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Article

Foliage biomass of the genera *Picea* spp. and *Quercus* spp. in winter temperature and annual precipitation gradients: Inter-genera paradox in the forests of Eurasia

V. A. Usoltsev[2,3], **H. Lin**[1,4,5,6] , **S.O. R. Shobairi**[1], **I. S. Tsepordey**[3], **Z. Ye**[1,4,5,6]

[1]Research Center of Forestry Remote Sensing & Information Engineering, Central South University of Forestry and Technology, Changsha 410004, China

[2]Ural State Forest Engineering University, Faculty of Forestry, Sibirskiy Trakt, 37, 620100 Yekaterinburg, Russia

[3]Botanical Garden of Ural Branch of RAS, Department of Forest Productivity, ul. 8 Marta, 202a, 620144 Yekaterinburg, Russia

[4]Key Laboratory of Forestry Remote Sensing Based Big Data & Ecological Security for Hunan Province, Changsha 410004, China

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

[6]Changsha Changchang Forestry Technology Consulting Co., Ltd., Changsha 410004, China

E-mails: Usoltsev50@mail.ru, linhui@csuft.edu.cn, Omidshobeyri214@gmail.com, common@botgard.uran.ru, 1053460198@qq.com

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Abstract

Current climate change make it increasingly important to assess the response of forest cover biomass to this change, which in turn determines the possibility of climate stabilization by reducing atmospheric CO_2. Climate change projections can been linked to significant changes in water deficits and natural disturbance regimes in forest ecosystems across many parts of the world.Since the carbon-deposing potential of a plant community is determined by the biomass of assimilating organs, we focused in this article on comparative analysis of foliage biomass in the dark-coniferous genus *Picea* spp. and of leaved genus *Quercus* spp. in gradients of annual precipitation and winter temperature on the territory of Eurasia. The database for modelling involves 870 and 570 sample plots for spruce and oak correspondingly. When studying changes in the biomass of spruce and oak foliage in the hydrothermal gradients of Eurasia, we obtained statistically reliable, but surprising and paradoxical results. When the temperature increases by 1°C, the most increase in spruce foliage biomass occurs in cold regions with insufficient moisture supply, while oak leaf biomass, on the contrary, has the largest percentage of its decrease. In cold regions, as the transition from dry conditions to wet ones, the percentage of foliage mass in spruce decreases, and in oak increases. When the precipitation increases by 100 mm, there is the opposite patterns for spruce and oak: in warm regions, spruce has a decrease in the percentage of foliage mass, and oak, on the contrary, its increase. In the cold regions, these patterns change to the opposite: the spruce negative percentage changes to positive, and the oak positive percentage changes to negative. This phenomenon seems to be related to the positive ratio of photosynthesis and respiration in the spruce during the winter period when the oak does not have photosynthesis, but only respiration. It 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. The development of such models 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.

Keywords hydrothermal gradients; foliage biomass; foliage efficiency; regression models; biomass equations; mean January temperature; annual precipitation.

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1 Introduction

The basis for the functioning of the biosphere is its biological productivity, and the life of humans and all heterotrophic organisms depends on it, but only in the last 50-60 years the idea of the biosphere's productive capacity has gone beyond "enlightened guesses" and received some quantitative confirmation (Whittaker et al., 1975). The main pool of recent publications on forest biomass is related to the assessment of possible changes in vegetation cover under the influence of climate, but most of them consider global estimates without taking into account the species composition, age and morphological structure, which do not answer the question of how the biological productivity of the planet's forest cover will change if the temperature changes by a certain number of degrees or precipitation changes by a certain number of mm (Anderson et al., 2006; Keeling and Phillips, 2007; Eggers et al., 2008; Huston and Wolverton, 2009; Shuman and Shugart, 2009; Poudel et al., 2011; Han et al., 2018; Zeller et al. 2018).

