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Additive Models of Single-tree Biomass Sensitive to Temperature and Precipitation in Eurasia – A Comparative Study for *Larix* spp. and *Quercus* spp.

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Abstract: In the context of current climate change, it is important to know the patterns characterising the response of forest trees to the dynamics of air temperature and precipitation. In this study, the first attempt to model changes of additive component composition of genera *Larix* spp. and *Quercus* spp. aboveground biomass according to Eurasian gradients of January's mean temperature and annual mean precipitation is made, taking into account regional particularities of tree age and morphology structure. In the process of modelling, the database of single-tree biomass for forest-forming species in Eurasia is used. According to our results, the factors limiting the biomass of trees differ not only between the two tree genera but also between different components of biomass within the genus. In larches, the reaction of the biomass of all components to an increase in precipitation in cold zones is directly opposite in comparison with oaks, i.e. it decreases as precipitation increases. But in warm areas, the reactions of the two genera to increased precipitation coincide, i.e. precipitation does not affect the biomass of all components, both in larches and oaks. In wet areas, larch biomass components react to temperature increases in the opposite way, i.e. the aboveground and stem biomass increases, but the biomass of foliage and branches decreases. In dry areas, the reaction to the temperature of all larch and oak biomass components is unambiguous and opposite, i.e. there is a decrease in the larch biomass of all components as temperatures rise, and in oak biomass vice versa. This situation is discussed in terms of limiting factors.

Keywords: Genera *Larix* spp. and *Quercus* spp.; Tree biomass; Allometric models; Additive biomass equations; Mean January temperature; Mean annual precipitation; The principle of limiting factors by Liebig-Shelford.

Introduction

Since ancient times climate change has largely determined the fate of human civilisation (Behrensmeyer, 2006; Miles-Novelo and Anderson, 2019), the great migrations of people (Laczko and Aghazarm, 2009) and changes in the structure and habitats of biota and their main terrestrial component – forest cover (Halofsky et al., 2018; Kosanic et al., 2018). Although it is believed that ancient civilisations died out largely as a result of forest harvesting, "still in no way and by no human device could the wood be exhausted" (Radkau, 2008:

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133), and the desertification of once-forested areas of ancient civilisations was the result of climate change.

Recently, a group of 11,258 scientists from 153 countries is declaring “clearly and unequivocally that planet Earth is facing a climate emergency”, and there is a “moral obligation to clearly warn humanity of any catastrophic threat” (Ripple et al., 2020). Therefore, international efforts are needed to prevent the rise in mean annual temperature and CO_2 emissions. Increased CO_2 emissions may be maintained while increasing vegetation biomass using effective forest management. Vegetation biomass and effective forest management help to reduce high mean annual temperature (IPCC, 2013). Forests support the livelihoods of more than a billion people living in extreme poverty worldwide and provide paid employment for over 100 million people. Moreover, they are home to more than 80 percent of the world’s terrestrial biodiversity. However, as climate change poses enormous challenges for forests and people, awareness is growing on the potential roles played by forests in mitigating and adapting to climate change, making, therefore, even more urgent, the need to improve forest monitoring and assessment (Matala et al., 2006; FAO, 2019). Although forest biomass is an important part of sustainable development and the main driver of succession changes in forests (Lohbeck et al., 2015), nevertheless the rate of recovery of their biomass is significantly faster than the rate of biodiversity recovery (Martin et al., 2013). This means a decrease in the stability of the biosphere and its gradual degradation. Therefore, the removal of uncertainties related to the assessment and monitoring of forest biological productivity and biodiversity in the condition of climate change is of paramount importance.

In the problem of climate stabilisation, great hopes are associated with the carbon-depositing capacity of forests. Therefore, in recent years, a lot of the world literature is devoted to the problem of the carbon-depositing capacity of forests. This needs the development of global biomass change models based on relevant world databases of biological productivity of forests, in relation to which the scientific community states the onset of the big data era (Kudyba, 2014; Poorter et al., 2015; Jucker et al., 2017; Serra-Diaz et al., 2017), and today, not just databases are being compiled, but the bases of databases (Kattge et al., 2020).

To estimate the biomass and carbon pools in the forested areas, allometric equations at tree and stand levels are developed based on the harvest data obtained on the sample plots. Allometry (Huxley, 1932) has a good biological basis but does not always fit well with empirical data (Fischer et al., 2019). On the allometry basis, several theories are proposed: the pipe model (Huber, 1925, 1927; Shinozaki and Yoda, 1964 a,b), the functional equilibrium model (Davidson, 1969), the fractal model (West et al., 1999), the metabolic scaling theory (when scaling exponent is constant) (West et al., 1997), the theory of adaptive mass distribution (when scaling exponent changes dynamically with size) (Poorter et al., 2015) and some of their modifications (Enquist and Niklas, 2001, 2002). However, when calculating allometric models of tree biomass there is always a residual variance, reflecting, in particular, the discrepancy between the annual dynamics of the crown mass, especially of the foliage, and the relative conservatism of stem diameter, as an accumulator of its annual increments (Usoltsev, 1988), as well as differences of age status and climatic conditions (Ouyang et al., 2019; Xiang, 2020). The problem of using allometric models in the assessment of biomass and carbon deposited by it remains extremely relevant, which is confirmed by the organisation of a special conference in 2013 within the framework of the UN-REDD programme (Cifuentes-Jara and Henry, 2013).

A comparative analysis of the accuracy of different methods for determining the biological productivity of some tree species showed that allometric models designed at a tree scale give a smaller prediction error compared to models performed at the forest stand scale (Zeng et al., 2018). Such single-tree allometric models for mixed stands are particularly relevant. The uncertainty associated with the variation of regression coefficients of allometric equations, both generic having one independent variable, and multi-predictor ones, is somewhat caused by climatic factors (Wirth et al., 2004; Zeng et al., 2017; Vasseur et al., 2018).

At the level of single-trees, allometric equations are related to the problem of internal consistency (compatibility, additivity) of the biomass component composition, according to which the total biomass of components (stems, branches, foliage) obtained by “component” equations would be equal to the value of biomass obtained by the total biomass equation (Young et al., 1964; Kurucz, 1969; Kozak, 1970; Chiyenda and Kozak, 1984; Cunia and Briggs, 1984, 1985; Reed and Green, 1985; Parresol, 1999, 2001; Tang et al., 2000; Carvalho, 2003; Carvalho and Parresol, 2003; Návar et al., 2004; Bi et al., 2004, 2015; Zeng and Tang, 2010; Salas et al., 2013; Daryaei and Sohrabi, 2015; Dong et al., 2015a,b; Sanquetta et al., 2015; Zheng et al., 2015; Magalhães and Seifert, 2015; Stankova et al., 2016; Zhuo et al., 2016; Zhang et al., 2016; Affleck, 2016;

Fu et al., 2016, 2017a,b; Zeng et al., 2018; Wang et al., 2018a), but these equations seldom include climatic variables and seldom relevant to the problem of climate change (Forrester et al., 2017; Zeng et al., 2017).

