecosystems. We hypothesise that the biomass structure of fir stands may be described by an additive system of equations based on two hydrothermal indices – mean January temperature and mean annual precipitation all over Eurasia (i.e. under a wide range of variation of hydrothermal indices). We decided to use the mean January temperature, because warming is most pronounced in the cold half of the year (Golubyatnikov & Denisenko 2009; Laing & Binyamin 2013; Felton et al. 2016) and also because winter temperature was found decisive for fir growth (Schwarz 1899; Bijak 2010; Toromani & Bojaxhi 2010).

2. Material and methods

A database describing biomass of forest-forming species of Eurasia (Usoltsev 2010, 2013), consisting of

data about the whole tree biomass and individual tree components published by a large number of authors, was used in this study. From this database, 272 sampling sites with the biomass data of fir forest stands were selected (Table 1, Fig. 1 and Fig. 2). At each site, several sample trees were selected for biomass sampling of individual tree components. In general, 5 to 10 trees were sampled from each site with the exception of 23 sites established in the Carpathians (Lakida & Domashovets 2009), from which only 3–4 trees per site were harvested and processed. From the sample trees, biomass samples were taken from every tree component to determine the dry matter content, and tissue density for wood and bark of stems. Individual biomass components are not equally presented in the database since not all components were determined at each site. Hence, the mass of stems above bark and needles was quantified for all 272 sites, while the mass of branches, stem bark and roots only for 255, 151, and 66 sites, respectively.

Sampling procedures for estimating biomass of tree components differed between the studies, since they were performed by representatives of different scientific fields in forestry. However, 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 morphological structure of a tree stand (Usoltsev 2007).

The matrix of biomass data representing individual components and forest stand characteristics was assessed against the main driver variables of mean January temperature (Fig. 1) and precipitation (Fig. 2) taken from World Weather Maps (2007). It is known that the

effectiveness of modelling of biological communities (of which a forest is the most complex one) depends on the implementation level of a meaningful analysis of the initial data, i.e. on a studied level of the structure of the impact of factors on an object, changing in time and space. To ensure the maximum stability of the model, each of the selected independent variables should be presented in the maximum range of its variation (Usoltsev 2004). In our case, mean January temperatures range from -40°C in the forest-tundra of the 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.

The matrix containing biomass data, stand variables, and climate characteristics was used as a source of data for the subsequent regression analysis to derive equations for estimation of total biomass and its components. Forest biomass was described using a power function, which belongs to the most widely used functions for such purposes (Picard et al. 2012). When choosing independent variables of the regression model, we adhered to the concept that there is only one definite variant of stand biomass structure corresponding to a given set of taxonomic parameters describing a forest stand (Usoltsev, 2007). The initial structure of the model included the main mass-forming factors of stands – age, stem volume, tree density, mean diameter and mean height. Mean diameter correlated with tree density and mean height correlated with age. Hence, they were excluded in the process of the regression analysis. The synergism $(\ln A) \cdot (\ln N)$ was introduced in the model to account for the decrease in tree density with age and its effect on the

Table 1. List of 272 sites with biomass data representing *Abies* spp. used for the construction of additive models.

Country	Species of <i>Abies</i>		Number of sampling sites	Range of					References
	English name	Latin name		Age [years]	Tree density [pcs ha^{-1}]	Stand volume [$\text{m}^3 \text{ha}^{-1}$]	Above ground biomass [t ha^{-1}]	Root biomass [t ha^{-1}]	
Italy	Silver fir	<i>A. alba</i> Mill.	16	20–95	512–2548	173–1095	86–467	Not available	Cantiani 1974; Hellrigl 1974
Romania	Silver fir	<i>A. alba</i> Mill.	1	110	485	1000	470	Not available	DeAngelis 1981
Czech Republic	Silver fir	<i>A. alba</i> Mill.	1	51	1667	216	119	15	Vyskot 1972, 1973
Ukraine	Silver fir	<i>A. alba</i> Mill.	46	6–99	223–7400	12–770	14–326	6–60	Odinak et al. 1986; Lakida and Domashovets 2009
Russia	Siberian fir	<i>A. sibirica</i> L.	142	20–200	165–54080	30–540	17–212	8–48	Khanbekov 1972; Krauklis et al. 1975; Kuzikov 1979; Onuchin & Borisov 1983; Mitrofanov et al. 1986; Usoltsev & Antropov, 2001; Andriyanova 2001; Koshurnikova 2007; Usoltsev et al. 2012
	Khingam fir	<i>A. nephrolepis</i> Maxim.	11	41–192	587–5125	68–383	40–189	38–51	Dyukarev & Rozenberg 1975; Opritova et al. 1982
	Nordmann fir	<i>A. nordmanniana</i> Spach.	5	160–283	332–544	601–1294	327–598	69–101	Orlov 1951; Veselov 1973
Nepal	Himalayan fir	<i>A. spectabilis</i> (D.Don) Mirb.	6	100	275–1450	336–758	158–417	38–102	Yoda 1967, 1968
Japan	Todo-fir	<i>A. sachalinensis</i> (F.Schmidt) Mast.	7	8–35	1178–2870	1–321	1–196	Not available	Yamamoto & Sanada 1970; Satoo 1973; Ueda 1974;
	Veitch's fir	<i>A. veitchii</i> Lindl.	26	13–126	1204–19500	114–568	68–257	4–62	Oshima et al. 1958; Kimura 1963; Oohata & Oniishi 1974; Tadaki et al. 1977
	Momi-fir	<i>A. firma</i> Sieb. et Zucc.	11	120	353–1250	157–930	90–502	145	Furuno & Kawanabe 1967; Ando et al. 1977; Furuno et al. 1979