At the level of forest communities, numerous studies of biomass structure are related to climate variables (Lieth, 1974; Monserud et al., 1996; Ni et al., 2001; Lapenis et al., 2005; Shuman et al., 2011; Stegen et al., 2011; Poudel et al., 2011; Pretzsch et al., 2012; Lewis et al., 2013; Berner et al., 2013; Frank et al., 2015; Schaphoff et al., 2016; Fang et al., 2016; Dong and Liu, 2017;Wang et al., 2017; Gu et al., 2017; Gustafson et al., 2017; Duan et al., 2018; Paquette et al., 2018; Sippel et al., 2018; Teets et al., 2018; Wang et al., 2018; Sperry et al., 2019; Khan et al., 2019a, b; Dolezal et al., 2021). 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 regional information is fragmentary and contradictory (Strömgren and Linder, 2002; Wilmking et al., 2004; Huang et al. 2010; Stegen et al., 2011; Fu et al., 2017; Forrester et al. 2017; Reichstein and Carvalhais, 2019).

However, there is the common agreement that vegetation responses to climate change are species-specific (Schulze and Mooney, 1994; Spathelf et al., 2018). It is well known that tree species (genera) occupy specific ecological niches and react differently to short-term stressful situations (Kusmin, 1930; Vassiljev, 1931; Gower and Richards, 1990; Suvorova et al., 1999; Suvorova, 2009; Sudachkova et al., 2012), and on long-term climate change too, but in the latter cases the plant trait responses are not only species (Pucko et al., 2011; Buckley and Kingsolver, 2012; Parmesan and Hanley, 2015; Gray and Brady, 2016; Baruah et al., 2017) but also community-specific ones (Dymond et al., 2016; Baruah et al., 2017; Noce et al., 2019; Ye et al., 2022).

It is believed that coniferous and deciduous species of the temperate zone do not differ in net primary production (Schulze, 1982; Reich and Bolstad, 2001). Since these two different functional types of forests are adapted to specific forest conditions and may occupy different ecological niches, the same type of forest conditions may, for example, be more suitable for coniferous than for deciduous, and vice versa (Givnish, 2002). Coniferous species are more adapted to harsh habitats that have a slow cycle of substances, which allows them to limit the amount of assimilates entering the needles. Deciduous species are often more adapted to a mild climate that provides an accelerated cycle of nutrients, which is necessary for deciduous species to meet the increased cost of annual leaf replacement (Schulze, 1982). Nevertheless, net primary production was consistently larger for deciduous than for evergreen boreal forests in each of the major boreal regions, especially for boreal forests in Alaska (Gower et al., 2001).

In comparison with these uncertainties and contradictions, we obtained a much more surprising and paradoxical result when studying changes in the foliage biomass of larch and pine in the hydrothermal gradients of Eurasia, which is described in this article.

The genus *Picea* spp. includes about 45 species, but a relatively intensive hybridisation complicates even their simple description. Usually Mayr’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. 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 believed that *Picea* spp. has a mountain origin, which is confirmed by the surface type of root system and the unique feature of natural renewal, most successful on detritus - rotting remnants of fallen trees, and in different types of forests and in different climatic conditions within its natural range (Usoltsev, 2019).

The genus *Quercus* spp. includes about 600 species in the temperate and tropical zone of the Northern Hemisphere, a distinguishing dependence of oak forests on climate is their affiliation with the humid regions with reduced continentality. In the temperate climate of Western Europe, they range from the Mediterranean Sea and deep into the north whereas in more continental conditions in the East European Plain geographically they are localized in a relatively narrow band. In Russia the oak forests are less than 1% of the forested area. So, the genus *Quercus* is divided into the western and eastern parts of the Eurasian continent, developed in the Tertiary period and varied by biological and especially ecological characteristics. There deciduous and ever-green trees, slow and fast growing at the young age, large trees and sub-shrubs, drought resistant and long-term water logging tolerated species. However, there is one common feature for all these species, which is the affiliation with the humid region with the reduced continentality (Usoltsev, 2019).