At the level of forest communities (phytocenoses), 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, 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., 2018b; Sperry et al., 2019), but are seldom related to the problem of component composition additivity (Bi et al., 2010).

It is known that the structure of tree biomass has regional features which are revealed on the basis of inclusion in allometric equations of a block of dummy variables coding regional accessory of some set of trees (Jacobs and Cunia, 1980; Zeng et al., 2011; Fu et al., 2012; Zheng and Zeng, 2013; Zeng, 2015, 2017), including additive ones (Usoltsev and Tsepordey, 2018; Usoltsev et al., 2018 a,b; Usoltsev et al., 2019a), but seldom related to climatic variables (Fu et al., 2017b). In the latter case, climate variables are used indirectly, through climate subzones. The authors (Fu et al., 2017b) proposed an allometric model for aboveground biomass (without separation in component composition), in which, in addition to the stem diameter, two blocks of dummy variables are introduced: one block encoded three species of larches, and the other block - five climatic subzones. Thus, it is possible to use this model to predict changes in aboveground biomass under the influence of climate shifts only indirectly, according to the principle: “What will happen if...?”, i.e. only if we know what climate change is coming in each of the five subzones. A similar situation is in the work by Usoltsev (2016), where allometric models of single-tree biomass for the main tree species of Eurasia, including stem diameter and height as independent variables, are distributed across ecoregions through a block of dummy variables.

Since climate variables are geographically determined, it can be expected that the development of allometric biomass models, including not only the age, height and stem diameter as independent variables, but also climate indices, will allow to isolate and quantify some changes in the biomass structure of equal-aged and equal-sized trees in relation to climate variables and will provide climate-sensitivity of such models (Forrester et al., 2017; Zeng et al., 2017; Fu et al., 2017b).

Today, the influence of climate change on the biomass of trees of a particular tree species in the format of additive models according to trans-continental hydrothermal gradients has not been studied at all. Our database on single-tree biomass (Usoltsev, 2020) for forest-forming species of Eurasia made it possible to implement modern methodological developments at a completely different, higher level, namely, to start modelling additive biomass at the trans-continental level. In this study, the first attempt at modelling changes in the additive component composition of *Larix* spp. aboveground biomass according to hydrothermal Trans-Eurasian gradients in comparison with other deciduous genera *Quercus* spp. is made.

Material and Methods

The distribution aboveground biomass harvest data by regions, tree species and taxation indices are presented in Table 1. Each sample plot on which tree biomass estimating was performed is positioned relative to the isolines of the mean January temperature and relatively to the isolines of mean annual precipitation (Figures 1 and 2). The use of evapotranspiration as a combined index in the assessment of tree production is futile since it explains only 24% of its variability compared to 42%, which provides the relation to mean annual precipitation, and compared to 31%, which provides the relation to mean annual temperature (Ni et al., 2001). Therefore, the use of temperature and precipitation indices are preferable as the most informative climatic factors. Our preference is given to using the mean January (not annual one) temperature as one of the climatic variables since winter temperatures in the Northern hemisphere increased faster than summer ones during the 20th century (Emanuel et al., 1985; Folland et al., 2001). Morley et al. (2017) have summarised: “We found that winter temperatures were particularly useful for explaining inter-annual variation in species’ distribution and biomass, although the direction and magnitude of the response varied among species from strongly negative, to little response, to strongly positive. Across species, the response to winter temperature varied greatly, with much of this variation being explained by thermal preference” (P. 2590). 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

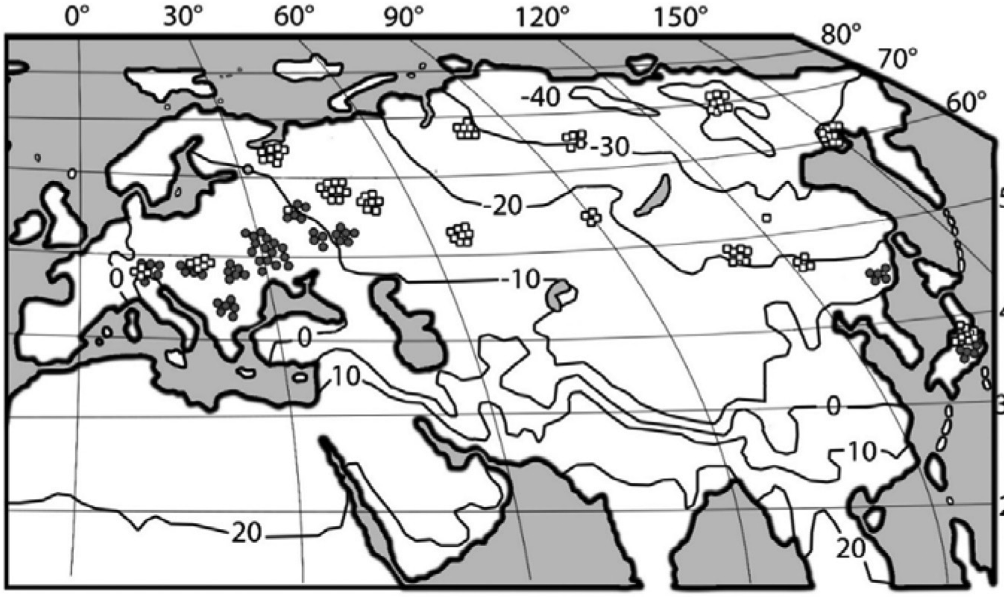

Figure 1: Distribution of biomass harvest data of *Larix* spp. (rings) and *Quercus* spp. (squares) sample trees on the map of the mean January temperature, °C (World Weather Maps, 2007; https://store.mapsofworld.com/image/cache/data/map_2014/currents-and-temperature-jan-enlarge-900×700.jpg).

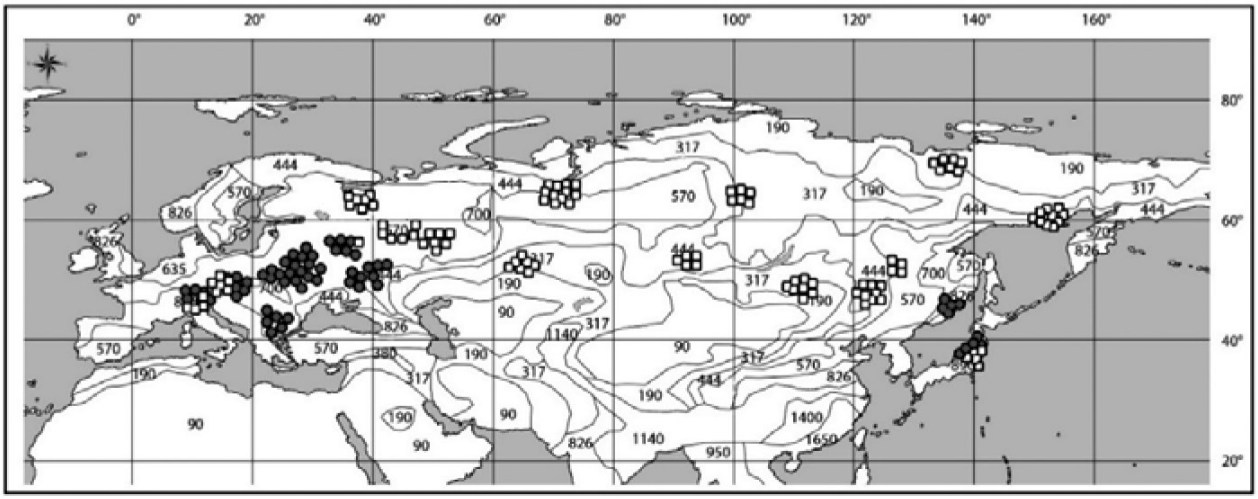

Figure 2: Distribution of biomass harvest data of *Larix* spp. (rings) and *Quercus* spp. (squares) sample trees on the map of the mean annual precipitation, mm (World Weather Maps, 2007; https://www.eldoradoweather.com/climate/world-maps/world-annual-precip-map.html).

regression. Taking the mean winter temperature as one of the independent variables, we get a more reliable dependence having a higher predictive ability.

