

# Changes in foliage's biomass of two-needled pine subgenus (*Pinus* spp.) and genus *Betula* spp. along the gradients of winter temperature and precipitation: inter-genera paradox in the forests of Eurasia

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## Research

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## Abstract

## Background

The main pool of publications on this topic is related to the assessment of possible changes in vegetation growth under the influence of climate, but few of them actually took account the impacts of global change on species composition and morphological (taxational) structure, so led to an unanswered question, how the biological productivity of the forests will change if air temperature and/or precipitation change up to a certain extent. This is a subject of the study.

## Methods

In this study, our database is used in a number of 2,110 sample plots for pine and 510 for birch. In each sample plot, the biomass of the forest stands was positioned in maps of January mean temperature isolines and to mean annual precipitation ones, and the input data matrix was compiled in which the values of biomass components and of stand taxation characteristics are mated with corresponding values of climate indices. The matrix was then subjected to regression analysis.

## Results

It is stated, in cold and insufficiently moisture-rich climate zones, temperature increase causes a decrease in biomass of *Pinus* foliage, and in other regions its increase, but the *Betula* pattern is the opposite. With an increase in precipitation, the *Pinus* foliage biomass in warm zones increase, and in cold ones it decreases, but the *Betula* pattern is the opposite.

## Conclusion

The biomass of pine and birch stands change in gradients of winter temperature and precipitation as propeller-formed but opposite patterns, which can be explained by the different winter physiology of evergreen and deciduous species.

## Introduction

In recent decades, numerous world-wide studies have proved that the irreversible climate change would result in biota catastrophe and a problem with the survival of mankind (Emanuel et al., 1985, Toman et al., 1996, Behrensmeier, 2006, Halofsky et al., 2018, Kosanic et al., 2018, Miles-Novelo and Anderson, 2019, Xu et al., 2020). The main pool of publications on this topic is related to the assessment of possible changes in vegetation growth under the influence of climate, but few of them actually took account the impacts of global change on species composition and morphological (taxational) structure, so led to an unanswered question, how the biological productivity of the forests will change if air temperature and/or precipitation change up to a certain extent (Anderson et al., 2006, Keeling and Phillips, 2007, Eggers et al., 2008, Huston and Wolverton, 2009, Shuman, Shugart, 2009, Poudel et al., 2011, Han et al., 2018, Zeller et al. 2018), and how these altered forests will affect the gas composition of the atmosphere changed due to climate shifts. In other words, we are dealing with a typical rigid feedback scheme that is common to all complex biological systems (Abramova, 1968, P. 169).

Long before Charles Darwin, Russian academician Ivan Lepekhin proposed the idea of changing the properties of plants and animals under the influence of environmental changes. In the descriptions of his expedition across the Ural Mountains in Russia, he noted: "Plants and animals can get used to different climates and, depending on the habitat conditions, they can acquire properties that make their behavior reborn" (Lepekhin, 1780. P. 93). Though there is the common agreement that vegetation responses to climate change are species-specific (Schulze & Mooney, 1994, Spathelf et al., 2018), how the biological production of stands for certain tree species (genera) would be impacted in the Trans-Eurasian climatic gradients of temperature and precipitation is unknown, because the available regional information is fragmentary and contradictory (Strömngren, Linder, 2002, Wilmking et al., 2004, Huang et al. 2010, Stegen et al., 2011, Fu et al., 2017, Forrester et al. 2017).

It was reported that in Canada the temperature of January and humidity conditions had a positive effect on the growth of *Betula papyrifera*, and the growth of *Picea mariana* was positively affected by the winter and spring temperatures in the current year (Huang et al. 2010). High temperature and precipitation in growth season could depict positive impact on tree biomass (Zhou et al. 2008). Furthermore, extra sugar is stored in winter tree, which will be available for tree growth till next summer (LaMarche 1974). The dendroclimatological analyses showed that the positive moisture balance in current April and previous September was the dominant climatic factor favoring the radial growth of *Quercus cerris* in Albania (Stafasani, and Toromani, 2015). Some discrepancies in the regional responses of the studied species mean that regional patterns of stand productivity may be not necessarily extrapolated to the transcontinental level (Huang et al. 2010).

The dependence of the radial growth of European spruce, Scots pine and European beech trees on the climate and water balance of the soil was studied using data from 24 sample plots in Germany for the period from 1951 to 2006. By combining the obtained models with climate forecast data published by the IPCC expert group for the period up to 2100, a forecast of the dynamics of growth of three tree species up to 2100 is made. It turned out that for spruce, environmental conditions become more and more unfavorable over time, which leads to a gradual decrease in growth. For Scots pine and for beech, the negative effect on radial growth of simulated climate scenarios and soil water balance could not be detected until 2100 (Röhle et al. 2010). All of the above uncertain and contradictory patterns indicate that the results obtained were not reproducible. The lack of reproducibility of scientific results is a critical feature of modern science (Ioannidis 2005). A special study found that more than 70% of researchers tried and failed to reproduce the experiments of another scientist, and more than half of them failed to reproduce their own experiments (Baker 2016). At the same time, the limits of reproducibility in science are discussed (Guttinger 2020).

A paradoxical conclusion was reached in Russian Siberia with respect to forest cover (Lapenis et al., 2005), where with a warming climate and a simultaneous decrease in precipitation, the share of assimilation mass decreases, and the share of wood components increases. Even more, it was found that in pure forest stands, net primary production reacts to temperature increases in different climatic zones in different ways: it increases in temperate forests, remains stable in boreal forests, and decreases in wet forests in the Mediterranean, but as the biodiversity index increases, different zonal trends gradually transform into a common, unified negative trend. These patterns do not yet find any biological or ecological explanation (Paquette et al., 2018). In comparison with these uncertainties and contradictions, we obtained a much more surprising and paradoxical result when studying changes in the biomass of pine and birch foliage in the hydrothermal gradients of Eurasia, which is described in this article.