The specificity of the response of tree species to climate change may be related to their interaction in different forest growing conditions (Lavrinenko, 1965). The question of relationship between spruce and oak in the forest-steppe of Russia has its own history. It is known the theoretical dispute between botanists (Korzhinsky, 1888) and foresters (Morozov, 1949) broking out on the relationship between oak and spruce in this zone. Geobotanists argued that the spruce that settled in the oak forests will inevitably displace the oak. Foresters were of the opinion that after the introduction of spruce under the canopy of oak forests, spruce is doomed to extinction (Morozov, 1949), which was later confirmed by Yarutkin (1968). Khitrovo (1907) was the most categorical, and gave an example when the spruce and oak ecosystems have been facing each other for thousands of years, separated by the Volga only, without any noticeable tendency to displace the oak from the spruce and vice versa.

To avoid uncertain results mentioned above, a transcontinental level of analysis was chosen in our study, using the opportunities and prospects that are opening up today through "big data" technologies (Niu et al., 2020). The purpose of this study was to show how much thefoliagebiomass of the genus *Picea* 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 the genus *Quercus* spp. in Eurasia. Leaf biomass can provide information about plant investments in leaf tissue and correlates with functional types of woody plants, such as the specific leaf area that can used in modeling plant water consumption (Mencuccini et al., 2019). Since the productive and carbon-deposing 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.

2 Material and Methods

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 (Usoltsev, 2020) in a number of 870 and 570 sample plots with estimations of spruce and oak forest stand biomass (t/ha) is extracted. Their fragment one can see in Table 1.

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

Picea forests						*Quercus* forests					
A	***N***	***V***	P_f	***Tm***	***PRm***	***A***	***N***	***V***	P_f	***Tm***	***PRm***
17	5.000	76	24.0	-3	826	70	0.880	277	5.70	-2	826
10	5.500	10	8.00	-3	826	70	0.572	180	4.10	-2	826
20	4.128	58	19.7	-3	826	80	0.490	450	7.23	-2	826
115	0.300	523	12.66	-2	600	60	0.820	328	5.37	-7	570
116	0.300	561	12.83	-2	600	70	0.628	376	5.71	-7	570
117	0.284	541	12.32	-2	600	80	0.498	417	6.04	-7	570
30	17.72	52	5.91	-14	570	55	1.486	129	3.46	3	635
40	7.267	82	8.38	-14	570	20	7.000	73	3.40	3	635
50	3.775	111	10.8	-14	570	28	7.000	74	2.50	3	635
46	0.756	252	14.7	-5	826	47	0.618	164	1.64	5	826
45	0.914	193	16.9	-5	826	44	0.890	117	2.17	5	826
39	2.240	368	23.9	0	890	21	10.102	44	3.38	5	826
30	1.072	269	24.6	0	890	100	0.500	207	16.1	10	1140
92	0.568	614	9.20	0	635	100	0.570	290	21.6	10	1140
85	0.475	900	20.8	0	635	100	0.725	325	23.5	10	1140
50	1.931	144	1.21	-20	317	20	15.47	59	4.74	-15	570
70	1.142	257	1.80	-20	317	40	1.240	133	3.19	-15	570
90	0.806	344	1.97	-20	317	60	0.634	202	3.57	-15	570
100	1.670	276	9.10	-30	570	80	0.615	165	1.00	-6	570
210	0.247	91	2.70	-30	570	55	1.648	346	6.01	-6	570
220	1.000	221	7.30	-30	570	59	1.723	378	6.84	-6	570
48	1.082	113	11.51	5	1140	80	4.000	150	6.00	3	890
214	0.401	637	7.69	5	1140	80	3.700	170	7.60	3	890
317	0.405	1143	10.0	5	1140	80	5.200	195	7.10	3	890
164	0.501	472	8.81	5	1140	13	10.30	124	5.30	0	826

*Designations here and further: *A* = stand age, yrs; *V* = stem volume, m^3/ha; *N* = tree density, 1000/ha; P_f = foliage biomass, t per ha; *Tm* = mean January temperature, °C; *PRm* = mean annual precipitation, mm.

Distribution of data collected from different sites is shown in Fig. 1. We can see that the coverage of the territory of Eurasia by *Picea* and *Quercus*is quite different, apparently, due to the difference in their ecological niches. Each sample plot, in which the biomass of the forest stands was estimated, is positioned inaccordance to January mean annual temperature isolines and tomeanannual precipitation isolines,and the initial data matrix is compiled inwhich the values of biomass components and of stand taxation characteristicsare mated with corresponding values of mean January temperatureand precipitationtaken from World Weather Maps (2007). The matrix is then subjected to regression analysis.