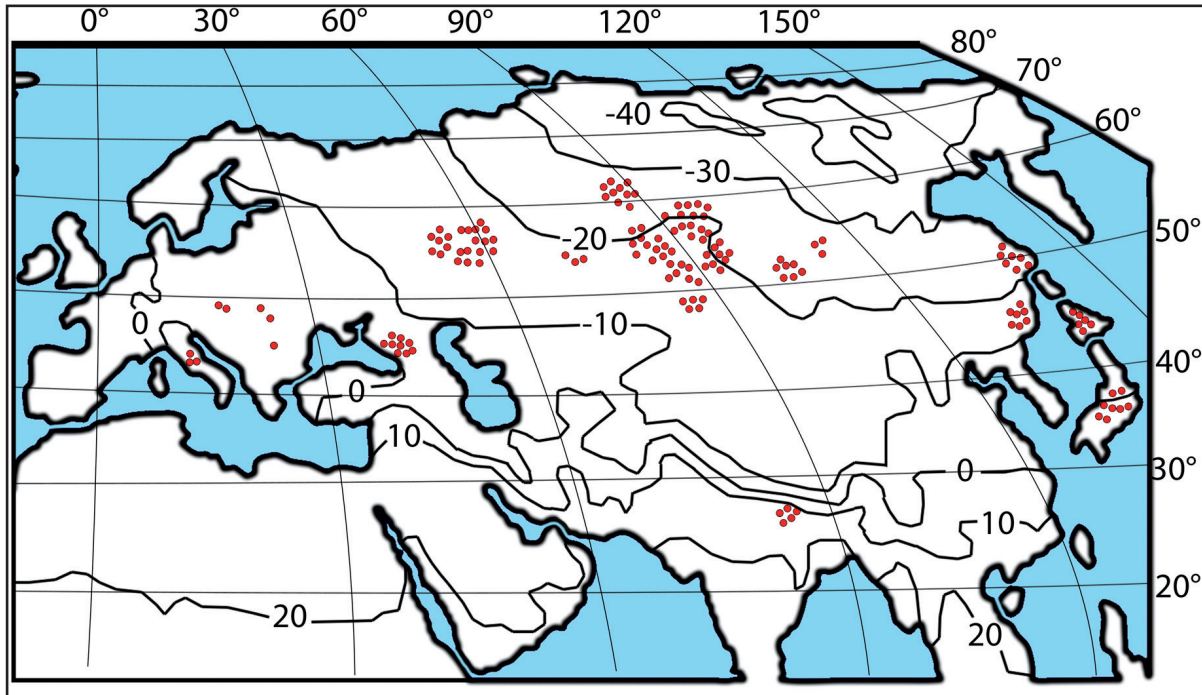


Fig. 1. Location of 272 *Abies* spp. for biomass sampling sites (in most cases biomass was determined specifically for each tree component; i.e. needles, branches, stem bark, stem wood, and roots) with regard to the mean January temperature [°C] (source: World Weather Maps 2007; see also https://store.mapsofworld.com/image/cache/data/map_2014/currents-and-temperature-jan-enlarge-900x700.jpg).

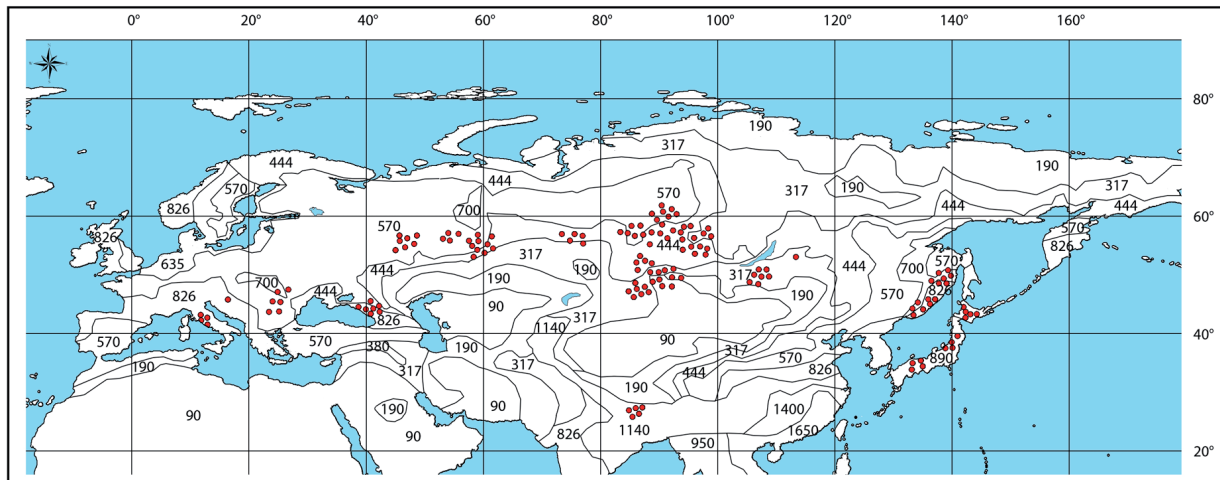


Fig. 2. Location of 272 *Abies* spp. biomass sampling sites (in most cases biomass was determined specifically for each tree component; i.e. needles, branches, stem bark, stem wood, and roots) with regard to the mean annual precipitation [mm] (source: World Weather Maps 2007; see also <http://www.mapmost.com/world-precipitation-map/free-world-precipitation-map/>).