The two-needled subgenus (*Pinus* spp.) (the diploxylon, or hard pines) is divided into the predominantly Eurasian and Mediterranean section *Pinus*, composed of subsections *Pinus* and *Pinaster*, includes about 100 species spread in boreal and mid-latitude zones and also in the mountain regions of the subtropical zone of the northern Hemisphere (Gernandt et al., 2005). There are about 10 species in Russia. Of the two-needled pines, the Scots pine (*Pinus sylvestris* L.) is the most common in Eurasia and among conifers only larches occupy a bigger area than pines. This is a large evergreen whorl-branching light-demanding tree with a transparent crown. Its needle foliage is adapted to conservative water consumption, tolerates temperatures of -50 °C to + 50 °C and lives for 5–6 years long. At the Northern limit of Eurasia, its growth is limited by a small crop of cones and very low seed quality (Boychenko, 1970). The bark is thick, scaly dark grey-brown on the lower trunk, and thin, flaky and orange on the upper trunk and branches (Bobrov, 1978, Mamaev, 1983).

Birch belongs to *Betulaceae* family. This family has 120–150 species (Grimm and Renner 2013). Majority of species are present in northern zones and have a wide natural distribution area on the Eurasian continent, ranging from the Atlantic to eastern Siberia. Genus *Betula* spp. is among ten common species in Russia, and 40 its species are presented in Russia. It plays an important ecological role in the formation of woody vegetation throughout the Quaternary period (Denisov, 2002), and in dry steppe conditions with high ground water forms pure stands that are resistant to droughts (Perov, 2008). There are several species in the common birch category from the section *Albae* Rgl.: silver birch (*B. pendula* Roth.), downy birch (*B. pubescens* Ehrh.), mountain birch (*B. tortuosa* Ldb.) and Japanese white birch (*B. platyphylla* Sukacz.) (Hynynen et al. 2009, Usoltsev, 2019).

To reduce the uncertainty results mentioned above, a transcontinental level of analysis was chosen in our study. The purpose of this study was to show how much the foliage biomass of the light-coniferous subgenus *Pinus* spp. can change with a possible increase in temperature by 1 °C at constant precipitation and with a possible increase in precipitation by 100 mm per year at constant temperature, and to compare the results with similar data for small-leaved genus *Betula* spp. in Eurasia. Since the productive and carbon-depositing potential of a plant community is determined by the biomass of assimilating organs, we have focused in this article not on the total biomass of forest stands, but only on the mass of foliage.

## Material And Methods

The database used in this study involves 3,020 sample plots with *Pinus* and 650 sample plots with *Betula* stand biomass in tons per hectares, including both pure stands and stands with admixture of other species (Usoltsev 2020). Since the response to climate change differs between pure and mixed stands (Paquette et al., 2018), in our comparative study we used harvest data only from pure stands that were selected from our database in a number of 2,110 sample plots for pine and 510 for birch. Subgenus *Pinus* sp. is presented in 86% by Scots pine (*Pinus sylvestris* L.) and in smaller quantities by the following species: *P. tabuliformis* Carr. *P. densiflora* S. et Z., *P. nigra* Arn., *P. pinaster* Aiton, *P. brutia* var. *pityusa* (Steven) Silba, and *P. thunbergii* Parl. Of the 650 sample plots for *Betula*, about 80% are presented by white birches, i.e. silver birch (*Betula pendula* Roth) and downy birch (*Betula pubescens* Ehrh.) We are not able to distinguish in our database these two types of birch forests, differing in their ecology and possibly in their response to climate change (Hynynen et al. 2010). However, they are very adaptive to changes in their growth environment (Laitakari 1935, Köstler et al. 1968, Ostonen et al. 2007).

In most cases, sample trees were taken on each of sample plots in a number from 5 to 10 copies. 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) after drying the samples at the temperature of 80-100<sup>0</sup> C. The quantity of each biomass component per 1 ha was determined by regression method. 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. The locations of sampling sites are shown in Fig. 1. We can see that despite the different number of sample plots for *Pinus* and *Betula*, the coverage of the territory of Eurasia by these genera is approximately the same.

In each sample plot, the biomass of the forest stands was positioned in accordance to January mean temperature isolines and to mean annual precipitation ones, and the input data matrix was compiled in which the values of biomass components and of stand taxation characteristics are mated with corresponding values of mean January temperature and precipitation taken from World Weather Maps (2007). The matrix was then subjected to regression analysis.

The question may arise why modelling was performed at a level of genera, and not for individual pine and birch species. If we adhere to the concept of species-specific responses of forest biomass to changes in the main climatic characteristics, then when we reach the transcontinental level, we are faced with the obvious fact that no species grows throughout the continent, precisely because of regional climate differences. Moving from refuges under the influence of geological processes and climate changes, the particular species adapted to changing environmental conditions, forming a series of vicariate species within a genus (Hultén 1937, Tolmachev 1962, Chernyshev 1974). This gives grounds for analyzing the response of tree species to changes in climate characteristics, to combine them into one climate-dependent set within the entire genus, since differences in ecological and physiological properties of different species of the genus, for example, *Betula pendula* Roth vs. *B. utilis* D. Don vs. *B. maximowicziana* Regel are derived from regional climatic features.

It is well known that when estimating stem biomass growth by using the annual ring width, the greatest contribution to explaining its variability being made by summer temperature. Moreover, it was established that this relationship is positive with the maximum intra-annual temperature and negative with the minimum and average annual temperature (Khan et al. 2019). With an inter-annual time step, the predominant influence of summer temperature is quite normal (Levanič et al., 2015, Zubairov et al., 2018, Bocharnikov, 2019). But against the background of long-term climatic shifts for decades, the prevailing influence is acquired by winter temperatures (Toromani, Bojaxhi, 2010, Bijak, 2010, Morley et al., 2017), having in mind that

winter air temperatures in the Northern hemisphere were increased faster than in summer during the 20th century (Emanuel et al., 1985, Folland et al., 2001, Laing and Binyamin, 2013, Felton et al., 2016). This phenomenon may be associated with the shift of the earth's magnetic pole towards Siberia (Olsen and Manda 2007).