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. In the latter cases, the plant trait responses are not only species-specific (Pucko et al., 2011; Buckley and Kingsolver, 2012; Parmesan and Hanley, 2015; Gray and Brady, 2016; Baruah et al., 2017) but also community-specific (Baruah et al., 2017). As shown in Figures 1 and 2, larches and oaks occupy different climatic regions of Eurasia, and this phenomenon suggests that their reactions to regional changes in temperature and precipitation will be different.

The matrices of harvest data were compiled, in which the biomass component values and mensuration tree parameters were related with the corresponding values of mean January temperature and precipitation, and then included in the regression analysis procedure.

We do not consider underground biomass here, due to insufficient harvest data and because of the enormous uncertainties involved in determining the biomass and primary production of roots (Reich et al., 2014), especially the fine fraction (Yuan and Chen, 2012; Železnik et al., 2016; Sinacore et al., 2017). The analysis of the world data of underground tree biomass has shown 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 noted above, the main predictors included in the allometric model of biomass are usually the tree height and stem diameter at breast height. In this study, the task is to extract the climatic component from the residual dispersion of a model calculated. For climatic factors to be predominant and "recoverable" from this "information noise", it is necessary to take into account in a model, in addition to diameter and height, also tree age, which is a factor determining the structure of tree biomass too (Nikitin, 1965; Kazaryan, 1966; Usoltsev, 1972; Tsel'niker, 1994; Vanninen et al., 1996; Genet et al., 2011; Ochał et al., 2013; Qiu et al., 2018).

Based on the above, the following structure of the regression model is suggested:

$$\begin{aligned}\ln P_i = {} & a_{0i}+a_{1i}(\ln A)+a_{2i}(\ln D)+a_{3i}(\ln H)\\ & +a_{4i}(\ln D)(\ln H)+a_{5i}[\ln(T+\mathrm{X})]\\ & +a_{6i}(\ln PR)+a_{7i}[\ln(T+\mathrm{X})]\times(\ln PR) \qquad (1)\end{aligned}$$

where P_i is the biomass of *i*-th component, kg; A is tree age, yrs; D is stem diameter at breast height, cm; H is tree biomass, m; i is the index of biomass component: aboveground (*a*), crown (*c*), foliage (*f*), branches (*b*), stem above bark (*s*), stem wood (*w*) and stem bark (*bk*); T is mean January temperature, °C; PR is mean annual precipitation, mm; X = 50 and 20 for *Larix* and *Quercus* correspondingly. Along with the three main mass-forming variables - tree age, diameter and height, the product of variables (ln*D*)(ln*H*) was introduced as an additional predictor. The trees in the database are represented in a wide range of diameters and heights (Table 1). When experimental data is included in equation (1) for the entire range of diameters and heights, the allometry is violated. In small trees, the diameter at breast height shifts to the apex, resulting in a correlation of residues, and the residual dispersion becomes heterogeneous: in small and large trees, biomass estimates are underestimated, and in medium-sized trees, they are overestimated. The introduction of synergy, or product (ln*D*)(ln*H*) eliminates the correlation of residuals (Usoltsev et al., 2019b). Since the mean January temperature in the northern part of Eurasia has negative values, the corresponding independent variable is modified to be subjected to log-log procedure as *T*+50 and *T*+20.

Results

The initial Equation (1) is calculated including the biomass data in the above mentioned database and after the correction for logarithmic transformation by Baskerville (1972) is suggested (Table 2). Regression coefficients of Equation (1) are characterised by the significance level of 0.05 and better, and the resulting equations are adequate to the original values presented in the available database. Determination coefficients $adjR^2$ ranged from 0.873 to 0.908 for foliage and branches, and from 0.990 to 0.992 for stem and aboveground biomass.

Using the results of regression analysis when calculating Equation (1) (Table 2), we can estimate the contributions of structural (taxation) and climatic (temperature and precipitation) independent variables to explain the variability of biomass components and compare their differences in *Larix* and Q*uercus*. The proportions of the contribution of independent variables to the explanation of the variability of the dependent variables in Equation (1) are given in Table 3. It shows the contribution of various independent variables to the explanation of the variability of the desired indices of biomass. We can see that mass-forming (taxation) variables explain in averaged about 77% and 75% of the variability of all biomass components in *Larix* and *Quercus* correspondingly, including 37% and 46% of the contribution from the stem diameter. Climate variables explain about 23% and 25% of the total biomass variability in *Larix* and Quercus correspondingly, i.e. less than about 3.4 and 3.0 times as much as mass-forming variables in *Larix* and *Quercus* correspondingly. Given that environmental correlations often have R^2 values significantly below 0.50 (Møller and Jennions, 2002), our result can be considered quite acceptable.

According to the structure of disaggregation two-step additive models, the aboveground biomass P_a estimated by an initial equation is subdivided into components according to the scheme presented by Zheng et al. (2015). The procedure for transforming the initial equations to additive form has been described in detail in previous publications (Usoltsev et al., 2018 a,b;

Table 1: Distribution of the sample trees by species, countries, regions and mensuration indices

Regions	*Species of the genus*	*Ranges:*			*Data number*
		Ages, yrs	*DBH, cm*	*Heights, m*	
Larix spp.*					
West Europa	*L. decidua* Mill.	34÷210	7.1÷47.8	9.8÷34.0	19
European Russia	*L. sukaczewii* N.Dyl.	10÷70	1.0÷35.0	2.3÷28.0	25
Turgay deflection	*L. sukaczewii* N.Dyl.	26÷42	6.2÷28.0	7.9÷17.8	28
North of West Siberia	*L. sibirica* L. *L. gmelinii* Rupr.	10÷70	2.1÷38.0	2.9÷24.8	116
North of Eastern Siberia	*L. cajanderi* Mayr.	44÷400	0.3÷22.7	1.4÷14.8	66
North of Russian Far East	*L. cajanderi* Mayr.	30÷424	3.9÷52.8	2.9÷30.0	43
Mongolia. China	*L. sibirica* L. *L. gmelinii* Rupr.	14÷186	0.5÷31.0	1.5÷24.3	50
Japan	*L. leptolepis* Gord.	9÷56	4.0÷35.9	4.3÷26.7	73
Total					420
Quercus spp.					
Czech Republic	*Q. robur* L.	13÷104	4.0÷69.7	26.7÷32.6	7
Bulgaria	*Q. rubra* L., *Q. longipes* Stev., *Q. sessiliflora* Sal., *Q. frainetto* Ten.	17÷70	1.5÷29.5	2.7÷26.4	49
The Ukraine	*Q. robur* L.	6÷128	2.5÷50.5	3.1÷31.5	370
European part of Russia	*Q. robur* L.	12÷130	1.1÷46.9	2.5÷32.4	54
Russian Far East	*Q. mongolica* Fisch. *ex* L.	56÷166	9.5÷34.5	12.0÷23.2	7
Japan	*Q. serrata* Murray, *Q. mongolica* Fisch. *ex* L.	4÷40	1.1÷16.5	2.7÷8.9	13
Total					500