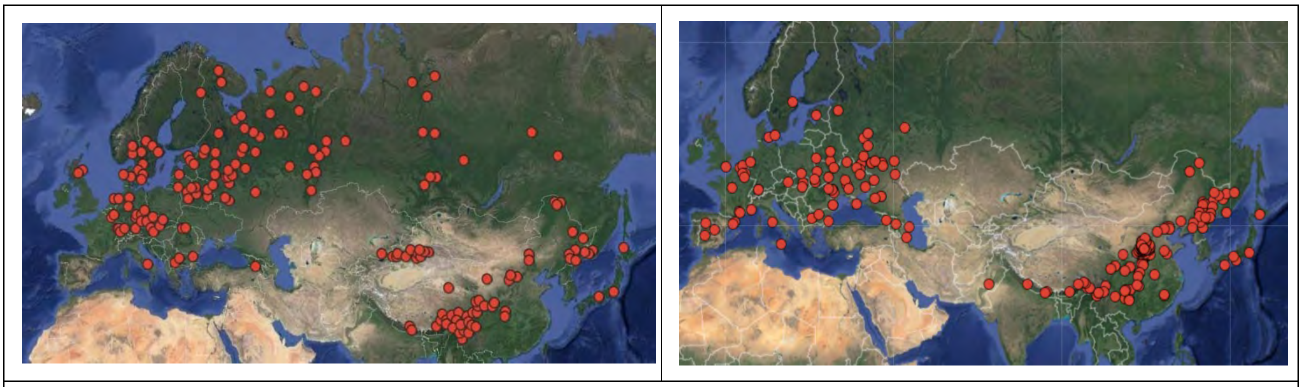

Fig. 1 The distribution of 870 sampling sites of *Picea* (on the left) and 570sampling sites of *Quercus* (on the right) on the territory of Eurasia.

The question may arise why modelling was performed at a level of genera, and not for individual spruce and oak 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, *P. abies* (L.) H. Karst. *vs*. *P. obovata* L. *vs*. *P. koraiensis* Nakaiare derived from regional climatic features.

It is wellknown 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 and Bojaxhi, 2010; Bijak, 2010; Morley et al., 2017), having in mind that winter temperatures in the Northern Hemisphere are increased faster than summer ones 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 Mandea, 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°C in the forest-tundra of the North–Eastern Siberia to +10°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.

The matrix was used as a source of data in the subsequent regression analysis.It is well known, 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 multicollinearity arises in empirical modeling of biomass. One of the solutions to the problem is to harmonize the system by constructing recursive (recurrent, related) equationsfor 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; Usoltsev, 1990; Zhao et al., 2022). This approachas one of the methods for model harmonization (JacobsandCunia, 1980), provides a multivariate conditionality of factors that provide flexibility and universality of the regression system describing the dynamics of biomass of stands.

When 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 final structure of the recursive system of equations included only those mass-forming indices that were statistically significant for foliage biomass component:

$$\begin{aligned}
&\ln N = \mathrm{f}\,\{\ln A, \ln(Tm+\mathrm{M}), \ln PRm, [\ln(Tm+\mathrm{M})]\cdot(\ln PRm)\} \rightarrow \\
&\rightarrow \ln V = \mathrm{f}\,[\ln A, \ln N, (\ln A)(\ln N), \ln(Tm+\mathrm{M}), \ln PRm, [\ln(Tm+\mathrm{M})]\cdot(\ln PRm)\} \rightarrow \\
&\rightarrow \ln Pi = \mathrm{f}\,\{\ln A, \ln V, \ln N, (\ln A)(\ln N), \ln(Tm+\mathrm{M}), \ln PRm, [\ln(Tm+\mathrm{M})]\cdot(\ln PRm)\}. \qquad (1)
\end{aligned}$$

3 Results and Discussion

The calculated equations (1) for foliage biomass are 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 *Picea*and M = 30 for *Quercus.* The synergism $(\mathrm{lnA})\cdot(\mathrm{lnN})$ was introduced in the model to account for the decrease in the tree density with age and its effect on the foliage biomass. All the necessary calculations were carried out in Statgraphics software (http://www.statgraphics.com/).