In terms of regression analysis, a weak temporal trend of summer temperatures compared to a steep trend of winter ones means a smaller regression slope and a worse ratio of residual variance to the total variance explained by this regression. Obviously, taking the mean winter temperature as one of the independent variables, we get a more reliable dependence having the higher predictive ability. 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 2003). In our example, mean January temperatures ranged from  $-40^{\circ}\text{C}$  in the forest-tundra of the North-Eastern Siberia to  $+10^{\circ}\text{C}$  in the subtropics of China. We compiled precipitation data ranging from 190 mm in permafrost regions of North-Eastern Siberia to 1,140 mm in South of China and to 2,500 in Greenland.

The matrix was used as a source of data (their fragment one can see in Table 1) in the subsequent regression analysis. It is well known that the biomass of a stand represented by a particular tree species is primarily determined by its age and morphological (taxation) structure, i.e., a set of characteristics such as age, mean height, mean diameter at breast height, the basal area, and the volume stock, which are interrelated. The problem of multi co-linearity arises in empirical modeling of biomass. One of the solutions to the problem is to harmonize the system by constructing recursive (recurrent, related) equations for the different mensuration indices and foliage biomass, in which the dependent variable of the previous equation is included as one of the independent variables of the subsequent one (Draper and Smith 1966). This approach as one of the methods for model harmonization (Jacobs and Cunia 1980), provides a multivariate conditionality of factors that provide flexibility and universality of the regression system describing the dynamics of biomass of stands.

Table 1  
A fragment of the original matrix of experimental data \*.

Pine forests						Birch forests					
A	N	V	P <sub>f</sub>	T <sub>m</sub>	PR <sub>m</sub>	A	N	V	P <sub>f</sub>	T <sub>m</sub>	PR <sub>m</sub>
20	2.275	15	1.4	-6	570	20	9.48	36	2.34	-5	800
25	3.838	50	2.69	-6	570	30	3.56	34	1.27	-5	800
25	4.516	60	1.63	-6	570	80	0.856	60	1.67	-7	570
23	3.640	94	5.06	5	730	25	4.00	88	1.50	5	800
31	2.370	174	8.28	5	730	30	2.85	115	1.40	5	800
35	1.890	210	9.83	5	730	79	2.15	23	1.20	-5	2500
55	0.760	206	7.24	5	730	23	2.68	127	2.43	-20	317
18	5.189	25	3.10	6	826	36	1.655	136	2.44	-20	317
28	3.608	65	4.80	6	826	60	0.918	224	2.71	-17	317
80	0.528	461	5.74	-4	570	100	0.500	97	2.78	-25	570
100	0.349	508	5.73	-4	570	46	0.513	32	0.37	-12	190
120	0.258	528	5.70	-4	570	35	0.600	164	1.95	-10	570
13	82.40	63	7.10	-15	260	60	1.640	172	3.40	-20	300
20	44.43	126	7.17	-15	260	37	3.930	83	3.51	-12	570
20	19.76	68	8.10	-15	260	40	3.440	75	3.25	-12	570
22	43.81	142	8.40	-15	260	55	1.886	294	3.42	-12	570
32	19.91	196	6.11	-15	260	75	0.880	389	3.23	-12	570
30	1.475	50	10.54	-10	500	69	1.765	410	8.96	-12	570
26	2.543	59	6.39	-10	500	71	0.686	22	0.48	-12	570
25	1.533	84	7.62	-10	500	20	12.08	32	2.39	-15	444
35	2.104	217	7.00	-5	980	80	8.250	16	1.20	-15	444
28	0.542	162	7.51	0	1300	12	35.00	41	3.70	-15	570
32	0.546	199	9.63	0	1300	24	5.925	104	5.65	-15	570
28	0.540	167	7.77	0	1300	46	1.015	148	3.67	-15	570
50	0.101	264	10.8	10	1140	85	0.315	328	3.55	-15	570
50	0.389	214	9.24	10	1140	55	0.625	237	3.38	-22	444
110	0.091	326	13.0	10	1140	70	0.777	195	2.67	-22	444
100	0.661	144	2.70	-12	444	90	1.870	11.6	0.28	-40	317
210	0.722	190	1.6	-12	444	90	0.706	92	0.7	-25	800

\* Designations here and further: A = stand age, yrs; V = stem volume, m<sup>3</sup>/ha; N = tree density, 1000/ha; P<sub>f</sub> = foliage biomass, t per ha; T<sub>m</sub> = mean January temperature, °C; PR<sub>m</sub> = mean annual precipitation, mm.

Pine forests						Birch forests					
25	1.329	88	5.2	-5	570	50	0.755	234	6.68	-5	570
29	1.707	169	6.6	-5	570	57	0.637	268	1.51	-5	570
18	36.93	93.2	6.3	0	890	43	0.900	131	1.48	-5	890
* Designations here and further: $A$ = stand age, yrs; $V$ = stem volume, m <sup>3</sup> /ha; $N$ = tree density, 1000/ha; $P_f$ = foliage biomass, t per ha; $Tm$ = mean January temperature, °C; $PRm$ = mean annual precipitation, mm.											

As for choosing the structure of the regression model, we adhered to the concept that there is only one definite variant of stand biomass structure corresponding to a given structure of taxonomic parameters (morphological structure) of a tree stand (Usoltsev 2007). The initial structure of the model included the main mass-forming indices of stands – age, stem volume, tree density, mean diameter and mean height. Mean diameter, and mean height were excluded in the process of the regression analysis as these factors were not statistically significant. The synergism  $(\ln A) \cdot (\ln N)$  was introduced in the model to account for the decrease in the tree density with age and its effect on the foliage biomass. The final structure of the model included only those mass-forming indices that were statistically significant for foliage biomass component.

