Macedonian Journal of Ecology and Environment
Vol. 22, issue 1
pp. 59 - 70
Skopje (2020)
ISSN 1857 - 8330 (on-line)
Original scientific paper
Available online at www.mjee.org.mk

Compatible models for *Quercus* spp. stand biomass and net primary production sensitive to precipitation and winter temperature in Eurasia

Компатибилни модели за биомасата и нето примарната продукција на состоини од *Quercus* spp. кои се чувствителни на врнежи и зимски температури во Евроазија

Vladimir Andreevich Usoltsev[1,2], Seyed Omid Reza Shobairi[1*], Ivan Stepanovich Tsepordey[2]

[1] *Ural State Forest Engineering University, 620100 Yekaterinburg, Sibirskiy Trakt, 37, Russia*

[2] *Botanical Garden of Ural Branch of RAS, 620144 Yekaterinburg, ul. 8 Marta, 202a, Russia*

Abstract

Since ancient times, climate change has largely determined the fate of human civilization, which was related mainly with changes in the structure and habitats of forest cover. In the context of current climate change, one must know a change of forest sustainability and productivity under future climate conditions. For this purpose, the authors compiled the database of biomass and net primary production (NPP) of *Quercus* spp. on Eurasian area in the amount of 663 and 260 sample plots correspondingly and used the methodology of multivariate regression analysis. The first attempt of modeling changes in compatible component composition of biomass and NPP on the Trans-Eurasian hydrothermal gradients involving regional peculiarities of age and morphology of the forests is fulfilled. It is found significant positive relationship of aboveground and total biomass with the mean temperature of January, and negative relationship with the level of moisture, was established. For the biomass of foliage, branches and roots, the positive pattern is only for wet regions, but as we move towards arid regions, this relationship becomes negative, and in 3D interpretation, the pattern looks as a propeller -like surface. The patterns of changes in the total and aboveground NPP are similar to the corresponding patterns for total and aboveground biomass, and the patterns of changes in the NPP of foliage, branches, roots and stems in climatic gradients correspond to the same propeller-like 3D picture. It is necessary to create compatible transcontinental models of biomass and NPP, sensitive to climate change, for each tree species (genus) separately and to find out the biological and ecological reasons for the differences in the results.

Key words: genus *Quercus* spp., biosphere role of forests, forest biomass, net primary production, compatible models, mean January temperature, annual mean precipitation.

Submitted: 01.08.2020
Accepted: 14.09.2020

---

* Author for correspondence: Omidshobeyri214@gmail.com

Апстракт

Уште од дамнешни времиња, промените во климата ја определувале судбината на човечката цивилизација што е во најголем дел резултат на промените во структурата и хабитатите на шумската вегетација. Во контекст на моменталните климатски промени, треба да се познава одржливоста на шумите и нивната продуктивност во идните климатски услови. За таа цел, авторите направија база на податоци за *Quercus* spp. во Евроазија за биомасата и нето примарната продукција (НПП) во која се вклучени 663 и 220 плотови соодветно, а беше искористена мултиваријантна регресиска анализа. Ова е прв обид за моделирање на промените во составот на биомасата и НПП низ транс-европски хидротермички градиент, вклучувајќи ги регионалните особености на возраста и морфологијата на шумите. Значајна позитивна корелација беше констатирана помеѓу надземната и вкупната биомаса со средната јануарска температура, а негативна со влажноста. Кога станува збор за биомасата на листови, гранки и корења, позитивна врска е утврдена само за влажни региони, но придвижувајќи се кон сушни региони, корелацијата се менува во негативна, а во 3d интерпретација, образецот потсетува на површина од пропелер. Неопходно е да се развијат компатибилен трансконтинентални модели за биомасата и НПП, чувствителни на климатските промени за секој дрвенест вид одделно (и родови) со цел да се откријат биолошките и еколошките причини за разликите во добиените резултати.

Клучни зборови: *Quercus* spp., улога на шумите во биосферата, шумска биомаса, нето примарна продукција, компатибилни модели, средна јануарска температура, средногодишни врнежи.

Introduction

Active human economic activity has led to significant global changes in the functioning of the biosphere, and the observed climate warming has a significant impact on the vegetation cover of the planet (Halofsky et al. 2018; Kosanic et al. 2018), threatening humanity with going beyond its ecological niche (Xu et al. 2020). Study of biosphere role and climate conditionality of biological productivity of world forest is one of the most priority directions of ecology and biogeography sciences. Sustainable models to describe the carbon-sequestering capacity of forests within world or continents are needed.