First of all, we should pay attention to the signs for climate variables in the equations for spruce and oak (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 +3.9064, +1.8125 and -0.6126 for spruce, and to -3.0578, -0.8465 and +0.4607 for oak correspondingly, i.e. we have mirror patterns for the foliage biomass of spruce and oak. These regression coefficients are significant at the probability level of 0.99 for spruce, and of0.95 in two climate variables out of the available three ones for oak, and the corresponding values of t-Student are +3.45, +2.95, and -3.37 for spruce foliage, and. -2.05, -1.14, and +2.00 for oak foliage.

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 84, and 70% of the variability of foliage biomass in *Picea*, and *Quercus* correspondingly, including 54, and 29% of the contribution from the stem volume. Climate variables explain about 16, and 30% of the foliage biomass variability in *Picea*, and *Quercus* correspondingly, i.e. less than about 5.1, and 2.2 times as much as mass-forming variables in *Picea*, and *Quercus* correspondingly.

When tabulating a multifactorial biomass model that includes age, number of trees and volume stock as independent variables, a problem arises. This problem consists in the fact that we can insert only the desired age values into the model, and the values of the other two independent variables are unknown to us. The recursive principle of model construction gives us a solution to the problem by sequentially tabulating the equations. The recursive system of equations (1) was tabulated in the sequence indicated by the arrows: 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 spruce and for oak) are taken, and 3-D graphs showing statistically significant transcontinental trends of biomass in temperature and precipitation gradients are designed (Fig. 2).

Table 2 Characteristic of equations (1) for forest stands of the *Picea,* and *Quercus* in Eurasia.

ln(Y)(1)	a_0(2)	ln$A$	ln$V$	ln$N$	(ln$A$)·(ln$N$)	ln(Tm+M)	lnPRm	[ln(Tm+M)]·(lnPRm)	adjR^2(3)	SE(4)
Picea										
ln(N)	-11.5190	-1.0091	-	-	-	5.2191	3.0637	-0.9733	0.569	0.61
ln(V)	-11.2252	0.8455	-	-1.1457	0.2699	-2.9798	-2.4759	0.7765	0.642	0.59
ln(Pf)	-10.8564	-0.3423	0.5893	-0.2302	0.1047	3.9064	1.8125	-0.6126	0.669	0.42
Quercus										
ln(N)	8.7044	-1.2007	-	-	-	-1.2007	-0.9147	0.2921	0.618	0.59
ln(V)	-5.2849	0.9559	-	-0.2394	0.0600	3.2725	0.8354	-0.4472	0.579	0.52
ln(Pf)	5.3121	0.2723	0.1575	-0.0081	0.0428	-3.0578	-0.8465	0.4607	0.403	0.40

(1)Dependent variables;

(2)The constant corrected for logarithmic retransformation by Baskerville (1972);

(3)$adjR^2$ – determination coefficient adjusted for the number of variables;

(4)SE – standard error of the equations.

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$A$)·(ln$N$) (IV)	I+II+III+IV	ln(Tm+M) (V)	lnPRm(VI)	[ln(Tm+M)]·(ln PRm) (VII)	V+VI+VII
Picea									
ln(Pf)	15.1	53.9	5.2	9.5	83.7	5.8	4.9	5.6	16.3
Quercus									
ln(Pf)	29.7	28.7	0.5	10.7	69.6	12.0	6.7	11.7	30.4