## Results

The matrix was used as a source of data in the subsequent regression analysis, and after correcting on logarithmic transformation by G.L. Baskerville (1972), the recursive equations for the mensuration indices and foliage biomass were derived:

$$\ln N = f \{ \ln A, \ln(Tm + M), \ln PRm, [\ln(Tm + M)] \cdot (\ln PRm) \} \rightarrow$$

$$\rightarrow \ln V = f \{ \ln A, \ln N, (\ln A)(\ln N), \ln(Tm + M), \ln PRm, [\ln(Tm + M)] \cdot (\ln PRm) \} \rightarrow$$

$$\rightarrow \ln P_f = f \{ \ln A, \ln V, \ln N, (\ln A)(\ln N), \ln(Tm + M), \ln PRm, [\ln(Tm + M)] \cdot (\ln PRm) \}. \quad (1)$$

Equation (1) for foliage biomass is presented in Table 2. Because mean January temperature in northern part of Eurasia has negative values, the corresponding independent variable was increased by  $M$  ( $Tm + M$ ) to enable a logarithmic transformation according to (Baskerville 1972), where  $M = 40$  for *Pinus* and  $M = 50$  for *Betula*. All the necessary calculations were carried out in Stat graphics software (<http://www.statgraphics.com/>). First of all, we should pay attention to the signs for climate variables in the equations for pine and birch (Table 2). In the equations for the foliage biomass, the regression coefficients for the variables: temperature, precipitation and their combined effect (synergy) are equal to -3.6140, -1.6842 and + 0.5555 for pine and + 8.2177, + 4.3173 and - 1.2789 for birch, correspondingly, i.e. we have mirror patterns for the foliage biomass of pine and birch. These regression coefficients are significant at the probability level of 0.9999, and the corresponding values of  $t$ -Student are - 6.20, -5.31, and + 6.03 for pine foliage, and + 4.87, + 4.33, and - 4.68 for birch foliage.

Table 2  
Characteristic of equations (1) for forest stands of the *Pinus*, and *Betula* in Eurasia

$\ln(Y)^{(1)}$	$a_0^{(2)}$	$\ln A$	$\ln V$	$\ln N$	$(\ln A) \cdot (\ln N)$	$\ln(Tm + M)$	$\ln PRm$	$[\ln(Tm + M)] \cdot (\ln PRm)$	$adjR^{2(3)}$	$SE^{(4)}$
<i>Pinus</i>										
$\ln(N)$	2.8168	-1.0696	-	-	-	1.9165	0.5011	-0.3577	0.566	0.72
$\ln(V)$	16.4304	0.7200	-	-0.7996	0.2065	-3.3579	-2.5007	0.6225	0.472	0.69
$\ln(Pf)$	11.8492	-0.3495	0.4313	0.1311	-0.0289	-3.6140	-1.6842	0.5555	0.424	0.36
<i>Betula</i>										
$\ln(N)$	-14.3298	- 1.7556	-	-	-	4.9674	4.1687	-0.9833	0.715	0.75
$\ln(V)$	-26.8621	0.7441	-	-0.4407	0.1195	8.0501	4.4803	-1.2297	0.707	0.47
$\ln(Pf)$	-29.6226	-0.0321	0.5605	0.2644	-0.0287	8.2177	4.3173	-1.2789	0.425	0.42
Designations for Table 1:										
<sup>1</sup> Dependent variables; <sup>2</sup> The constant corrected for logarithmic retransformation by: Baskerville (1972); <sup>(3)</sup> $adjR^2$ – determination coefficient adjusted for the number of variables; <sup>(4)</sup> $SE$ – standard error of the equations.										

The proportions of the contribution of independent variables to the explanation of the variability of the forest biomass in equations (1) are shown in Table 3. We can see that mass-forming variables explain in averaged about 78, and 61% of the variability of foliage biomass in *Pinus*, and *Betula* correspondingly, including 47, and 39% of the contribution from the stem volume. Climate variables explain about 22, and 39% of the foliage biomass variability in *Pinus*, and *Betula* correspondingly, i.e. less than about 3.5, and 1.6 times as much as mass-forming variables in *Pinus*, and *Betula* correspondingly.

Table 3  
Contribution of independent variables of equations (1) to the explanation of variability of dependent variables, %

$\ln(Y)$	Independent variables								
	$\ln A(I)$	$\ln V(II)$	$\ln N(III)$	$(\ln A) \cdot (\ln N)(IV)$	I + II + III + IV	$\ln(Tm + M)(V)$	$\ln PRm(VI)$	$[\ln(Tm + M)] \cdot (\ln PRm)(VII)$	V + VI + VII
<i>Pinus</i>									
$\ln(Pf)$	22.4	47.3	4.3	3.6	77.6	7.9	6.8	7.7	22.4
<i>Betula</i>									
$\ln(Pf)$	1.5	38.6	15.0	5.5	60.6	13.8	12.3	13.3	39.4

The recursive system of Eq. (1) was tabulated in the sequence indicated by the arrows as follows: first, the values of tree density according to the given values of age, temperature and precipitation were obtained, then the volume stock according to the given values of age, temperature and rainfall and the calculated values of the tree density were obtained, and finally, the values of the foliage biomass according to the given values of age, temperature and precipitation, the calculated values of tree density and the volume stock were obtained. From the resulting tables, the values of the foliage biomass for the age of maturity (100 years for pine and 50 years for birch) are taken, and 3-D graphs showing statistically significant transcontinental trends of biomass in temperature and precipitation gradients are designed (Fig. 2).