The concept of biological productivity includes two components, i.e. biomass and net primary production (NPP). When revealing transcontinental trends in the carbon-deposition capacity of forests, it is needed to study the component composition not only of biomass, but also of NPP. It should be noted that current attempts of quantitative geographical analysis of the global distribution of forest NPP are sometimes reduced to its analysis only on the latitudinal gradient, without taking into account their species composition, age and morphology, and the resulting patterns are characterized by a large degree of uncertainty (Anderson et al. 2006; Keeling & Phillips 2007; Huston & Wolverton 2009). The modern attempts to identify global patterns of changes in forest NPP in relation to climate indices such as temperature and precipitation, but without taking into account their species composition mass-forming variables, do not show statistically significant patterns (Luyssaert et al. 2007). The reason is that the biological productivity influenced by forest morphology varies in natural conditions in a wide range that overlaps the range of NPP variation under the influence of temperature and precipitation only. Ignoring the morphological structure of stands when modeling regional patterns of their biological productivity gives significant biases, reaching 40-60 % compared with models that take into account the structure of stands (Usoltsev & Salnikov 1998).

There are theoretical reasons to assume a relationship between forest NPP and biomass, as both may be influenced by similar ecological factors. However, the attempt to identify the global dependence of the NPP upon the biomass of stands without taking into account the biomass component composition and mass-forming variables showed the presence of a poor coefficient of determination in the range only from 0.020 to 0.370 (Keeling & Phillips 2007). Similarly, the calculation of the dependence of the NPP of China‘s forests of all natural zones upon the average annual temperature and annual precipitation without taking into account the biomass component composition and mass-forming variables showed the presence of determination coefficients of only 0.196 and 0.054 respectively (Liu et al. 2016). The calculation of Russian forest NPP using species-specific regression models depending on the age and volume stock of stands (Zamolodchikov & Utkin 2000) resulted in a 2-3-fold overestimation in relation to the true value (Shvidenko et al. 2008, Usoltsev et al. 2011). Such models are not stable enough and cannot be used as predictive ones.

An improved calculation of the NPP based on a system of related equations, including not only mass-forming indicators of stands, but also biomass indices as independent variables (Usoltsev et al. 2011), showed deviations within only 8% from the results of two other alternative methods (Voronin et al. 2004; Shvidenko et al. 2008). Such method of combining biomass and NPP data suites for our study as having a logical justification.

In relation to a forest ecosystem, the regression model is the result of statistical estimation of the parameters of a system of mathematical expressions that characterize a certain biological concept of the relationship of phenomena. The variability of forest ecosystem parameters can be explained using not one, but several variables that are partially or completely interdependent. Separate modeling of such dependencies leads to the fact that the obtained estimates will not be balanced, or harmonized. Mathematical dependencies combined into a single logically consistent concept form a system of related (compatible) equations. Their main advantage is the internal consistency of the described chain of equations, according to which the dependent variable of the previous equation is included in the subsequent one as one of the independent variables (Clutter 1963; Borders 1989). Another method of harmonizing the patterns of biomass and NPP suggests regionalization of a model by introducing dummy variables (Draper & Smith 1966) encoding ecoregions or tree species affiliation of the harvest data. Biomass and NPP models that include mass-forming indices and dummy variables as regressors are known as mixed-effect models (Usoltsev et al. 2002; Fu et al. 2012, 2017; Zheng & Zeng 2013; Zeng 2017).

In the development of transcontinental models of biomass and NPP distribution, these two methods of harmonization seem promising. It is known that changes in the vegetation cover of Eurasia occur both in the latitudinal direction due to changes in the solar radiation (Grigoriev & Budyko 1956), and in the meridional direction due to changes in the continental climate (Komarov 1921). When using biomass and NPP databases compiled by the authors for six forest-forming species of Eurasia, a system of transcontinental species-specific models of forest NPP was designed that includes both the principle of recursive compatibility of variables, and encoding regions with dummy variables following subsequent analysis of the results in connection with the natural zonality and climate continentality (Usoltsev et al. 2017).

However, models describing changes in NPP in gradients of natural zoning and climate continentality do not match the current trends of climate variables of temperature and precipitation (Hubau et al. 2020). Besides, models that include mass-forming indices and dummy variables as regressors (mixed-effect models) have the disadvantage that they take into account regional shifts in the calculated values only by the intercept term, but the regression coefficients are assumed to be unchanged for regions, what is not true.

The purposes of this study are:

- to calculate models of the biomass component composition of *Quercus* spp. stands in Eurasia in dependence of the mass-forming indices of stands, as well as of average temperatures and precipitation;
- to calculate models of the NPP component composition of *Quercus* spp. stands depending on mass-forming indices, as well as on average temperatures and precipitation, combined with models of biomass on a recursive, or compatible principle;
- to analyze changes in the biomass components of oak stands in the Trans-Eurasian temperature and precipitation gradients.