stand biomass. In addition, the climate characteristics, namely mean January temperature and annual precipitation total, were included in the model to account for the impact of environmental conditions. The final model included only those variables that were found significant for all biomass components. Hence, the general regression equation was:

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

where P_i is biomass of i^{th} component, t per ha; A is stand age, yrs; V is stand stem volume above bark, m^3 per ha; N is tree number, 1000 per ha; i is index of biomass components as follows: total (t), aboveground (a), roots (r), crown (c), stem above bark (s), foliage (f), branches (b), stem wood (w), and stem bark (bk); PRm is mean annual precipitation total, mm; Tm is mean January temperature, °C. Since the mean January temperature at the northern limit of Eurasia is negative (Fig. 2), the corresponding independent variable was increased by 40 ($Tm+40$) to enable a logarithmic transformation according to Baskerville (1972). The problem of transforming the model (1) into a tabular form

is that we can specify only stand age, temperature, and precipitation, while stem volume and tree density can be obtained by a system of auxiliary recursive equations having the general form:

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

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

The regression coefficients of multiple regression equations [1], [2], and [3] were calculated using the Statgraphics software (see <http://www.statgraphics.com/> for more information).

First, an initial equation for the estimation of the total tree biomass was derived. Then, a three-step additive disaggregation system of equations was applied (e.g. Dong et al. 2015; Zheng et al. 2015). Hence, the total biomass estimated from the initial equation was divided into its constituent parts according to the scheme presented in Fig. 3. In the first step, the total tree biomass was divided into roots and the aboveground part in accordance with their shares in the total biomass represented by the corresponding component equations (step 1). Afterwards, the resulting aboveground biomass was divided in the same way into the crown and the stem above bark (step 2). Finally, the crown biomass was divided into foliage and branches (step 3a), and stem biomass into wood and bark (step 3b) (Fig. 3). Such an algorithm enables the simulation of a component structure of forest stand biomass despite different representation of the components in the total biomass, because their relative proportions are used as a basis instead of absolute values, which minimises the bias of estimates.

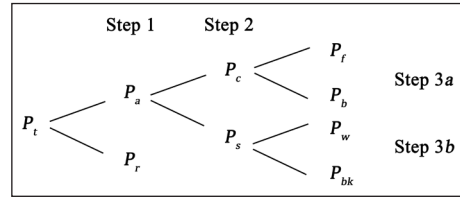


Fig. 3. The pattern of the disaggregating three-step proportional weighting additive model. Designation: P_t , P_r , P_a , P_c , P_s , P_f , P_b , P_w and P_{bk} represent stand biomass in t per ha as follows: total, underground (roots), aboveground, crown (foliage and branches), stems above bark (wood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

3. Results

The initial equations after the correction for logarithmic transformation by Baskerville (1972) and anti-log transforming are characterised by the significance level of at most 0.05 (Table 2). The equations represent the biomass data included in the above mentioned database. These equations were modified to the additive form according to the algorithm presented in Fig. 3. As a result, we obtained the final form of the transcontinental additive model of component composition of fir biomass, shown in Table 3.

The comparison of observed biomass with the predicted values using the initial (Table 2) and additive (Table 3) equations confirmed the adequacy of the

Table 2. Characteristics of initial models (1) after their anti-log transformation. Designation: A is stand age, yrs; V is stand stem volume above bark, m^3 per ha; N is tree number, 1000 per ha; PRm is mean annual precipitation total, mm; Tm is mean January temperature, $^{\circ}C$, P is stand biomass, t per ha, in biomass components as follows: total (t), aboveground (a), roots (r), crown (c), stem above bark (s), foliage (f), branches (b), stem wood (w), and stem bark (bk). The abbreviation $adjR^2$ is a coefficient of determination adjusted for the number of parameters; SE – equation standard error.