## Discussion

We can see in Fig. 2 that there are two patterns of significantly differential changes in the pine and birch foliage biomass in precipitation and winter temperature gradients in the form of two oppositely directed propellers. The most interesting question is how much the foliage biomass would change with an air temperature deviation from the usual norm, for example, by 1 °C and with a precipitation deviation from the usual norm, or by 100 mm per year. The constructed models give us the answer to such question in relation to pine and birch stands. To do this, we took the first derivative of 3-Dimensional surfaces (Fig. 2), and not analytically, but graphically, i.e. we took off the biomass difference interval ( $\Delta$ , %) corresponding to temperature interval 1 °C and precipitation interval 100 mm directly from the graphs or from the corresponding tables, and get the answer in the form of 3-Dimensional surfaces divided into plus and minus areas that correspond to the increase or decrease in the biomass of stands having the age of 100 years for *Pinus* (Fig. 2a) and 50 years for *Betula* (Fig. 2b). 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  $-30\Delta$  ( $-40\Delta$ ) ...  $+10\Delta$  ( $0\Delta$ ). It is also assumed that climate change does not affect temperatures, which change only geographically (by ecoregions), while as a result of expected climate change, annual precipitation increases by 100 mm at various territorial precipitation levels, designated as  $300\Delta$  ...  $900\Delta$ .

Figure 3a shows the change in *Pinus* foliage biomass ( $\Delta$ , %) with a temperature increase of 1 °C in different ecoregions characterized by different temperature and precipitation ratios. Thus, Fig. 3a demonstrates a common pattern in *Pinus* of the Eurasian scale: in cold ( $T_m = -30$  °C) and insufficiently moisture-rich ( $PR_m = 300-400$  mm) climate zones, temperature increase with constant precipitation causes a decrease in biomass of foliage (the location of the increment surface below the zero plane), and in other regions - its increase (the location of the increment surface above the zero plane). In the contrary, Fig. 3b demonstrates a common pattern in *Betula* of the Eurasian scale: in cold ( $T_m = -30$  °C) and insufficiently moisture-rich ( $PR_m = 300-400$  mm) climate zones, temperature increase with constant precipitation causes an increase in biomass of foliage (the location of the increment surface above the zero plane), and in other regions - its decrease (the location of the increment surface below the zero plane).

Figure 4a shows the change ( $\Delta$ , %) in the *Pinus* foliage biomass with an increase in precipitation of 100 mm in different ecoregions. In warm zones (0 °C to 10 °C), with an increase in precipitation of 100 mm, foliage biomass increase (the location of the increment surface above the zero plane), and in cold ones ( $\approx 20$  °C to  $\approx 30$  °C) it decreases (the location of the increment surface under the zero plane). In contrary, Fig. 4b demonstrates a common pattern in *Betula* of the Eurasian scale: in cold ( $T_m = -40$  °C) and insufficiently moisture-rich ( $PR_m = 300-400$  mm) climate zones, temperature increase with a constant precipitation causes an increase in foliage biomass (the location of the increment surface above the zero plane), and in other regions - its decrease (the location of the increment surface below the zero plane).

We can see in Fig. 2a, that pine forests show a monotonous increase in foliage biomass in the gradient of temperature increase but only when there is sufficient water supply ( $PR_m = 900$  mm), and as the transition from moist areas ( $PR_m = 900$  mm) to areas of nonsufficient water supply ( $PR_m = 300$  mm), the trend changes to the opposite (Fig. 2a). In the gradient of increasing precipitation, pine forests show a monotonous increase in foliage biomass but only in cold areas ( $T_m = -30$  °C), and as the transition from cold areas to warm ones ( $T_m = 10$  °C), the trend changes to the opposite (Fig. 2a). A similar general pattern was observed earlier at the local level in the marsh forests of Siberia, where 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 and Litvinenko, 1976). According to the results obtained by Molchanov (1976), in the North of Eurasia the greatest influence on the growth of the annual tree ring is the air temperature, and in the conditions of the southern forest-steppe the dominant role is played by precipitation.

It is well known the Liebig's law of the minimum (1840), according to which a growth rate depends on the factor that is at the minimum in relation to its needs. Although J. Liebig, followed by J. Esslen (1905), had shown that a limiting factor can be not

only a lack, but also an excess of such factors as light, heat and moisture (a lot of "good" is also "not good"), nevertheless, he focused his attention mainly on the effect of the minimum of chemicals (oxygen, phosphorus, boron, etc.), and as a result of that, this phenomenon was established in science as the law (principle) of the minimum by Liebig. The idea of the limiting influence of the maximum on a par with the minimum was developed by V. Shelford (1913), who extended the limiting principle to any environmental factors and became known as the author of Shelford's law of tolerance. W.P. Taylor (1934) followed the same concept. Later A.A. Molchanov (1971) interpreted the limiting principle in relation to forest ecosystems as an "extended concept of limiting factors", according to which "any state approaching or exceeding the limit of resistance for any organism and groups of interest can be considered as a limiting factor" (p. 271). Recently, this phenomenon has become widespread as the principle of limiting factors by Liebig-Shelford (Rozenberg et al., 2016). The reaction of pine foliage biomass (Fig. 2) on temperature and precipitation corresponds to the principle by Liebig-Shelford: since the minimum values of biomass occur in regions with minimum precipitation ( $PR_m = 300$  mm) in warm climate and minimum temperature ( $T_m = -30$  °C) with sufficient water supply, these two factors are limiting in relation to pine foliage biomass.