Objects and methods

From the database on the biomass and NPP of forests of Eurasia (Usoltsev 2020) the materials in the amount of 663 sample plots with the estimates of biomass of 20 species of *Quercus spp*. and 260 plots with the estimates of not only biomass, but also annual NPP (t/ha), are selected. The distribution of sample plots with stand biomass definitions on the map of Eurasia is shown in Fig. 1, and by tree species and countries in Table 1.

Fig. 1. Distribution of sample plolts with measurements of biomass (t/ha) of 663 oak stands (genus *Quercus* spp.) on the territory of Eurasia.

Table 1. Distribution of the number of sample plots with definitions of oak biomass (t / ha) by species and countries

Species	Country	Number of sample plots
Quercus robur L.	Russia, Belarus, Ukraine, Belgium, Great Britain, Denmark, Moldova, Switzerland, Sweden, Spain, Czech Republic, France, Poland, Estonia	388
Q. acutissima Carruth.	China	157
Q. petraea Liebl.	France, Bulgaria, Moldova, Hungary, Belarus, Belgium, United Kingdom, Netherlands	35
Q. mongolica Fisch. *ex* Ledeb.	Russia	15
Q. serrata Murray	China, Japan	10
Q. coccifera L.	Spain	8
Q. ilex L.	Spain, Italy, France	7
Q. imeretina Stev.	Georgia	6
Q. rubra L.	Bulgaria, United Kingdom	5
Q. pubescens Willd.	Moldova, France, Romania	4
Q. iberica Stev.	Georgia, Azerbaijan	4
Q. pyrenaica Willd.	Spain	4
Q. leucotrichophora A.Camus	Georgia, Pakistan	4
Q. castaneifolia C. A. Mey.	Azerbaijan	3
Q. glauca Thunb.	Japan	3
Q. phillyraeoides Gray.	Japan	3
Q. crispula Blume	Japan	2
Q. longipes Stev.	Bulgaria	2
Q. lanuginosa Thuill.	Pakistan	2
Q. robur subsp. *pedunculiflora* (K.Koch) Menitsky	Romania	1
Total		663

In the database, the time of establishment of sample plots covers the period from 1947 to 2009. Sample trees were usually taken on each of the sample plots in a number from 5 to 10 trees, and then samples were taken from each biomass component to determine the dry matter content (and for wood and bark of stems also to determine the basic density) and after drying the samples at the temperature of 80-100^0 C, the results were recalculated for the whole tree. The procedure for determining NPP was more time-consuming, the review of methods for its obtaining on sample plots was shown earlier (Usoltsev 2007). The quantity of each biomass and NPP component per 1 ha was determined by allometric method. Not all biomass components are equally presented in the database: if the aboveground biomass is determined on the all 663 plots, the mass roots only in 390 ones. NPP data were obtained from 260 and 225 plots correspondingly.

Each sample plot, at which biomass and NPP of forest stands was estimated, is positioned in accordance to mean January temperature isolines (World Weather Maps 2007) and to mean annual precipitation ones (http://www.mapmost.com/world-precipitation-map/free-world-precipitation-map/), and the initial data matrix is compiled in which the values of biomass components and of stand taxation characteristics are mated with corresponding values of mean January temperature and annual precipitation. A similar matrix is compiled for the NPP values. The matrices are included then into regression analysis procedure. The regression coefficients of multiple regression equations were calculated using the Statgraphics software (see http://www.statgraphics.com/for more information).

A schematic map of the isolines of the mean January temperature was used, rather than the mean annual temperature, since the influence of warming on the environment is most pronounced in Northern latitudes, and in the cold half of the year (Laing & Binyamin 2013, Morley et al. 2017). Obviously, taking the mean January temperature as one of the independent variables, we get a more reliable dependence having the higher predictive ability.

Besides, to ensure the maximum stability of the model, each of the selected factors (independent variables) should be presented in the maximum range of its variation (Usoltsev 2004). In our example, mean January temperatures range from -20°C in the Far East of Russia to +10°C in the subtropics of China, and mean annual precipitation from 317 mm in the Central Asia to 1,650 mm in the territory of the south-eastern China.

Results and discussion

The initial recursive dependencies are calculated:

$$\ln N = a_0 + a_1(\ln A) + a_2[\ln(Tm+30)] + a_3(\ln PRm) + a_4[\ln(Tm+30)](\ln PRm); \quad (1)$$

$$\downarrow$$

$$\ln V = a_0 + a_1(\ln A) + a_2(\ln N) + a_3(\ln A)(\ln N) + a_4[\ln(Tm+30)] + a_5(\ln PRm) + a_6[\ln(Tm+30)](\ln PRm); \quad (2)$$

$$\downarrow$$

$$\ln P_i = a_0 + a_1(\ln A) + a_2(\ln V) + a_3(\ln N) + a_4[\ln(Tm+30)] + a_5(\ln PRm) + a_6[\ln(Tm+30)](\ln PRm); \quad (3)$$

$$\downarrow$$

$$\ln Zi = a_0 + a_1(\ln A) + a_2(\ln V) + a_3(\ln N) + a_4(\ln P_i) + a_5[\ln(Tm+30)] + a_6(\ln PRm) + a_7[\ln(Tm+30)](\ln PRm) \quad (4)$$