Biomass component	Initial model characteristics				
P_t	2.79E-02	$A^{0.1288}$	$V^{0.7793}$	$A^{0.0114 \ln(N)}$	$(Tm+40)^{0.5654}$
Step 1					
P_a	2.66E+03	$A^{0.0762}$	$V^{0.8415}$	$A^{0.0092 \ln(N)}$	$(Tm+40)^{-2.8453}$
P_r	1.98E-01	$A^{0.1440}$	$V^{0.7773}$	$A^{0.0289 \ln(N)}$	$(Tm+40)^{-1.0832}$
Step 2					
P_c	1.21E+06	$A^{0.0042}$	$V^{0.5849}$	$A^{0.0188 \ln(N)}$	$(Tm+40)^{-4.8792}$
P_s	1.19E+02	$A^{0.1163}$	$V^{0.9601}$	$A^{0.0060 \ln(N)}$	$(Tm+40)^{-2.1101}$
Step 3a					
P_f	1.04E-06	$A^{-0.1735}$	$V^{0.5351}$	$A^{0.0214 \ln(N)}$	$(Tm+40)^{3.3463}$
P_b	2.77E+09	$A^{0.1344}$	$V^{0.6633}$	$A^{0.0141 \ln(N)}$	$(Tm+40)^{-7.5829}$
Step 3b					
P_w	4.14E-10	$A^{0.2061}$	$V^{0.9849}$	$A^{0.0225 \ln(N)}$	$(Tm+40)^{6.0684}$
P_{bk}	3.40E+07	$A^{0.2179}$	$V^{0.7755}$	$A^{0.0345 \ln(N)}$	$(Tm+40)^{-6.0017}$
Biomass components	Initial model characteristics			$adjR^{2*}$	SE^*
P_t	$PRm^{0.4209}$	$(Tm+40)^{-0.0396 \ln(PRm)}$		0.961	1.16
Step 1					
P_a	$PRm^{-1.3083}$	$(Tm+40)^{0.4588 \ln(PRm)}$		0.971	1.15
P_r	$PRm^{-0.0796}$	$(Tm+40)^{0.1917 \ln(PRm)}$		0.868	1.34
Step 2					
P_c	$PRm^{-2.1828}$	$(Tm+40)^{0.7610 \ln(PRm)}$		0.805	1.32
P_s	$PRm^{-0.9855}$	$(Tm+40)^{0.3414 \ln(PRm)}$		0.983	1.13
Step 3a					
P_f	$PRm^{2.1635}$	$(Tm+40)^{-0.5177 \ln(PRm)}$		0.628	1.47
P_b	$PRm^{-3.5753}$	$(Tm+40)^{1.1677 \ln(PRm)}$		0.804	1.40
Step 3b					
P_w	$PRm^{2.8542}$	$(Tm+40)^{-0.8792 \ln(PRm)}$		0.978	1.13
P_{bk}	$PRm^{-3.3007}$	$(Tm+40)^{0.9810 \ln(PRm)}$		0.928	1.20

derived models, since they usually explained more than 50% of variability in biomass depending on the biomass component (Fig. 4). The variability of aboveground and stem biomass was captured well, as our equations explained more than 90% of observed variance (Fig. 4). High correlation between predicted and observed biomass was also observed for stem wood (R^2 of around 0.8), followed by roots, branches, and crown (R^2 of around 0.7). The model explained the least variability in the biomass of foliage and stem bark (Fig. 4).

The equations [2] and [3] derived from the data on fir stands were significant at a level of 0.05 and explained 68% and 61% of variability of number of trees and stand volume per ha, respectively (Table 4). As Fig. 5 shows, the biomass of all components in 100-year-old fir stands grows as mean annual precipitation total and mean January temperature increase.

Under an assumed increase in temperature by 1°C, the model results showed that more biomass was accumulated in 100-year-old fir stands regardless of precipitation conditions in comparison to current temperature conditions (Fig. 6). Similarly, an increase in precipitation by 100 mm resulted in the increase in biomass of fir stands under all temperature and precipitation combinations present in this study of Eurasia (Fig. 7). The exceptions were the patterns for the foliage and branches, for which a slight decrease of their biomass was estimated in warm climatic zones ($Tm = 10^\circ\text{C}$, Fig. 7) regardless of the existing level of precipitation.

4. Discussion

Our modelling suggested that biomass of all fir 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 $+10^\circ\text{C}$ (Fig. 5). 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 & Li 2011). However, this trend does not correspond to the results obtained using similar models for biomass quantification in two-needled pine forests of Eurasia (Usoltsev et al. 2019b). The pine models manifested different trends, since in cold zones ($Tm = -20^\circ\text{C}$) precipitation increase leads to a decrease of biomass, while in warm zones ($Tm = 10^\circ\text{C}$) to their increase, with the exception of root biomass. Correspondingly, temperature increase in wet areas ($PRm = 900$ mm) causes an increase of biomass in two-needled pine forests, while in dry areas ($PRm = 300$ mm) it causes their decrease, with the exception of roots. Derived additive models of fir stand biomass allow us to determine quantitative changes in the biomass structure due to the climate change, in particular, the mean January temperature and mean annual precipitation.

The change in the biomass structure is associated with the changes of these two climatic parameters. For example, if the mean January temperature in the central part of European Russia, characterised by the mean January temperature equal to -10°C and the mean annual precipitation equal to 400 mm (Fig. 1 and Fig. 2) is increased by 1°C, the model suggests that the biomass of all compo-

Table 3. Final three-step additive model of *Abies* forest biomass derived for Eurasia. Designation: *A* is stand age, yrs; *V* is stand stem volume above bark, m^3 per ha; *N* is tree number, 1000 per ha; *PRm* is mean annual precipitation total, mm; *Tm* is mean January temperature, $^\circ\text{C}$, *P* is stand biomass, *t* per ha, in biomass components as follows: total (*t*), aboveground (*a*), roots (*r*), crown (*c*), stem above bark (*s*), foliage (*f*), branches (*b*), stem wood (*w*), and stem bark (*bk*).