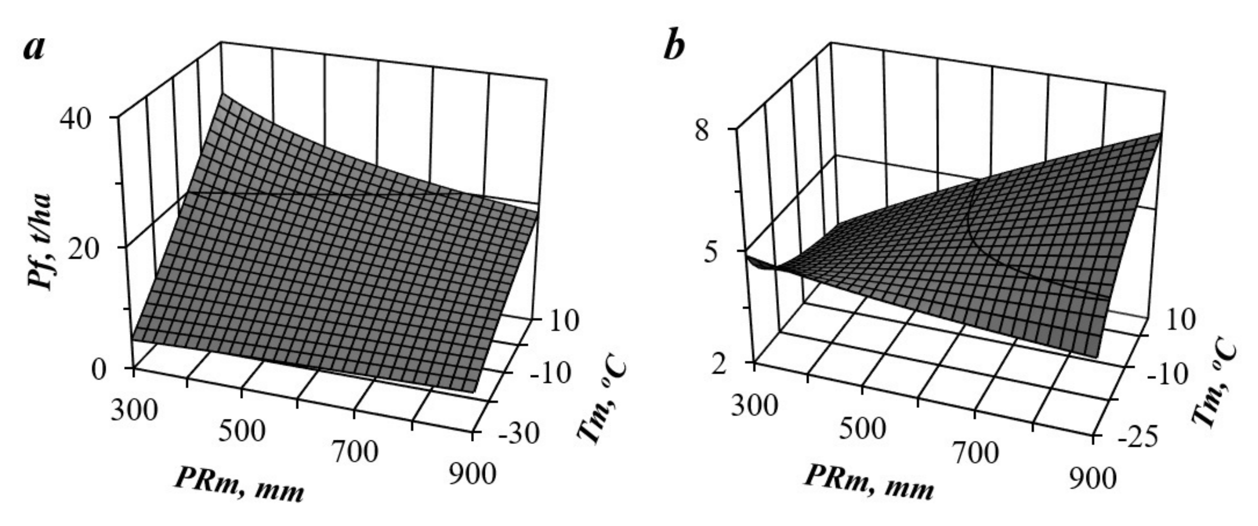

Fig. 2 Dependence of spruce (a) and oak (b) foliage biomass (*Pf*) of Eurasia upon the mean January temperature (*Tm*) and mean annual precipitation (*PRm*).

We can see in Fig. 2 two patterns significant differed in changes in the spruce and oak foliage biomass in precipitation and winter temperature gradientsin the form of two oppositely directed propellers. Similar oppositely directed 3D patterns were obtained earlier for larches and two-needled pines (Usoltsev et al., 2022).

Using the 3-D pattern in Fig. 2, we can find out,how much the foliage biomass will change with an air temperature deviationfrom the usual norm, for example, by 1°C and with a precipitation deviation from the usual norm, for example, by 100 mm per year. To do this, we take the first derivative of 3-D surfaces (Fig. 2), and not analytically, but graphically, i.e. we take off the biomass difference interval (Δ, %) 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-D surfaces divided into plus and minus areas that correspond to the increase or decrease in the foliage biomass for spruce (Fig. 2a) and foroak (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 -25Δ (-30Δ) ... +10Δ. 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 300Δ ... 900Δ.

As we can see on Fig. 3a, there is an increase in *Picea*foliage biomass (Δ, %) with a temperature increase of 1°C regardless of regional temperature and precipitation indicators(the location of the increment surface above the zero plane), and the largest percentage of increase occurs in cold regions (*Tm* = -30°C) with insufficient moisture supply (*PRm* = 300-400 mm), while *Quercus* leaf biomass in the same conditions, on the contrary, has the largest percentage of its decrease (the location of the increment surface below the zero plane) (Fig. 3b). In cold regions (*Tm* = -30°C), as the transition from dry conditions (*PRm* = 300 mm) to wet ones (*PRm* = 900 mm), the percentage of foliage mass in spruce decreases, and in oak increases (Fig. 3a, b).