In equations (1)-(4): P_i – biomass of i-th component, t/ha; Z_i – annual NPP of i-th component, t/ha; A – stand age, yrs; V – stem volume, m^3/ha; N – tree density, 1000/ha; i – index of biomass component: total (t), aboveground (a), underground, or roots (r), stem over the bark (s), foliage (f), and branches (b); PRm – mean annual precipitation, мм; Tm – mean January temperature, °C. Because mean January temperature in northern part of Eurasia has negative values, corresponding independent variable is modified to the form ($Tm+30$).

The results of calculating equations (1)-(4) are shown in Table 2. The equations here and below show only variables that are significant at the probability level of P_{95} or better. The only exception was the coefficients a_4, a_5 and a_6 of equation (3) for stem biomass, which means that climate variables do not affect the variability of this component of biomass. The proportions of the contribution of independent variables to the explanation of the variability of the dependent variable in equations (3) and (4) are shown in Table 3.

The equations (1)-(4) are tabulated in the sequence indicated by arrows for the specified age values in the range from 10 to 100 years (not shown here). For oak biomass and NPP, the values of the required indices for the age of 100 years are taken from the resulting table and presented as 3-dimensional graphs of their relationship with the average temperatures of January and with the average annual precipitation (Figs. 2 and 3).

Before discussing the patterns shown in Figures 2 and 3, let‘s turn to Table 3, which describes the contribution of various independent variables to the explanation of the variability of the desired indices of biomass and NPP. We can see that mass-forming variables explain in average about

Table 2. Characteristic of equations (1)-(4) for forest stands of the genus *Quercus* in Eurasia

$\ln(Y)$*	a_0**	$\ln A$	$\ln V$	$\ln N$	$(\ln A)(\ln N)$	$\ln Pi$	$\ln(Tm+30)$	$\ln PRm$	$[\ln(Tm+30)](\ln PRm)$	SE***	adjR^2****
$\ln(N)$	3.3600	-1.1895	-	-	-	-	0.4477	0.0132	0.0037	0.62	0.616
$\ln(V)$	0.0824	0.9743	-	-0.2683	0.0738	-	1.4433	0.0221	-0.1717	0.58	0.560
$\ln(Pt)$	7.7739	0.1625	0.7306	0.0597	-	-	-2.1252	-1.2538	0.3776	0.18	0.924
$\ln(Pa)$	5.8799	0.1071	0.8223	-0.0043	-	-	-1.7786	-0.9870	0.3097	0.17	0.951
$\ln(Pr)$	22.4276	0.4038	0.4973	0.2658	-	-	-6.7516	-3.7174	1.0893	0.42	0.623
$\ln(Ps)$	0.3418	0.0684	0.9518	0.0180	-	-	-0.0089	-0.2311	0.0303	0.16	0.967
$\ln(Pf)$	10.0733	0.2212	0.2063	0.1469	-	-	-4.6694	-1.6037	0.7131	0.41	0.423
$\ln(Pb)$	25.3852	0.2394	0.5305	-0.0735	-	-	-8.9476	-4.0631	1.4012	0.46	0.673
$\ln(Zt)$	-6.7529	-0.3700	-0.1192	0.0574	-	0.8681	1.3145	1.1916	-0.2429	0.16	0.746
$\ln(Za)$	-6.6107	-0.3824	-0.1444	0.0680	-	0.9253	0.8727	1.2679	-0.2085	0.18	0.739
$\ln(Zr)$	9.3663	-0.8626	0.0696	-0.0074	-	0.8372	-2.9004	-1.5248	0.4940	0.31	0.725
$\ln(Zs)$	12.1985	-0.8382	0.6158	0.0711	-	0.3332	-4.4102	-1.8139	0.6535	0.22	0.855
$\ln(Zf)$	-4.6195	-0.0085	-0.0294	-0.0070	-	0.9958	1.5064	0.7735	-0.2433	0.07	0.969
$\ln(Zb)$	10.9323	-0.9176	0.1793	-0.1354	-	0.9177	-2.4562	-1.6738	0.3855	0.36	0.717

* Dependent variables; ** The constant corrected for logarithmic retransformation by: Baskerville (1972); *** *SE* – standard error of the equations.

**** *adjR*^{2} – determination coefficient adjusted for the number of variables;

78 % of the variability of all components of biomass, including 57% of the contribution from the stem volume. Climate variables explain only about 22 % of the total variability of biomass, i.e. less than about four times as much as mass-forming variables. At the same time, the variability of stem mass is explained by mass-forming variables by almost 99%, including 93% of the stem volume. Climate variables explain only about 1 % of the total variability of stem biomass. Since climate variables do not have any significant effect on the variability of stem biomass and explain the negligible share of the total variability of stem biomass, the diagram for this biomass component on Fig. 2 is not shown.