* *Larix sukaczewii* N.Dyl. is a synonym of *L. sibirica* Ledebour; *L. cajanderi* Mayr. is a synonym of *L. gmelinii* (Rupr.) Kuzen.; and *L. sibirica* Ledebour = *L. decidua* Mill. ssp *sibirica* (Ledeb.) Domin.

Table 2: Characteristics of initial Equation (1)

Initial models (1)	*adjR*^{2}*	*SE**
Larix		
$\mathrm{lnP_a}$ =4.6168-0.0285(lnA)+1.4200(lnD)+0.3531(lnH)+0.1864(lnH)(lnD)-1.6980[ln(T+50)]-1.0497(lnPR)+0.2763(lnPR)[ln(T+50)]	0.990	0.18
$\mathrm{lnP_c}$ =5.8313-0.4750(lnA)+2.0494(lnD)-1.5901(lnH)+0.3572(lnH)(lnD)-1.7519[ln(T+50)]-0.6997(lnPR)+0.2213(lnPR)[ln(T+50)]	0.909	0.50
$\mathrm{lnP_s}$ =3.7903+0.0454(lnA)+1.3147(lnD)+0.8121(lnH)+0.1419(lnH)(lnD)-1.7511[ln(T+50)]-1.1176(lnPR)+0.2937(lnPR)[ln(T+50)]	0.991	0.18
$\mathrm{lnP_f}$ =4.7190-0.5758(lnA)+1.9697(lnD)-1.3881(lnH)+0.2974(lnH)(lnD)-1.4389[ln(T+50)]-0.6001(lnPR)+0.1423(lnPR)[ln(T+50)]	0.901	0.46
$\mathrm{lnP_b}$ =6.3496-0.4541(lnA)+2.1476(lnD)-1.5849(lnH)+0.3480(lnH)(lnD)-2.1004[ln(T+50)]-0.8932(lnPR)+0.2846(lnPR)[ln(T+50)]	0.908	0.52
$\mathrm{lnP_w}$ =6.1040+0.0288(lnA)+1.2741(lnD)+0.8612(lnH)+0.1705(lnH)(lnD)-2.7437[ln(T+50)]-1.5993(lnPR)+0.4723(lnPR)[ln(T+50)]	0.992	0.18
$\mathrm{lnP_{bk}}$ =10.4148-0.0024(lnA)+1.2221(lnD)+0.5373(lnH)+0.1706(lnH)(lnD)-3.9433[ln(T+50)]-2.4096(lnPR)+0.6761(lnPR)[ln(T+50)]	0.968	0.31
Quercus		
$\mathrm{lnP_a}$ =-16.3528+0.0254(lnA)+1.6723(lnD)+0.2228(lnH)+0.1413(lnH)(lnD)+4.4574[ln(T+20)]+2.2228(lnPR)-0.6737(lnPR)[ln(T+20)]	0.992	0.17
$\mathrm{lnP_c}$ =-33.9823-0.2153(lnA)+2.3605(lnD)-1.0038(lnH)+0.1659(lnH)(lnD)+9.8556[ln(T+20)]+5.0538(lnPR)-1.5157(lnPR)[ln(T+20)]	0.915	0.52
$\mathrm{lnP_s}$ =-10.0271+0.0667(lnA)+1.4733(lnD)+0.5684(lnH)+0.1399(lnH)(lnD)+2.1479[ln(T+20)]+1.1454(lnPR)-0.3236(lnPR)[ln(T+20)]	0.993	0.17
$\mathrm{lnP_f}$ =-26.3688-0.4527(lnA)+2.0980(lnD)-0.8138(lnH)+0.1138(lnH)(lnD)+8.6857[ln(T+20)]+3.7759(lnPR)-1.3286(lnPR)[ln(T+20)]	0.873	0.51
$\mathrm{lnP_b}$ =-33.7298-0.1362(lnA)+2.5273(lnD)-0.8758(lnH)+0.1243(lnH)(lnD)+8.87554[ln(T+20)]+4.8775(lnPR)-1.3646(lnPR)[ln(T+20)]	0.904	0.59
$\mathrm{lnP_w}$ =-6.9610+0.0744(lnA)+1.5935(lnD)+0.7738(lnH)+0.0939(lnH)(lnD)+0.9671[ln(T+20)]+0.5896(lnPR)-0.1543(lnPR)[ln(T+20)]	0.991	0.18
$\mathrm{lnP_{bk}}$ =-14.4224-0.1233(lnA)+0.7839(lnD)+0.2179(lnH)+0.3397(lnH)(lnD)+3.6427[ln(T+20)]+1.8868(lnPR)-0.5671(lnPR)[ln(T+20)]	0.969	0.29

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

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

ln(Y)	*Independent variables*[2]								
	lnA(I)	*lnD(II)*	*lnH(III)*	*(lnH)·(lnD) (IV)*	*I+II+III+IV*	*ln(T+X) (V)*	*lnPR (VI)*	*(lnPR)·[ln(T+X)] (VII)*	*V+VI+VII*
Larix									
ln(*Pa*)	1.9	42.6	7.5	16.7	68.7	10.7	10.6	10.0	31.3
ln(*Ps*)	2.9	37.6	16.3	12.0	68.8	10.5	10.7	10.0	31.2
ln(*Pf*)	23.0	33.2	16.8	15.4	88.4	5.2	3.5	2.9	11.6
ln(*Pb*)	16.0	33.5	17.4	16.2	83.1	6.9	4.7	5.3	16.9
X±σ[1]	11.0±10.3	36.7±4.4	14.5±4.7	15.1±2.1	77.3±10.1	8.3±2.7	7.4±3.8	7.1±3.5	22.8±10.1
Quercus									
ln(*Pa*)	1.5	52.6	6.1	13.5	73.7	8.3	9.8	8.2	26.3
ln(*Ps*)	4.1	50.6	17.0	14.4	86.1	4.3	5.4	4.2	13.9
ln(*Pf*)	15.0	37.8	12.9	6.2	71.9	9.3	9.5	9.3	28.1
ln(*Pb*)	4.4	44.7	13.6	6.7	69.4	9.3	12.0	9.3	30.6
X±σ	6.3±6.0	46.4±6.7	12.4±4.6	10.2±4.4	75.3±7.4	7.8±2.4	9.2±2.8	7.8±2.4	24.7±7.4

[1] X±σ – mean ± standard deviation;

[2] Designations of independent variables see in characteristics of equations (1).