At the same time, birch demonstrates the opposite 3-D pattern under the same conditions, i.e. the minimum values of biomass occur in regions with minimum precipitation ( $PR_m = 300$  mm) in warm climate and minimum temperature ( $-40$  °C) with nonsufficient water supply. As we can see from Fig. 1, the areas of the sample areas distribution in Eurasia are approximately the same, and therefore the presented temperature and precipitation ranges for pines and birches are the same, and, consequently, the limits of applicability of the models for pines and birches are the same. However, the biomass of birch stands in the database is 4 times less than that of pine, but even if we equalize the harvest data pools for pines and birches, the limits of applicability of the models will not change, and, of course, this will not lead to a change of signs in birches for independent variables - temperatures, precipitation, and their synergy. Then what can be the reason for the opposite trends in foliage biomass in pine and birch, which are statistically significant probability level reaches 0.9999, i.e.  $p\text{-value} < 0.00001$ .

Let us try to link the obtained counterintuitive patterns of changes in foliage biomass with previously published Trans-Eurasian trends in foliage productivity as the ratio of annual growth in the stem volume or aboveground biomass to the biomass of the assimilation apparatus. It is known as foliage efficiency (FE) (Usoltsev et al., 2018). It was found that in the direction from the northern moderate zonal belt to the subequatorial one, FE increases in pine and decreases in birch in the same zonal range. This phenomenon seems to be related to the fundamental difference between the winter physiology of evergreen and deciduous species, namely the ability of the former to assimilate atmospheric carbon dioxide and prolong the assimilation process beyond the vegetation period, which is usual for deciduous species (Jumelle, 1892, Ewart, 1896, Matthaei, 1902, Henrici, 1921, Iwanoff, Kossowitsch, 1929, Zacharowa, 1929, Ivanov & Orlova 1931, Printz, 1933, Cartellieri, 1935, Ålvik, 1939, Freeland, 1944, Zeller, 1951, Pisek, Rehner, 1958, Pisek, 1960, Lyr et al. 1974, Kramer & Kozlovsky 1983, Schaberg et al., 1995, Wieser, 1997, Smashevskiy, 2014).

In pine trees in the southern direction, due to higher winter temperatures, the winter accumulation of assimilates increases as a result of excess of photosynthesis over respiration, which is associated with the autumn-winter litter fall of foliage (Zalesov, et al., 1994), which apparently determines the trend of increasing FE in the direction from the northern temperate zone to the subequatorial one.

In birch trees, FE in the direction from the northern temperate to the subequatorial zone does not increase, as in pine, but decreases, possibly due to an increase in the respiration losses during a shorter physiologically active period (due to leaf shedding) compared to pine. In essence, everything depends on the ratio of photosynthesis and respiration in the pine, especially during the period when the birch does not have photosynthesis, but only respiration. If we assume the presence of a positive ratio of foliage biomass and FE, then in our case, the opposite FE trends of two species coincide with opposite trends in foliage biomass, but only in regions of sufficient moisture ( $PR_m = 800\text{--}900$  mm) (Fig. 2a, b), and as we move to areas of insufficient moisture ( $PR_m = 300$  mm), this coincidence is replaced by a complete contradiction.

The differences between pine and birch in FE values are also apparent as the climate continentality (summer aridity of the climate) increases: FE decreases most intensively in pine forests, and significantly less intensively in birch communities. As

the continentality index by Khromov (1957) increases from 55 to 95%, the FE in pine decreases by 8 times, and in birch the corresponding decrease in FE is less than 2%. The decrease in foliage biomass coincides with the decrease in FE as the climate increases in aridity only in pine trees and only in warm regions ( $T_m = 0$  to  $10$  °C), and when moving to cold regions, this coincidence is replaced by a complete contradiction. For birch, the decrease in leaf biomass as the climate increases in aridity coincides with a decrease in FE only in cold regions ( $T_m = -30$  to  $-40$  °C), and as the transition to warm regions, this coincidence is replaced by a complete contradiction.

The patterns of biomass amount change under assumed changed climatic conditions (Figs. 2–4) 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 (Givnish, 2002, Berner et al., 2013, Schaphoff et al., 2016, Spathelf et al., 2018, Vasseur et al., 2018, DeLeo et al., 2020, Denney and Anderson, 2020). The law of limiting factors (Liebig 1840, Shelford 1913) works well in stationary conditions. With a rapid change in limiting factors (such as air temperature or precipitation), forest ecosystems are in a transitional (non-stationary) state, in which some factors that were still not significant may come to the fore, and the end result may be determined by other limiting factors (Odum, 1971, Du et al., 2019).

The main pool of our harvest data on forest biomass in Eurasia were obtained since 1970s to 1990s, and the climate maps used cover the period of the late 1990s and early 2000s. Some discrepancy between the two time periods may cause possible biases in the results obtained, but for such a small time difference in the initial data, the inclusion of compensatory mechanisms or phenological shifts in forest communities is unlikely (Anderegg et al., 2019, DeLeo et al., 2020). There is an uncertainty in assessing the impact of phenology on the biological productivity of stands, established for the cherry oak in the South of Russia: if the assessment of the biomass of oak stands did not reveal differences between the phenological varieties of oak, then the assessment of net primary production shows a 1.6-fold advantage of late-blooming variety over the early-blooming variety (Zhou Wen Nan, 1992).

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 site-specific and stand-specific data. A full explanation for both the obtained regularities and counterintuitive results can be obtained after conducting detailed physiological studies.

## Conclusions

A comparison of the reaction of pine and birch foliage biomass to changes in the average January temperature by  $1$  °C at constant precipitation and average precipitation by  $100$  mm per year at constant temperature showed counterintuitive result. If low temperature and heavy precipitation are the limiting factors for pine leaf biomass, then low temperature and insufficient precipitation are the limiting factors for birch. When the temperature increases by  $1$  °C, the change in leaf biomass in pine, which is negative in dry conditions, becomes positive in wet conditions, and in birch, a positive change in dry conditions becomes negative in wet conditions. When precipitation increases by  $100$  mm, the change in leaf biomass in pine trees that is negative in cold regions becomes positive in warm regions, and in birch trees, the positive change in leaf biomass in cold regions becomes negative in warm regions.