Table 3. Contribution of independent variables of equations (3) and (4) to the explanation of variability of dependent variables (%)

Y *	Independent variables***								
	A	*V*	*N*	*Pi*	*A+V+N+Pi*	*T*	*P*	*P·T*	*T+P+P·T*
Equation (3)									
Pt	10.6	67.8	6.9	-	85.3	4.4	5.2	5.1	14.7
Pa	6.3	80.7	0.5	-	87.5	3.7	4.1	4.2	12
Pr	17.5	32.9	20.7	-	71.1	9.1	10.1	9.7	28.9
Ps	3.9	92.7	2	-	98.6	0.02	1	0.4	1.42
Pf	17.4	27.5	21.4	-	66.3	12.6	8.7	12.4	33.7
Pb	12	40.2	6.2	-	58.4	14.2	13	14.4	41.6
X±σ**	11.3 ±2.3	57.0 ±11.1	9.6 ±3.7	-	77.9±6.1	7.3 ±2.3	7.0 ±1.8	7.7 ±2.2	22.1±6,2
Equation (4)									
Zt	32,7	5,9	9,3	33,5	81,4	4,7	8,3	5,6	18,6
Za	33.7	6.5	10.2	35.4	85.8	2.6	7.5	4.1	14.2
Zr	41.8	3.2	6	31.2	82.2	5.7	5.8	6.3	17.8
Zs	49.3	13.3	7.1	6.6	76.3	8.5	6.9	8.3	23.7
Zf	0.8	3	1.1	81.3	86.2	4.5	4.6	4.7	13.8
Zb	33	7.5	8.5	40.7	89.7	3	4.3	3	10.3
X±σ	31.9 ±6.7	6.6 ±1.5	7.0 ±1.3	38.1 ±9.9	83.6±1.9	4.8 ±0.9	6.2 ±0.6	5.3 ±0.7	16.4±1.9

* *Y* – dependent variables of equations (3) and (4);