2019a), and the results of the calculation of Equation (1) are given in Table 4. The ratio of harvest biomass data and values obtained by the calculation of initial and additive models biomass of *Larix* spp. and *Quercus* spp. shows the high correlation coefficients (R) and the absence of visible differences in the structure of residual dispersions between the two models (Figures 3 and 4).

Since the tabulation of additive equations using the given values A, D, H, T and PR results in a too cumbersome table, the 3D-figures of the tree biomass dependence upon temperature T and precipitation PR is designed using its fragment for trees of the age A equal 100 years, the diameter D equal 20 cm and the height H equal 18 m (Figures 5 and 6).

Discussion

Configuration analysis of the surfaces obtained in three-dimensional space in Figures 5 and 6 show that the two tree genera differ greatly in the response of their biomass structure to changes in temperature and precipitation. Moreover, the trends of their responses are in parts directly opposite.

The regularity common to all the biomass components of oaks: in the cold zones ($T = –20°C$) some precipitation increase leads to the increase of biomass but in the warm ones ($T = 0°C$), precipitation does not affect biomass. In wet areas ($PR = 800$ mm) some increase of temperature causes a decrease of biomass, and in dry areas ($PR = 300\text{-}400$ mm) it causes an increase.

In larches, the reaction of the biomass of all components to an increase in precipitation in cold zones is directly opposite in comparison with oaks, i.e. it decreases as precipitation increases. But in warm areas, the reactions of the two genera to increased precipitation coincide, i.e. precipitation does not affect the biomass of all components, both in larches and oaks. In wet areas, larch biomass components react to temperature increases in the opposite way, i.e. the aboveground and stem biomass increases, but the biomass of foliage and branches decreases. In dry areas, the reaction to the temperature of all larch and oak biomass components is unambiguous and opposite, i.e. there is a decrease in the larch biomass of all components as temperatures rise and in oak biomass vise versa. This situation can be commented on in terms of limiting factors.

It is well known that 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. Later, this principle was interpreted as the "Shelford's law of tolerance" or "extended concept of limiting factors" (Shelford, 1913; Esslen, 1905; Taylor, 1934; Molchanov, 1971; Odum, 1975). Today, this phenomenon has become widespread as the principle of limiting factors by Liebig-Shelford (Rozenberg et al., 2016).

Table 4: Final two-step additive models of tree biomass

	Larix spp.
	$Pa=101.1688\ A^{-0.0286} D^{1.4200} H^{0.3531} D^{0.1864(\ln H)} (T+50)^{-1.6980} PR^{-1.04978} (T+50)^{0.2763(\ln PR)}$
Step 1	$Pc=Pa[1+0.1299\ A^{0.5204} D^{-0.7347} H^{2.4023} D^{-0.2153(\ln H)} (T+50)^{0.0008} PR^{-0.4178} (T+50)^{0.0723(\ln PR)}]^{-1}$
	$Ps=Pa[1+7.6985\ A^{-0.5204} D^{0.7347} H^{-2.4023} D^{0.2153(\ln H)} (T+50)^{-0.0008} PR^{0.4178} (T+50)^{-0.0723(\ln PR)}]^{-1}$
Step 2a	$Pf=Pc[1+5.1072\ A^{0.1211} D^{0.1779} H^{-0.1968} D^{0.0506(\ln H)} (T+50)^{-0.6615} PR^{-0.2931} (T+50)^{0.1424(\ln PR)}]^{-1}$
	$Pb=Pc[1+0.19582\ A^{-0.1211} D^{-0.1779} H^{0.1968} D^{-0.0506(\ln H)} (T+50)^{0.6615} PR^{0.2931} (T+50)^{-0.1424(\ln PR)}]^{-1}$
Step 2b	$Pw=Ps[1+74.5051\ A^{-0.0312} D^{-0.0520} H^{-0.3239} D^{0.0002(\ln H)} (T+50)^{-1.1996} PR^{-0.8104} (T+50)^{0.2038(\ln PR)}]^{-1}$
	$Pbk=Ps[1+0.0134\ A^{0.0312} D^{0.0520} H^{0.3239} D^{-0.0002(\ln H)} (T+50)^{1.1996} PR^{0.8104} (T+50)^{-0.2038(\ln PR)}]^{-1}$
	Quercus spp.
	$P_a=7.96E\text{-}08\ A^{0.0254} D^{1.6723} H^{0.2228} D^{0.1413(\ln H)} (T+20)^{4.4574} PR^{2.2228} (T+20)^{-0.6737(\ln PR)}$
Step 1	$Pc=Pa[1+2.53E+10\ A^{0.2821} D^{-0.8871} H^{1.5722} D^{-0.0260(\ln H)} (T+20)^{-7.7077} PR^{-3.9084} (T+20)^{1.1921(\ln PR)}]^{-1}$
	$Ps=Pa[1+3.95E\text{-}11\ A^{-0.2821} D^{0.8871} H^{-1.5722} D^{0.0260(\ln H)} (T+20)^{7.7077} PR^{3.9084} (T+20)^{-1.1921(\ln PR)}]^{-1}$
Step 2a	$Pf=Pc[1+6.36E\text{-}04\ A^{0.3165} D^{0.4293} H^{-0.0620} D^{0.0106(\ln H)} (T+20)^{0.1897} PR^{1.1016} (T+20)^{-0.0359(\ln PR)}]^{-1}$
	$Pb=Pc[1+1.57E+03\ A^{-0.3165} D^{-0.4293} H^{0.0620} D^{-0.0106(\ln H)} (T+20)^{-0.1897} PR^{-1.1016} (T+20)^{0.0359(\ln PR)}]^{-1}$
Step 2b	$Pw=Ps[1+5.75E\text{-}04\ A^{-0.1977} D^{-0.8095} H^{-0.5559} D^{0.2458(\ln H)} (T+20)^{2.6756} PR^{1.2972} (T+20)^{-0.4128(\ln PR)}]^{-1}$
	$Pbk=Ps[1+1.74E+03\ A^{0.1977} D^{0.8095} H^{0.5559} D^{-0.2458(\ln H)} (T+20)^{-2.6756} PR^{-1.2972} (T+20)^{0.4128(\ln PR)}]^{-1}$