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 just an example of model sensitivity to changing climatic conditions. The development of such a model for the main forest-forming species of Eurasia allow us to predict changes in the foliage productivity of the forest cover of Eurasia in relation to climate change.

## Declarations

# Availability of data and materials

The datasets used and/or analysed during the current study are available at: <https://elar.usfeu.ru/handle/123456789/9648>

## Ethics approval and consent to participate

Not applicable.

## Consent for publication

Not applicable.

## Competing interests

The authors declare that they have no competing interests.

# Authors' contributions

Vladimir Andreevich Usoltsev and Baozhang Chen participated in study design, data processing, interpreting the results and writing the manuscript. Peng Leng took part in the

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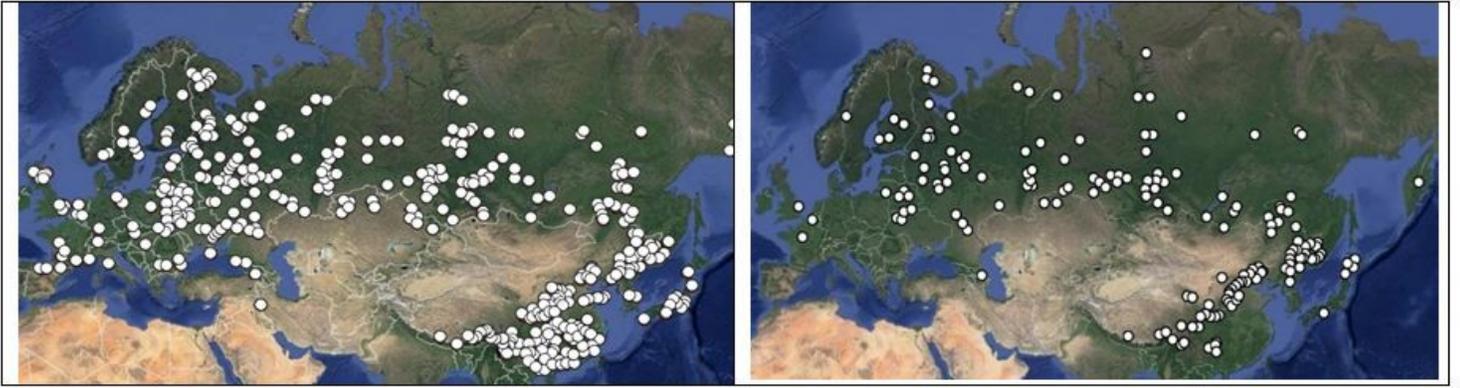
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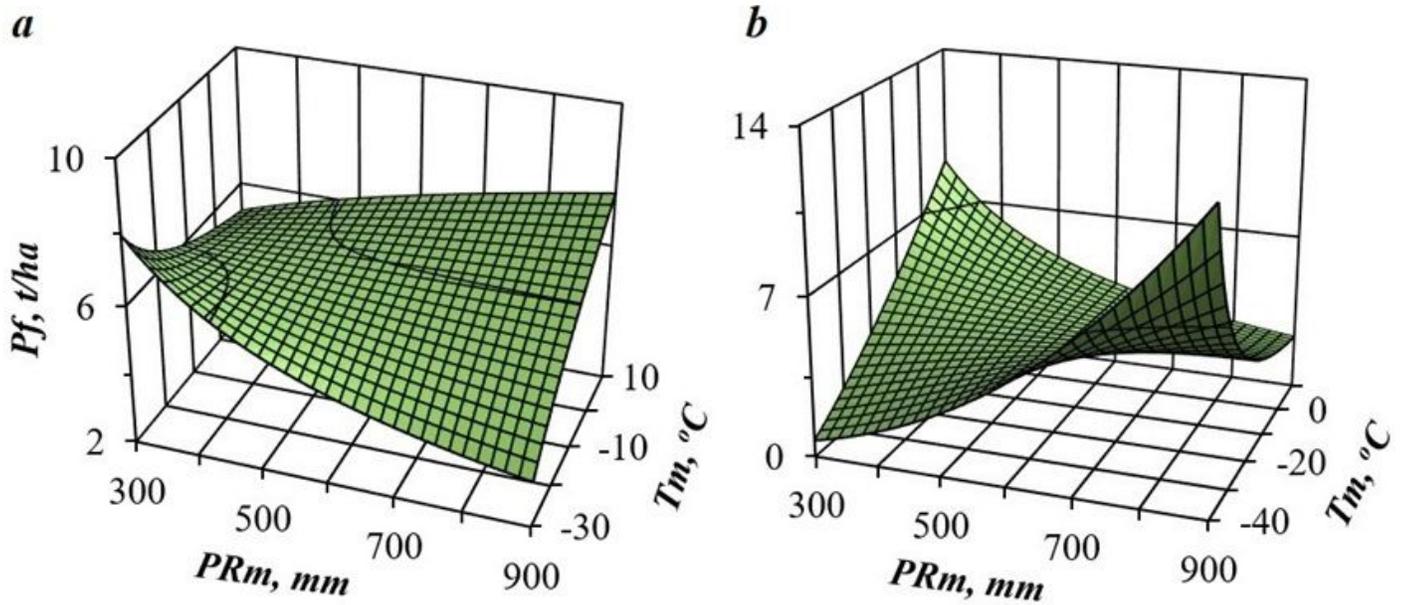
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## Figures



**Figure 1**

The distribution of 2,110 sampling sites of *Pinus* (left hand side) and 510 sampling sites of *Betula* (right hand side) on the territory of Eurasia.



**Figure 2**

Dependence of pine a and birch b forest biomass ( $P_f$ ) of Eurasia upon the mean January temperature ( $T_m$ ) and mean annual precipitation ( $PR_m$ ).