		Model	
		$Pt = 2.79\text{E-}02 A^{0.1288} V^{0.2793} A^{0.0114} \ln(N) (Tm+40)^{0.5654} PRm^{0.4209} (Tm+40)^{-0.0396} \ln(PRm)$	
Step 1	$Pa = \frac{1}{1+7.46\text{E-}05 A^{0.0678} V^{0.0642} A^{0.0197} \ln(N) (Tm+40)^{1.7621} PRm^{1.2287} (Tm+40)^{-0.2671} \ln(PRm)} \times Pt$		
	$Pr = \frac{1}{1+1.34\text{E+}04 A^{-0.0678} V^{0.0642} A^{-0.0197} \ln(N) (Tm+40)^{-1.7621} PRm^{-1.2287} (Tm+40)^{0.2671} \ln(PRm)} \times Pt$		
Step 2	$Pc = \frac{1}{1+9.87\text{E-}05 A^{0.1122} V^{0.3752} A^{-0.0128} \ln(N) (Tm+40)^{2.7691} PRm^{1.1973} (Tm+40)^{-0.4196} \ln(PRm)} \times Pa$		
	$P_s = \frac{1}{1+1.01\text{E+}04 A^{-0.1122} V^{-0.3752} A^{0.0128} \ln(N) (Tm+40)^{-2.7691} PRm^{-1.1973} (Tm+40)^{0.4196} \ln(PRm)} \times Pa$		
Step 3a	$Pf = \frac{1}{1+2.66\text{E+}15 A^{0.3079} V^{0.1283} A^{-0.0073} \ln(N) (Tm+40)^{-10.9291} PRm^{-5.7388} (Tm+40)^{1.6854} \ln(PRm)} \times Pc$		
	$Pb = \frac{1}{1+3.77\text{E-}16 A^{-0.3079} V^{-0.1283} A^{0.0073} \ln(N) (Tm+40)^{10.9291} PRm^{5.7388} (Tm+40)^{-1.6854} \ln(PRm)} \times Pc$		
Step 3b	$Pw = \frac{1}{1+8.23\text{E+}16 A^{0.0118} V^{-0.2094} A^{0.0120} \ln(N) (Tm+40)^{-12.0700} PRm^{-6.1548} (Tm+40)^{1.8602} \ln(PRm)} \times P_s$		
	$Pbk = \frac{1}{1+1.22\text{E-}17 A^{-0.0118} V^{0.2094} A^{-0.0120} \ln(N) (Tm+40)^{12.0700} PRm^{6.1548} (Tm+40)^{-1.8602} \ln(PRm)} \times P_s$		

Table 4. Characteristics of the recursive system of auxiliary equations for fir stand characteristics.

Stand characteristics	Equation				
Tree number per ha	1.05E+33	$A^{-1.1176}$	$\exp[9.5436 (1/A)]$	$(Tm+40)^{-25.1111}$	
Stand stem volume above bark	6.91E-05	$A^{0.7152}$	$N^{-0.4815}$	$(Tm+40)^{2.6481}$	
Stand characteristics		The auxiliary equations characteristics		adjR ²	SE
Tree number per ha	$PRm^{-9.9710}$		$(Tm+40)^{3.5812 \ln(PRm)}$	0.681	2.19
Stand stem volume above bark	$PRm^{1.5702}$		$(Tm+40)^{-0.3094 \ln(PRm)}$	0.613	1.76

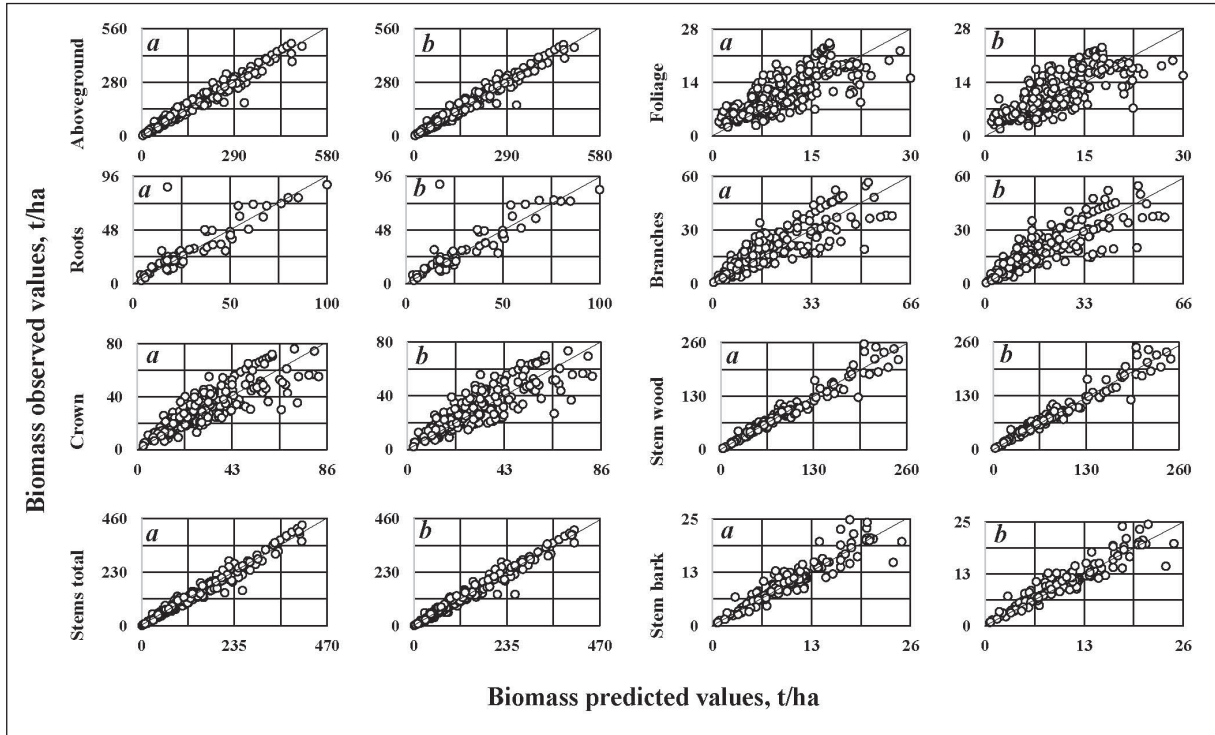


Fig. 4. Observed stand fir biomass plotted against predicted biomass obtained by calculating the initial (a) and additive (b) models.