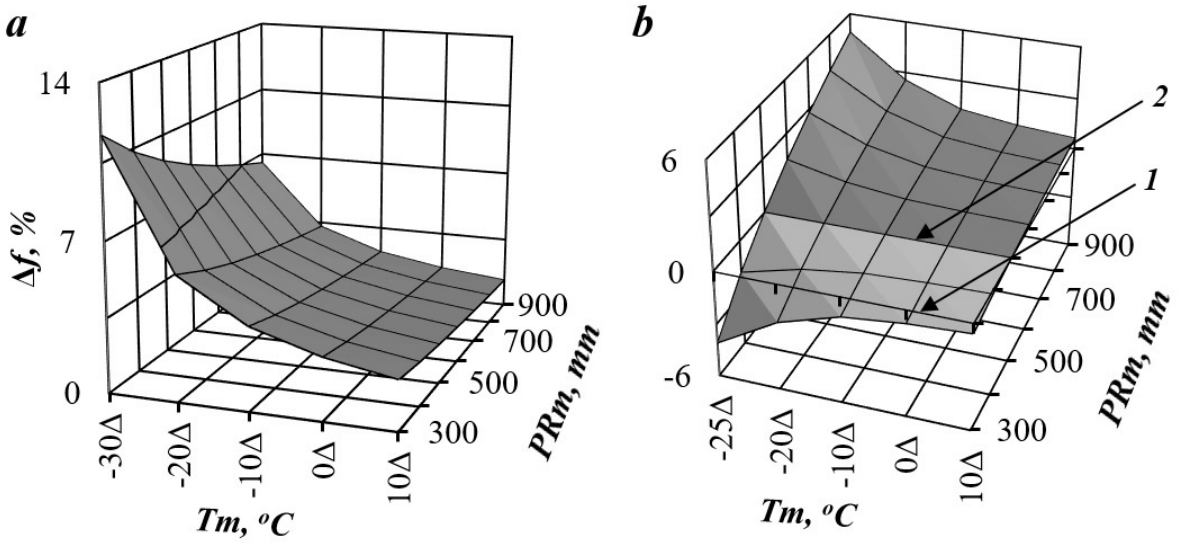

Fig. 3 Simulated changes in spruce (a) and oak (b) foliage biomass due to the assumed temperature increase of 1°C based on the derived model (for the stands aged 100 years). Here and further: the value 1 represents the plane corresponding to zero change of biomass at the expected temperature increase by 1°C; the value 2 represents the border between positive and negative changes in biomass (Δ,%) at the expected temperature increase by 1°C.

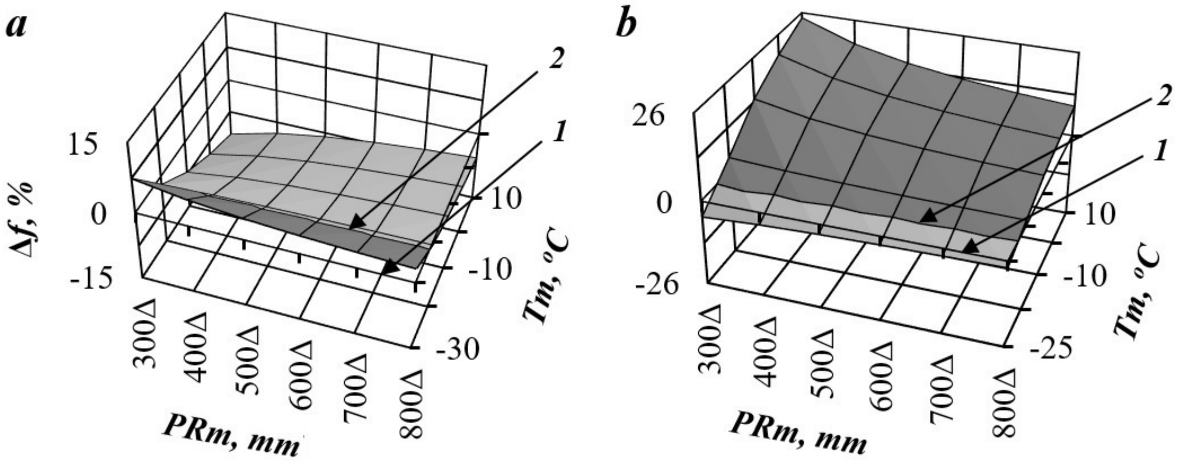

Fig. 4 Simulated changes in spruce (a) and oak (b) foliage biomass due to the assumed precipitation increase of 100 mm (for the stands aged 50 years).

If we assume an increase in precipitation by 100 mm at a constant winter temperature, we get exactly the opposite patterns for spruce and oak: in warm regions (*Tm* = 10°C), spruce has a decrease in the percentage of foliage mass (Fig. 4a), and oak, on the contrary, its increase (Fig. 4b). As we move to cold regions (*Tm* = -30°C), these patterns change to the opposite: the spruce negative percentage changes to positive, and the oak positive percentage changes to negative.