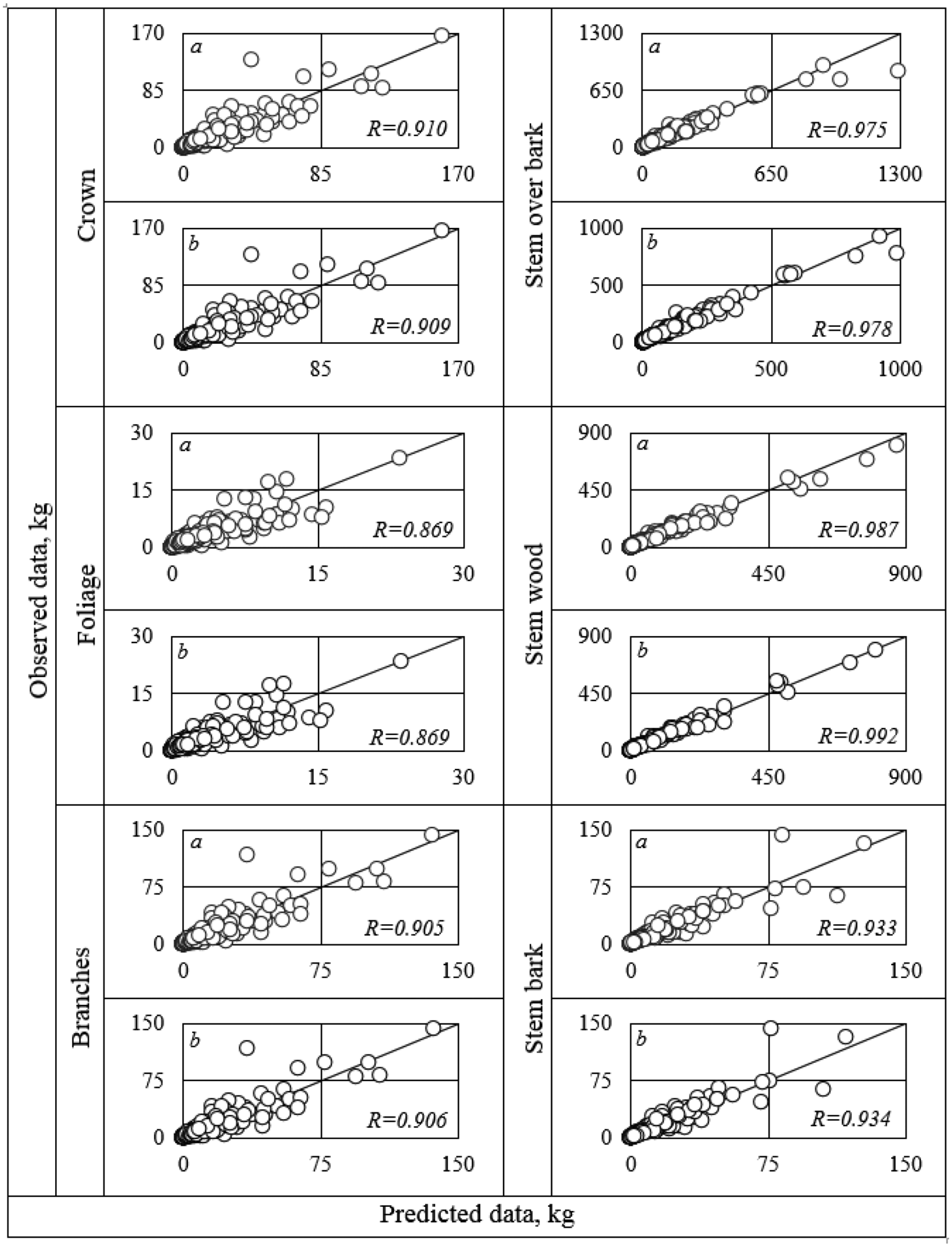

Figure 3: The ratio of the actual values and the values obtained by calculating the inital (a) and additive (b) models of the biomass of *Larix* spp. trees.

The manifestation of limiting factors was traced by researchers at regional and local levels in relation to the stem radial growth. In conditions of excessive moisture in the marshes in the Pre–Urals, where two limiting factors act simultaneously, i.e. excess of moisture and lack of oxygen in the soil, the cyclical radial growth

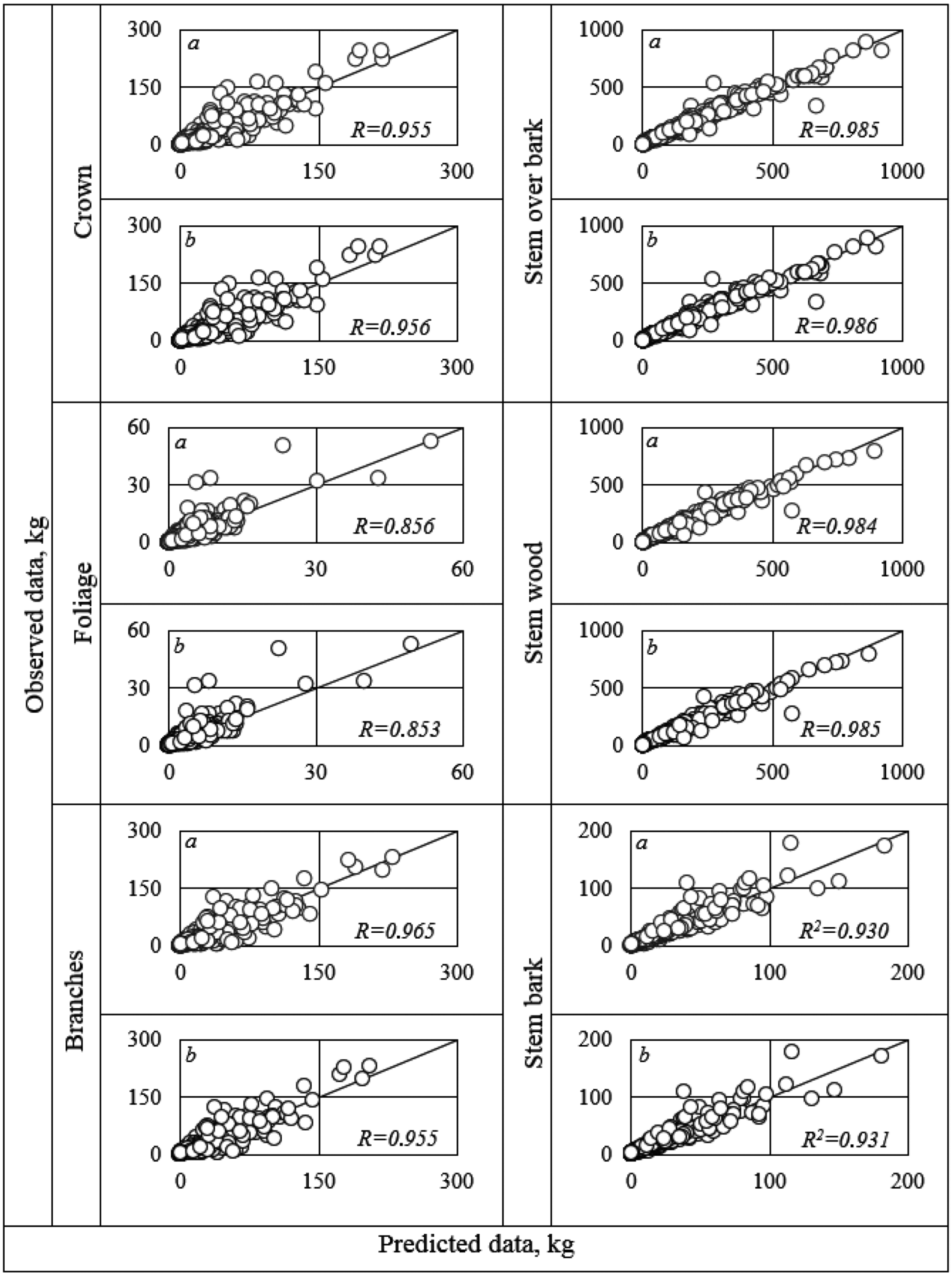

Figure 4: The ratio of the actual values and the values obtained by calculating the initial (a) and additive (b) models of the biomass of *Quercus* spp. trees.