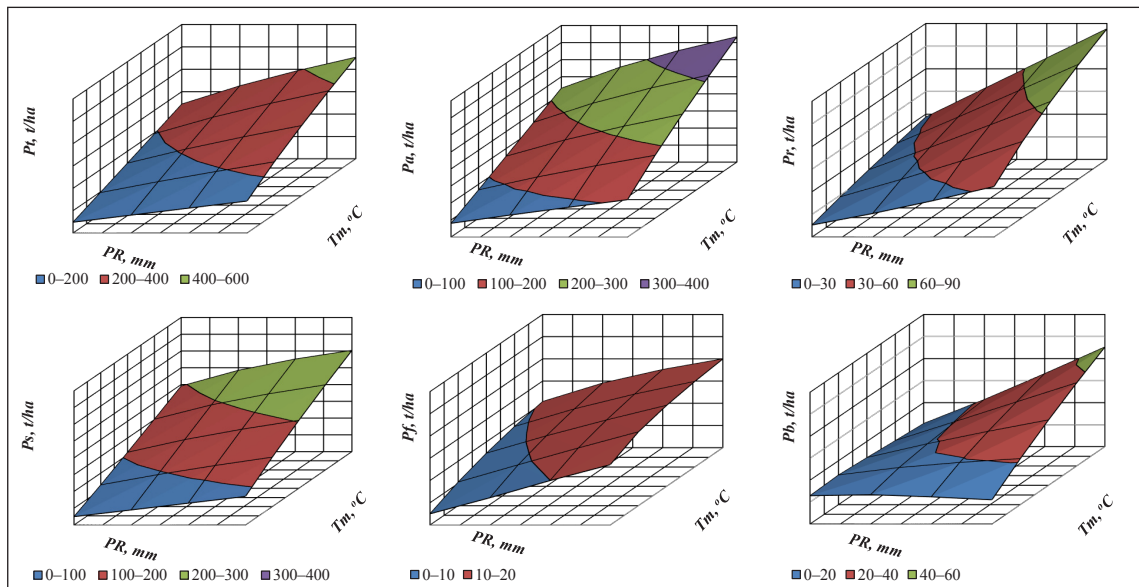


Fig. 5. The dependence of fir stand biomass upon mean January temperature (T_m) and annual precipitation (PR_m) at the stand age of 100 years. Designation: P_t , P_s , P_a , P_f , P_r , and P_b – total biomass, biomass in stems, aboveground, foliage, roots, and branches, t per ha, respectively.

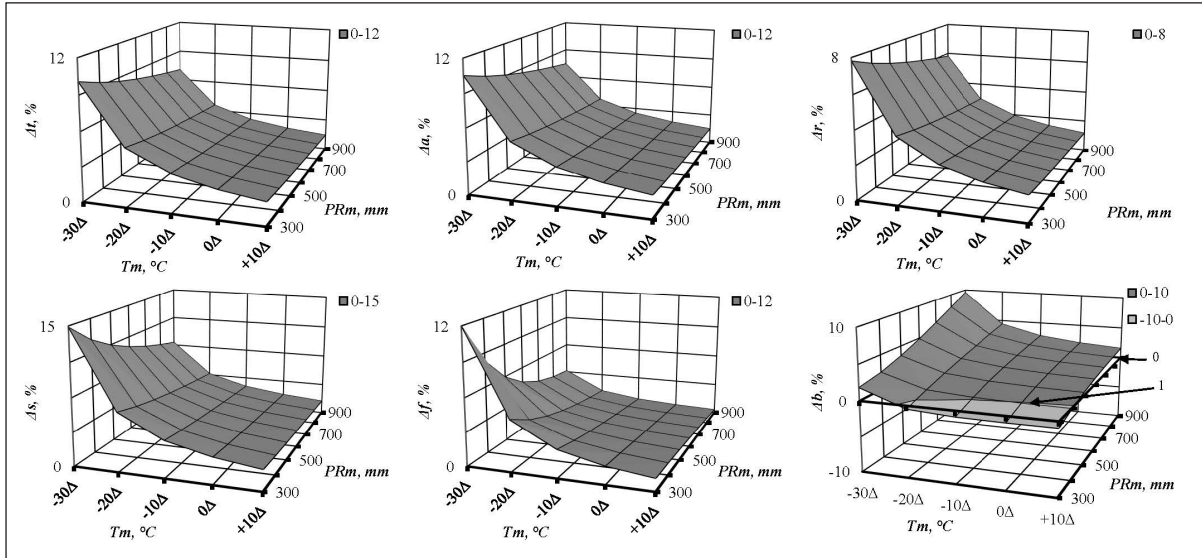


Fig. 6. Simulated changes in fir stand biomass due to the assumed temperature increase of 1°C based on the derived model (for the stands aged 100 years). T_m – mean January temperature, °C; PR_m – mean annual precipitation, mm. Temperature values on X axis designated as $-30\Delta\dots+10\Delta$ represent the mean January temperature increased by 1°C. The relative changes in individual biomass components (%) are marked as follows: total ΔP_t , aboveground ΔP_a , roots ΔP_r , stems ΔP_s , foliage ΔP_f and branches ΔP_b . The value 0 represents the plane corresponding to zero change of biomass at the expected temperature increase by 1°C; the value 1 represents the border between positive and negative changes in biomass ($\Delta, \%$) at the expected temperature increase by 1°C.