A next question: what can be the reason for the opposite trends in foliage biomass in spruce and oak, which are statistically reliable at the probability level equals 0.95and even 0.99? 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 aboveground biomass to the biomass of the assimilation apparatus, that is known as foliage efficiency (FE) (Cannell et al., 1983; Shi and Cao, 1997). This index was analyzed in 5 natural zones (subarctic, northern temperate, southern temperate, subtropical, and subequatorial) with a stable Khromov's index of continentality (Khromov, 1957). It was found that in the direction from the northern moderate zonal belt to the subequatorial one, FE increases in spruce and decreases in oak in the same zonal range (Usoltsev et al., 2018). Another production index, foliage biomass, on the contrary, decreases in the direction from moderate to subequatorial zone in spruce, and increases in oak (Usoltsev, 2016). Opposite patterns of foliage biomass in spruce and oak were also observed in the continental climate gradient: a negative trend in spruce and a positive trend in oak (Usoltsev, 2016).

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 and Kossowitsch, 1929; Zacharowa, 1929; Ivanov and Orlova 1931; Printz, 1933; Cartellieri, 1935; Ålvik, 1939; Freeland, 1944; Zeller, 1951; Pisek and Rehner, 1958; Pisek, 1960; Lyr et al. 1974; Kramer and Kozlovsky 1983; Schaberg et al., 1995; Wieser, 1997; Smashevskiy, 2014).

In spruce 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 litterfall 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 oak trees, FE in the direction from the northern temperate to the subequatorial zone does not increase, as in spruce, but decreases, possibly due to an increase in the respiration losses during a shorter physiologically active period (due to leaf shedding) compared to spruce. In essence, everything depends on the ratio of photosynthesis and respiration in the spruce, especially during the period when the oak 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 insufficient moisture (PRm = 300 mm) (Fig. 2 a, b), and as we move to areas of sufficient moisture (PRm = 900 mm), this coincidenceisonly in spruce, and in oak, this correspondence is replaced by a complete contradiction: the foliage mass increases during the transition from cold to warm regions, in contrast to the negative trend in the foliage efficiency.

The patterns of biomass amount change under assumed changed climatic conditions (Figs. 2-4) 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; Kannenberg et al., 2022). However, with a slow change in the environment, the effect of short-term stability of communities can be achieved (Baez et al., 2022). The law of limiting factors (Liebig, 1840) works well in stationary conditions. With a rapid change in limiting factors (for example, air temperature or precipitation), forest ecosystems are in a transitional 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 was 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, 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-specificdata. A full explanation of both the obtained regularities and counterintuitive results can be obtained after conducting detailed physiological studies, especially in relations between foliage biomass and foliage efficiency. Today, the most important question is whether the dryness of habitats will increase with climate warming. This determines the possible increase in carbon sink during climate warming, or, on the contrary, its decrease and the corresponding change to the source of carbon dioxide in the atmosphere (Tyrrell et al., 2012).

3 Conclusion

A comparison of the reaction of spruce and oak foliage biomass to changes in the mean January temperature by 1°C at constant precipitation and annual precipitation by 100 mm at constant temperature showed counterintuitive result.If low temperature regardless of regional precipitation is the limiting factor for spruce foliage biomass, then high temperature and insufficient precipitation are the limiting factors for oak.

When the temperature increases by 1°C, the most increase in spruce foliage biomass occurs in cold regions with insufficient moisture supply, while oak leaf biomass, on the contrary, has the largest percentage of its decrease. In cold regions, as the transition from dry conditions to wet ones, the percentage of foliage mass in spruce decreases, and in oak increases. When the precipitation increases by 100 mm, there is the opposite patterns for spruce and oak: in warm regions, spruce has a decrease in the percentage of foliage mass, and oak, on the contrary, its increase. In the cold regions, these patterns change to the opposite: the spruce negative percentage changes to positive, and the oak positive percentage changes to negative.

Our outputs represent an example of model sensitivity to changing climatic conditions. The development of such models 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.

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