is explained by the hydrological regime of a habitat (Olenin, 1982), and in the other extreme – lack of moisture in the steppe zone, there is increase in the sensitivity of tree growth to precipitation (Ricklefs, 1979). In the swamp forests of Western Siberia, under conditions of lack of heat, radial growth is limited by an increase in precipitation, and under conditions of lack of moisture in the soil, it is limited by an increase

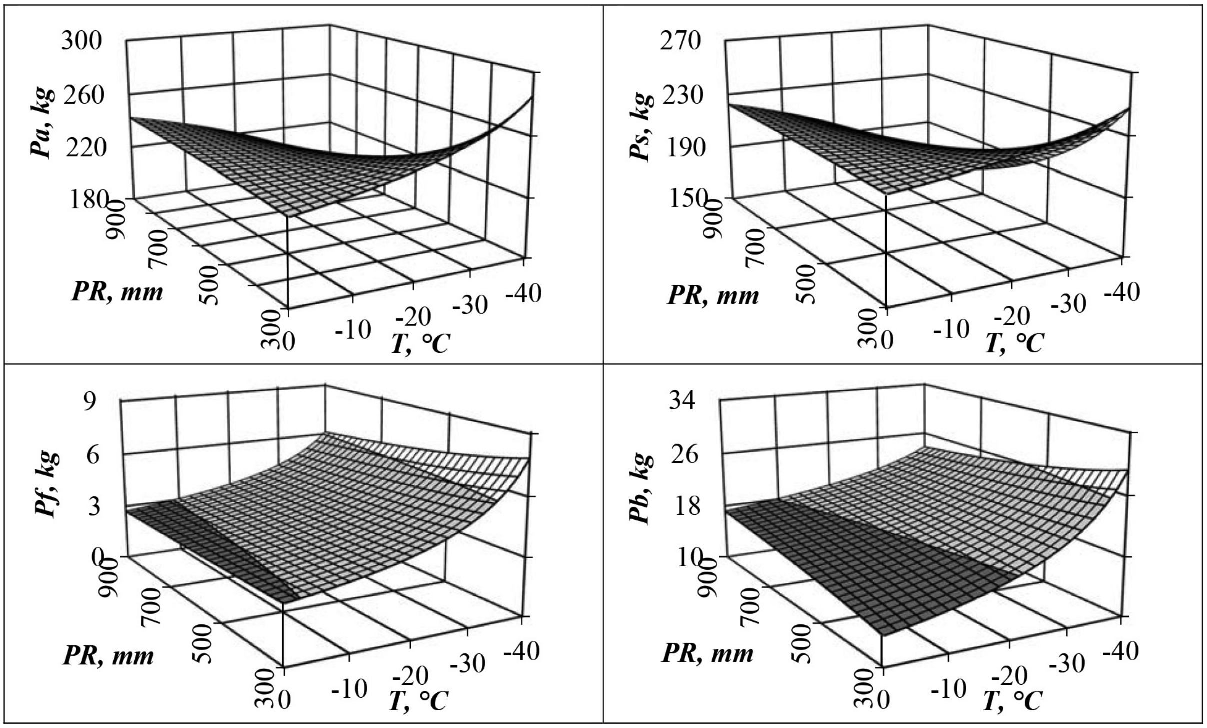

Figure 5: Dependence of biomass of *Larix* spp. equal-aged and equal-sized trees upon the January mean temperature (*T*) and precipitation (*PR*). Designations: *Pa, Ps, Pf,* and *Pb* are correspondingly biomass: aboveground, stems, foliage, and branches, kg.

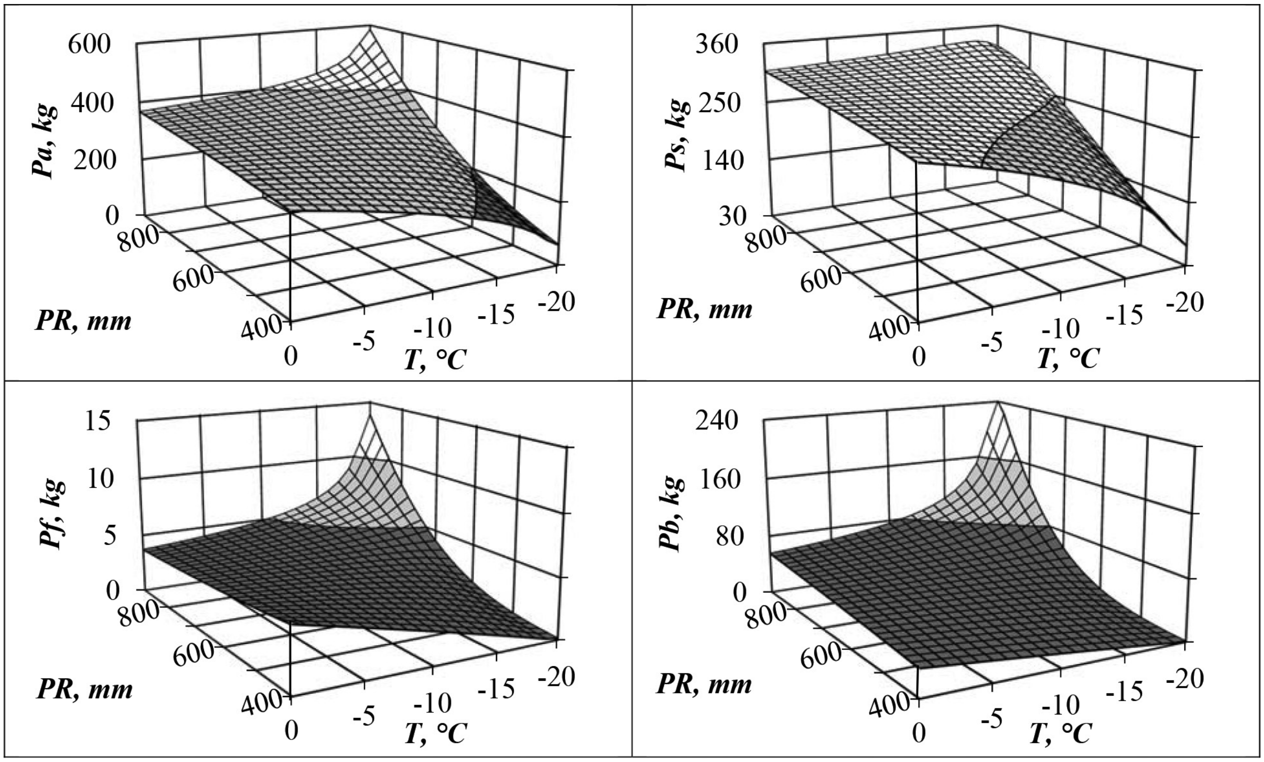

Figure 6: Dependence of biomass of *Quercus* spp. equal-aged and equal-sized trees upon the January mean temperature (*T*) and precipitation (*PR*). Designations see above.

in temperature (Glebov and Litvinenko, 1976). In conditions of lack of heat in the North of Eurasia, the productivity of forest cover increases with increasing temperature, and in the conditions of the southern forest-steppe, precipitation plays a dominant role (Molchanov, 1976; Berner et al., 2013).