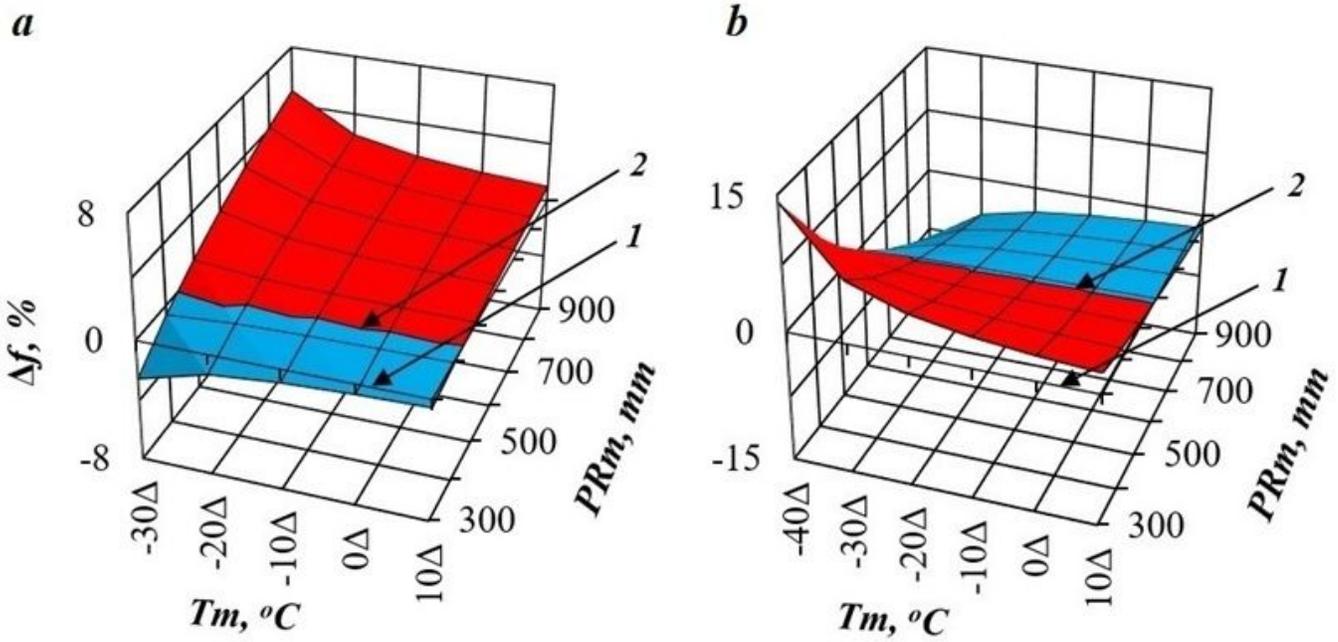


Figure 3

Simulated changes in pine a and birch foliage biomass due to temperature increase of 1°C based on the derived model (for the stands aged 100 years). Here the value 1 represents the plane corresponding to zero change of biomass at the expected temperature increase by 1°C; the value 2 represents the border between positive and negative changes in biomass ( $\Delta$ , %) at the expected temperature increase by 1°C.

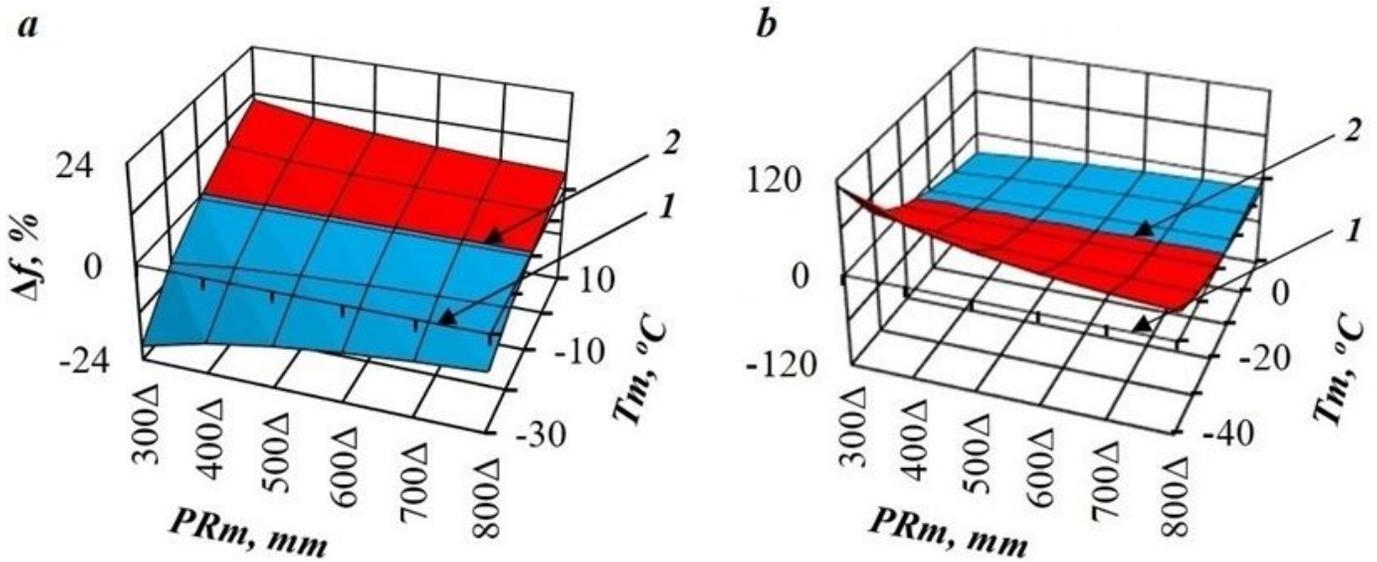


Figure 4

Simulated changes in pine a and birch b foliage biomass due to the assumed precipitation increase of 100 mm (for the stands aged 50 years).