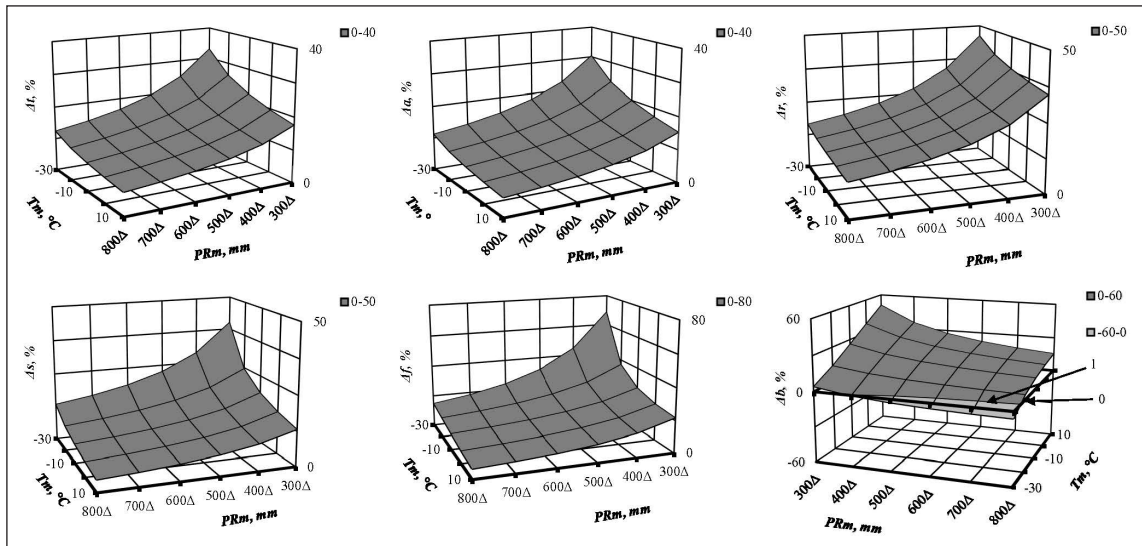


Fig. 7. Simulated changes in fir stand biomass due to the assumed precipitation increase of 100 mm (for the stands aged 100 years). T_m – mean January temperature, °C; PR_m – mean annual precipitation, mm. Precipitation values on X axis designated as $300\Delta\dots800\Delta$ represent the annual precipitation total increased by 100 mm. The relative changes in individual biomass components (%) are marked as follows: total ΔP_t , aboveground ΔP_a , roots ΔP_r , stems ΔP_s , foliage ΔP_f and branches ΔP_b . The value 0 represents the plane corresponding to zero change of biomass at the expected temperature increase by 1°C; the value 1 represents the border between positive and negative changes in biomass ($\Delta, \%$) at the expected temperature increase by 1°C.

nents in a 100-year-old stand would increase by 3.9, 3.8, 4.6, 3.8, 4.6, and 3.5 % in the case of total biomass, above-ground, roots, stems, foliage, and branches, respectively. Similarly, the increase in precipitation by 100 mm in the same region while keeping mean January temperature constant caused an increase in the total biomass, above-ground, roots, stems, foliage and branches by 12.5, 11.9, 15.3, 12.7, 1.4 and 1.9%, respectively. Our results show that both temperature and precipitation increases result in positive trends of biomass accumulation (Fig. 5). The exception is the foliage biomass, which in the warm zone ($T_m = +10^{\circ}\text{C}$) decreases with increasing precipitation during the transition from the regions of insufficient moisture ($PR_m = 300$ mm) to the regions of increased moisture ($PR_m = 900$ mm).

Here, we would like to point out that not only total quantity of forest stand biomass but also its allocation to individual tree components is important from carbon sequestration point of view. For instance, a ratio between foliage, i.e. a component with fast carbon turnover, and woody parts, i.e. long-run carbon turnover, determines the rate of carbon cycling via tree biomass (e.g. Šebeň et al. 2017). Moreover, the root to shoot ratio describes carbon proportion situated above ground and in the soil. Those two different environments represent contrasting conditions for wood decomposition and carbon emission after tree perishes (e.g. Laiho & Prescott 2004).

It is generally known that the efficiency of environmental object modelling depends on the level of implementation of a meaningful analysis of empirical data, i.e. on the studied level of impact factors changing in time and space. In relation to a single factor, this principle means identifying the most informative (active) range of its effects (Liepa 1980) in order to identify the optimal range within which the selected factor, ambiguous in its informativeness, would explain the largest proportion of variability of the resulting variable. Our study uses the winter temperature index as the most sensitive to climate change, and one can draw an analogy with a similar process at a global level: the temperature at the Earth poles increases at an accelerated rate compared to the mainland (Henderson 2006). In the future, the impact of temperatures representing different parts of the year should be tested and the most significant period should be used in the models.