According to our results, the factors limiting the biomass of trees differ not only between the two tree genera but also between different components of biomass within the genus. The limiting factor for all the biomass components of *Larix* at low temperatures (*T* = –40°C) is excessive precipitation, but in warm areas (*T* = 0°C) - excessive temperatures, irrespective of the level of precipitation. In regions of increased moisture supply (*PR* = 900 mm), the limiting factor for aboveground and stem biomass is a decrease in temperature, and for the biomass of foliage and branches – it increases. In regions of insufficient moisture supply (*PR* = 300 mm), the limiting factor for all biomass components is the temperature increase.

For all components of *Quercus* biomass in areas of low temperatures (*T* = –20°C), the limiting factor is the lack of moisture, and in warm regions (*T* = 0°C) – excessive humidity. In regions of increased moisture supply (*PR* = 800 mm), the limiting factor for aboveground, foliage and branches biomass – the warm increase. In regions of insufficient moisture supply (*PR* = 400 mm), the limiting factor for all biomass components is the temperature decrease.

The reasons why the biomass of foliage and stem in *Larix* react to temperature change in the opposite ways in regions of increased moisture supply (*PR* = 900 mm) are still difficult to explain in biological terms. It can only be noted that such a contradiction was revealed at the level of forest cover in Russian Siberia (Lapenis et al., 2005). An increase in the proportion of foliage and a decrease in the proportion of stem growth was found with a simultaneous increase in temperature and precipitation, which is associated with increased deposition of assimilates in intensively transpiring foliage when the temperature grows. However, as temperature increases and precipitation decreases, the proportion of foliage decreases while the proportion of aboveground and root biomass in the same condition increases (Lapenis et al., 2005).

It is easy to see that in the equations for the aboveground biomass of larches and oaks (Tables 2 and 4) regression coefficients for variables *T* and *PR* have opposite signs. Naturally, this pattern is reflected in Figures 5 and 6: in cold zones (*T* = –20°C and colder), with increasing precipitation, the aboveground and stem biomass in larches decreases, and oaks increases. On the biomass of the crown, the named contradiction is expressed to a lesser extent. This difference between the reactions of larch and oak biomass to precipitation, as mentioned above, can be explained by their growth in different climatic zones: the range of larch is confined mainly to areas of continental climate, the ranges of oaks—to areas approaching the coasts of the Atlantic and Pacific oceans (Figures 1 and 2). Accordingly, the two deciduous genera have developed different adaptation strategies.

Natural zoning is considered as a spatial form of the law of quantity-quality transition (Rodoman, 1999). In fact, all territorial zones are mobile. If it takes millennia and centuries to replace the natural zones seen by A. Humboldt, then in anthropogenic geosystems it takes years. Positional reduction assumes that it is possible and necessary to reduce the properties of objects to derivatives from their geographical position and to deduce the properties of objects and places from their geographical position (Rodoman, 1977). Geologically formed climates of two neighbouring ecoregions determine not only the separation of one genus into two species or the replacement of one species by another but also the difference in the morphological structure and biomass of stands. The adaptation of species to the different climates of these regions lasted for thousands of years. We extrapolated the territorial climate difference to the currently predicted climate difference, and not territorial, but temporary (the method of analogies, or the comparative Humboldt's method).

The proposed equations can be used in the practical implementation of IPCC in different regions of Eurasia, characterised by current climate indicators and current taxation characteristics. But for predictive purposes, the applicability of our models may have limitations. Our models obtained and the patterns shown are hypothetical as they reflect the long-term adaptive responses of forest stands to regional climatic conditions and do not take into account the rapid trends of current environmental changes, which place serious constraints on the ability of forests to adapt to new climatic conditions (Givnish, 2002; Alcamo et al., 2007; Berner et al., 2013; Schaphoff et al., 2016; Spathelf et al., 2018; Vasseur et al., 2018). The law of limiting factors work 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 a final result may be determined by other limiting factors (Odum, 1975).

We can see the problems associated with the application of our equations for predictive purposes. First, the main share of the explained variability of tree biomass is assumed by the taxation indicators of trees. We have built 3D-surfaces (Figures 5 and 6) using current taxation indicators, but we do not know what the ratio of taxation indicators will be in the face of future climate changes. The second problem is the validity of applying spatial climate trends to temporal aspects since we cannot predict changes in the adaptive traits of trees of different species due to climate shifts. The consequences of sudden fluctuations in precipitation due to increasing droughts are particularly unpredictable. For example, in the Moscow region (Russia), after the catastrophic drought of 1938, under the conditions of a long-term experiment with mixed pine-spruce plantations having the age of 72 years, there was a sharp drop-off of trees, mainly spruce (92%), whose surface roots were affected first due to the drying of the upper soil horizon (Timofeev, 1939). The unpredictability of the frequency and intensity of droughts is very significant uncertainty, and one can hope that the combined use of modern breakthrough technologies, such as “Big Data” and “Artificial Intelligence”, will have a positive effect in removing this uncertainty.

The presented patterns are related to larch and oak forests, which are either pure or with a slight admixture of other tree species. However, there is a lot 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). In mixed stands, our resulting models may have biases.

A disadvantage of the database used in this study is the uneven spatial distribution and different representation of sampling sites and individual species over Eurasia (Figures 1 and 2; Table 1). 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 may be biased due to the greater “information weight” of ecoregions with the largest number of sampling sites. Methodological uncertainties causing biases in biomass amounts in individual tree parts may also affect the accuracy of the estimates. The response of forests to climate change also depends on whether the photosynthetic benefit from increased atmospheric CO_2 compensates for increased physiological stresses from higher temperature (Sperry, 2019).

Based on the above uncertainties, it can be stated that the proposed models provide a solution to the problem only in the first approximation. 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).

Conclusions

The authors conclude that any response of forests to climate change is species-specific, it reflects the biological and ecological specificities of each tree genus and species and their different adaptive strategies. There is also a need for further research on the molecular mechanisms of the response of tree biomass to climate change and the associated effects with the simultaneous interaction of various factors (Pucko et al., 2011; Gray and Brady, 2016).

The obtained models of the two tree genera biomass make it possible to establish quantitative changes in the biomass structure due to climatic changes, in particular, the mean temperature of January and mean annual precipitation. The proposed additive models, adapted for use in the forest area of Eurasia, are designed for a more accurate assessment of the carbon-depositing ability of two deciduous species.

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