** X±σ – mean and standard deviation;

*** - Designations of independent variables see in characteristics of equations (1)-(4).

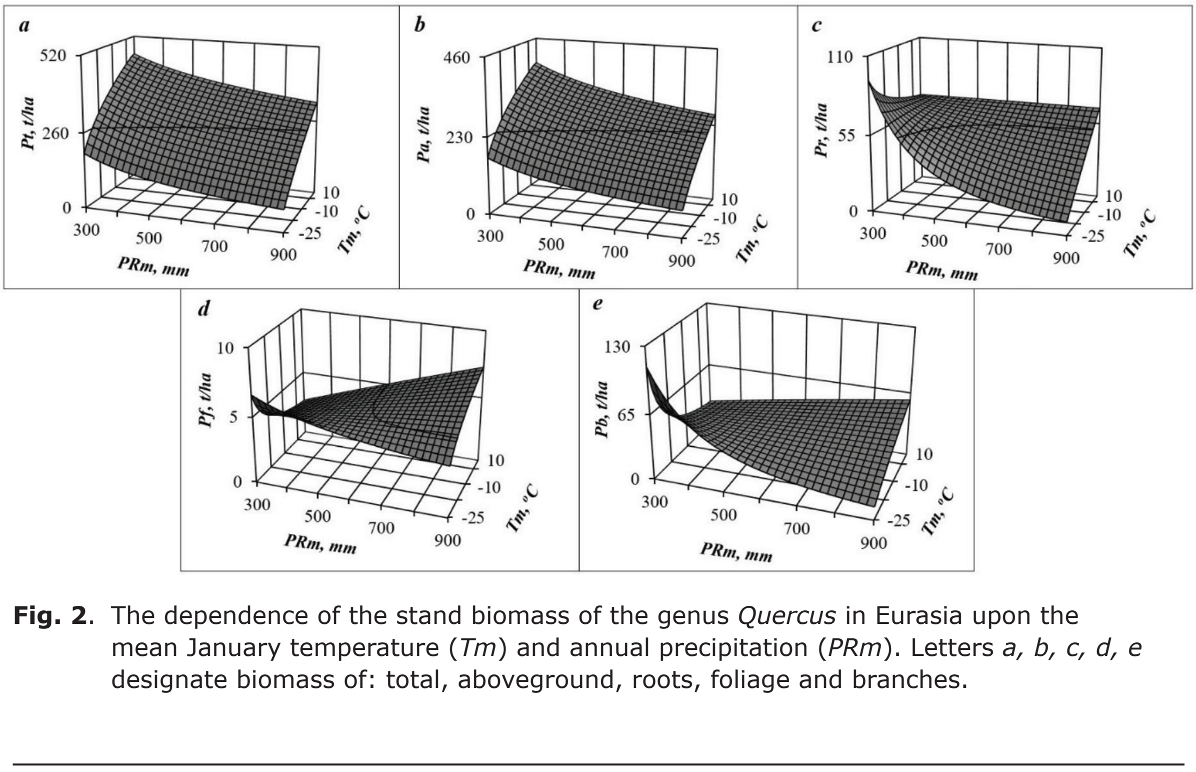

Fig. 2. The dependence of the stand biomass of the genus *Quercus* in Eurasia upon the mean January temperature (*Tm*) and annual precipitation (*PRm*). Letters *a, b, c, d, e* designate biomass of: total, aboveground, roots, foliage and branches.

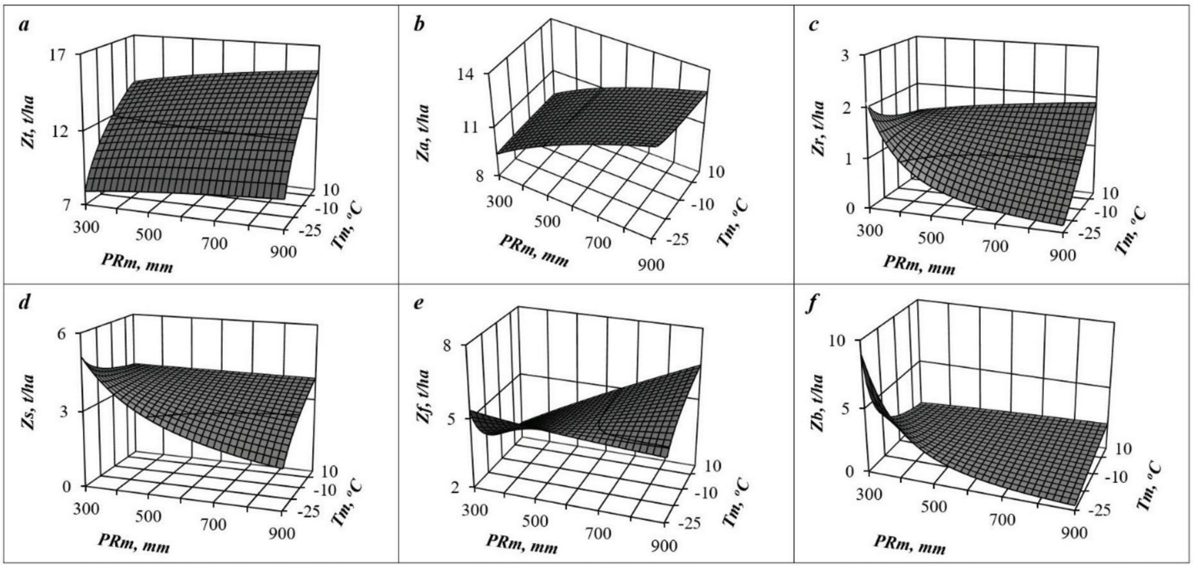

Fig. 3. The dependence of the stand NPP of the genus *Quercus* in Eurasia upon the mean January temperature (*Tm*) and annual precipitation (*PRm*). Letters *a, b, c, d, e, f* designate NPP of: total, aboveground, roots, stems, foliage and branches.

The relative contributions of independent variables to the explanation of NPP variability are different too: mass-forming variables account for about 84 % of the NPP variability, including the 38% contribution from the stem volume and the 32% contribution from the stand age. Climate variables explain about 16 % of the total NPP variability, i.e. less in comparison to the explained biomass variability. At the same time, the variability of stem NPP is explained by climate variables by almost 24%, i.e. more than the other components (10-19%).

When analyzing the reaction of the *Quercus* biomass structure to temperature and precipitation in their transcontinental gradients (Fig. 2), there are clearly expressed positive relations of aboveground and total biomass with the mean temperature of January. If for the named components this regularity occurs regardless of the level of water availability in the regions, then for the mass of foliage, branches and roots this positive relationship with temperature is characteristic only for sufficiently water-rich regions (*PRm* = 800-900 mm). As we move from moisture-rich to water-deficient regions (*PRm* = 300 mm), this positive trend of foliage, branches and roots biomass changes to a negative one (see Fig. 2).

Accordingly, during the transition from water-deficient to moisture-rich regions, aboveground and total biomass decreases in all warm zones. The mass of leaves, branches and roots under the same conditions (i.e. with increased water availability) decreases most intensively in cold climatic zones, and in warm climatic conditions either does not change (as in the roots), or increases (as in the foliage and branches) (see Fig. 2).