Presented approach of biomass calculation ensures that the sum of component biomass amounts obtained from component equations is equal to the value of the total biomass calculated with the general equation. Two algorithms have been proposed for this purpose: (1) an “aggregation” method based on the principle “from the particular (i.e. from component equations) to the general” (Parresol 2001), and (2) a “disaggregation” method of proportional weighing based on the principle “from general to particular” (Dong et al. 2015). When comparing aggregation and disaggregation methods using the data from 122 sample trees, Dong et al. (2015) concluded

that although the results obtained by the two methods were similar, the second one led to a smaller standard error of regression coefficients. An advantage of our chosen disaggregated structure of the model is that it can be used for global or transcontinental modelling, because it uses climate variables as independent input, which cannot be included in the “aggregated” model (Parresol 2001). Another possible approach is to construct a system of regional equations and use dummy variables that specify particular ecoregions (Usoltsev et al. 2019a).

In order to understand possible impacts of climate change on forest biological productivity and to obtain sufficiently adequate simulation results of this relationship, it is necessary to provide empirical data on productivity and climate variables in the widest possible range of their variation, i.e. at global or continental levels. In a recent work (Zeller et al. 2018), geographical coordinates of sample plots, as well as annual precipitation and temperature were included in the model of forest productivity for the territories of Germany and the United States along with main defining independent variables. We contend that the evidence of the authors is contradictory because: (1) climate variables are correlated with geographical coordinates of sample plots in this model, and (2) the ranges of variability of climate variables within a country were too small to obtain stable patterns. To avoid such uncertain results, a transcontinental level of analysis was chosen in our study, and geographical coordinates were not included among independent variables.

The question may arise why modelling was performed at the level of *Abies* genus, and not for individual fir species. In the world affected by climate change, large-scale analyses are needed as they can provide us with general trends. The spatial distribution of individual *Abies species* in Eurasia is rather scattered and complementary (Savill et al. 2016), which does not allow for a large-scale analysis of individual species based on the available empirical data. In plant horology, this distribution is known as species substitution, or replacing of species, which occurs in the cases of paleo-geographically protracted dissociation of once continuous plant habitat (Hultén 1937; Tolmachev 1962) or due to the climatologically caused morphogenesis (Chernyshev 1974). A disadvantage of the database used in this study is the uneven spatial distribution of sampling sites over Eurasia (Fig. 2) resulting in different representation of individual ecoregions. Since in the regression analysis of biomass data we used the least squares method, estimates of biomass in ecoregions with a minimum number of sampling sites (Romania and the Czech Republic) may be biased due to the greater “information weight” of ecoregions with the largest numbers of sampling sites (Central Siberia and China). Methodological uncertainties causing biases in biomass amounts in individual tree parts may also affect the accuracy of the estimates. This applies primarily to the underground biomass. The analysis of the world data of underground tree biomass has showed that due to the

imperfection of methods to estimate fine root biomass, the total underground biomass of stands may be underestimated two to five times (Usoltsev 2018).

As is usually the case, the solution of each new problem and the corresponding removal of the associated uncertainty generates several new ones. In our case, two main uncertainties have arisen:

1) The patterns of biomass amount change under assumed changed climatic conditions (Fig. 6 and Fig. 7) are hypothetical. They reflect long-term adaptive responses of forest stands to regional climatic conditions and do not take into account rapid trends of current environmental changes, which place serious constraints on the ability of forests to adapt to new climatic conditions (Alcamo et al. 2007).

2) The presented patterns are related to fir forests, which are either pure or with a slight admixture of other tree species. However, fir usually grows in mixed stands (Bosela et al. 2018). There is a body of evidence that mixed stands are more resistant to stress caused by abiotic factors and are more productive than pure stands (Liang et al. 2016). However, a recent study of net primary production (NPP) of aboveground biomass from forests in Spain and Canada over a wide range of biodiversity index values as well as of mean temperature and moisture conditions (Paquette et al. 2018) led to a paradoxical conclusion. The authors found that in pure forest stands (low value of biodiversity index), NPP reacts to temperature rise of 1 – 2°C in different climatic zones in different ways: it grows in temperate forests, remains stable in boreal forests and declines in the Mediterranean forests. However, as the biodiversity index increases, these trends gradually transform into a unified negative trend, common for all zones (Paquette et al. 2018). This result indicates that the revealed trajectories of changes in biomass and NPP of pure (or almost pure) forest communities may not hold under the conditions of variable climate: in forests with an increased biodiversity index, the patterns can be significantly modified and even reversed.

Taking into account the stated methodological and conceptual uncertainties, the results presented in this study should be considered as preliminary ones. They can be modified if the biomass database will be enlarged by additional data, mainly site-specific and stand-specific characteristics. Moreover, further inherent phenomena of climate change (especially CO₂ concentration in the atmosphere) could be potentially included in future models if the corresponding data were available.

5. Conclusion

This paper presents a model for calculating stand biomass of fir species along the trans-Eurasian hydrothermal gradient. The model was derived from the biomass data of nearly 300 fir stands and climate data. We revealed that all biomass components of examined stands changed in the same direction: fir stand biomass increased with the

increasing precipitation within the evaluated range from 300 to 900 mm per year, as well as due to the increase in the mean January temperature from –30°C to +10°C regardless of the precipitation level. A modelled increase of January temperature by 1°C, or of precipitation by 100 mm, caused an increase in biomass of all components of fir stands. Our results indicate that fir would not suffer from the projected climate change. However, from the long-term perspective, climate change might bring even more drastic modification of winter temperature and annual sum of precipitation than was considered here. Therefore, our outputs represent a reasonable example of model sensitivity to changing climatic conditions. The development of such models for the main forest-forming species of Eurasia allow predicting changes in the productivity of the forest cover of Eurasia in relation to climate change.

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