The patterns of changes in the total, aboveground, roots, foliage and branches NPP in climatic gradients are the same as for biomass (Fig. 3). Changes in the stem NPP in temperature and precipitation gradients are subject in this case to the same propeller-shaped 3D-pattern as in the biomass and NPP of roots, foliage and branches.

At first glance, it may seem paradoxical that the reaction of the mass of the assimilation apparatus in warm climatic conditions does not decrease with increasing precipitation, as is typical for wood components, but increases. However, such contradictory situations have been encountered before. In particular, it is shown (Lapenis et al. 2005) that in Siberia, with the simultaneous warming of the climate and a decrease in precipitation, the share of assimilation mass of forest cover decreases, and the share of wood components increases. This is explained by the specifics of the assimilation apparatus, namely its transpiration activity, when warming and a corresponding increase in transpiration requires an increase in the influx of assimilates into the foliage, and climate desiccation reduces this influx of assimilates by reducing transpiration activity. Perhaps this phenomenon demonstrates the future scenario of acclimatization of trees to continuing warming and changes in the water balance of territories.

The resulting models and patterns can be used to predict changes in the component composition of biomass and NPP of oak stands due to changes in climate variables. However, they are hypothetical, and not only because of the relatively small contribution of climate variables to explain the variability of biomass and NPP of oak stands: they reflect long-term adaptive responses of stands to regional climate conditions and do not take into account the rapid trends of current environmental changes, which impose serious restrictions on the ability of forests to adapt to new climate conditions (Givnish 2002; Alcamo et al. 2007; Berner et al. 2013; Schaphoff et al. 2016; Spathelf et al. 2018; Vasseur et al. 2018). Liebig's law of limiting factor works well in stationary conditions. When limiting factors change rapidly (for example, air temperature or precipitation), forest ecosystems are in a transient (non-stationary) state, in which some factors that have not yet been significant may come to the fore, and the final result may be determined by other limiting factors (Odum 1975). The disadvantage of the database used in our study is the uneven distribution of experimental sample plots with biomass and NPP data across the territory of Eurasia. Since regression analysis is performed using the common least squares method, its estimates in regions with the minimum number of sample plots may be skewed due to the greater „information weight" of those regions where their number is maximum. The response of forest biomass to climate change will also depend on how much the photosynthetic benefits of increased atmospheric CO_2 can offset the increased physiological stresses of climate change (Sperry et al. 2019).

As noted above, the main pool of our harvest data on forest biomass in Eurasia was obtained since 1947 to 2009, 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 phenologic varieties of oak, then the assessment of net primary production shows a 1.6-fold advantage of late-blooming variety over the early-blooming one (Zhou, 1992).

Given the noted methodological and conceptual uncertainties, the results presented in this study should be considered as preliminary ones. They may change as the original forest biomass and NPP databases will be updated and methods of analysis will be improved.

Conclusions

When using the database of 663 and 260 sample plots with estimates of biomass and net primary production (NPP) of stands of the genus *Quercus* in Eurasia, a statistically significant positive relationship of aboveground and total biomass with the mean temperature of January, regardless of the level of moisture, was established. For the biomass of foliage, branches and roots, the positive pattern is only characteristic for wet regions, but as we move towards arid regions, this relationship becomes negative, and in 3D interpretation, the pattern looks as a propeller -like surface.

The patterns of changes in the total and aboveground NPP are similar to the corresponding patterns for total and aboveground biomass, and the patterns of changes in the NPP of foliage, branches, roots and stems in climatic gradients correspond to the same propeller-like 3D picture.

The results obtained can be useful in managing the biosphere functions of forests, which is important in implementing climate stabilization measures, as well as in validating the results of simulation experiments to assess the carbon-deposition capacity of forests. They also provide a preliminary view of possible changes in oak forest biological productivity under the influence of climate change.

References

Alcamo J., Moreno J.M., Nováky B., Bindi M., Corobov R., Devoy R.J.N et al. (2007). *Europe: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. In: Parry M.L., Canziani O.F., Palutikof J.P., van der Linden P.J., Hanson C.E. (eds.): Climate change. Cambridge University Press, Cambridge: 541–580.

Anderegg W.R.L., Anderegg L.D.L., Kerr K.L., Trugman A.T. (2019). Widespread droughtinduced tree mortality at dry range edges indicates that climate stress exceeds species' compensating mechanisms. *Global Change Biology*, 25: 3793–3802.

Anderson K.J., Allen A.P., Gillooly J.F., & Brown J.H. (2006). Temperature-dependence of biomass accumulation rates during secondary succession. *Ecol. Lett.*, 9: 673-682.

Baskerville G.L (1972). Use of logarithmic regression in the estimation of plant biomass. *Can. J. For. Res.*, 2: 49-53.

Berner L.T., Beck P.S.A., Bunn A.G., & Goetz S.J. (2013). Plant response to climate change along the forest-tundra ecotone in northeastern Siberia. *Global Change Biol.*, 19 (11): 3449–3462. DOI: 10.1111/gcb.12304.

Borders B.E. (1989). Systems of equations in forest stand modelling. *Forest Sci.*, 35 (2): 548-556.

Clutter J.L. (1963). Compatible growth and yield models for loblolly pine. Forest Sci., 9 (3): 354-371.

DeLeo V.L., Menge D.N.L., Hanks E.M., et al. (2020). Effects of two centuries of global environmental variation on phenology and physiology of *Arabidopsis thaliana*. *Global Change Biology*, 26: 523–538.

Draper N. & Smith H. (1966). *Applied regression analysis*. New-York, Wiley. Translated under the title "Prikladnoy regressionnyi analiz". Moscow, Statistika, 1973. 362 pp.

Fu L., Sun W., & Wang G. (2017). A climate-sensitive aboveground biomass model for three larch species in northeastern and northern China. *Trees*, 31: 557–573.

Fu L.Y., Zeng W.S., Tang S.Z., Sharma R.P. & Li H.K. (2012). Using linear mixed model and dummy variable model approaches to construct compatible single-tree biomass equations at different scales – A case study for Masson pine in Southern China. *Journal of Forest Science*, 58(3): 101-115.

Givnish T.J. (2002). Adaptive significance of evergreen vs. deciduous leaves: Solving the triple paradox. *Silva Fenn*., 36 (3): 703–743.

Grigoriev A.A. & Budyko M.I. (1956). On the periodic law of geographical zoning. *Doklady Akadimii Nauk SSSR*, 110(1): 129-132.

Halofsky J.S., Conklin D.R., Donato D.C., Halofsky J.E., & Kim J.B. (2018). Climate change, wildfire, and vegetation shifts in a high-inertia forest landscape: Western Washington, U.S.A. *PLoS ONE*, 13 (12): 1-23. e0209490.

Hubau W., Lewis S.L., Phillips O.L., Affum-Baffoe K., Beeckman H., Cuní-Sanchez A., Daniels A.K., Ewango C.E.N., Fauset S., Mukinzi J.M., Sheil D., Sonké B., Sullivan M.J.P., Sunderland T.C.H., Taedoumg H., Thomas S.C., White L.J.T., Abernethy K.A., Adu-Bredu S., Amani C.A., Baker T.R., Banin L.F., Baya F., Begne S.K., Bennett A.C., Benedet F., Bitariho R., Bocko Y.E., Boeckx P., Boundja P., Brienen R.J.W., Brncic T., Chezeaux E., Chuyong G.B., Clark C.J., Collins M., Comiskey J.A., Coomes D.A., Dargie G.C., de Haulleville T., Kamdem M.N.D., Doucet J.L., Esquivel-Muelbert A., Feldpausch T.R., Fofanah A., Foli E.G., Gilpin M., Gloor E., Gonmadje C., Gourlet-Fleury S., Hall J.S., Hamilton A.C., Harris D.J., Hart T.B., Hockemba M.B.N., Hladik A., Ifo S.A., Jeffery K.J., Jucker T., Yakusu E.K., Kearsley E., Kenfack D., Koch A., Leal M.E., Levesley A., Lindsell J.A., Lisingo J., Lopez-Gonzalez G., Lovett J.C., Makana J.R., Malhi Y., Marshall A.R., Martin J., Martin E.H., Mbayu F.M., Medjibe V.P., Mihindou V., Mitchard E.T.A., Moore S., Munishi P.K.T., Bengone N.N., Ojo L., Ondo F.E., Peh K.S., Pickavance G.C., Poulsen A.D., Poulsen J.R., Qie L., Reitsma J., Rovero F., Swaine M.D., Talbot J., Taplin J., Taylor D.M., Thomas D.W., Toirambe B., Mukendi J.T., Tuagben D., Umunay P.M., van der Heijden G.M.F., Verbeeck H., Vleminckx J., Willcock S., Wöll H., Woods J.T. &, Zemagho L. (2020). Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, 579: 1-27.

Huston M.A., & Wolverton S. (2009). The global distribution of net primary production: resolving the paradox. *Ecol. Monogr.*, 79 (3): 343–377.

Keeling H.C., & Phillips O.L. (2007). The global relationship between forest productivity and biomass. *Global Ecol. Biogeogr.*, 16: 618-631.

Komarov V.L. (1921). Meridional'naya zonal'nost' organizmov (Meridional zonality of organisms), *Dnevnik I vserossiiskogo sezda russkikh botanikov v Petrograde (Diary of the 1st All-Russian Congress of Russian botanists in Petrograd)* 3: 27-28. (in Rus.).

Kosanic A., Anderson K., Harrison S., Turkington T., & Bennie J. (2018). Changes in the geographical distribution of plant species and climatic variables on the West Cornwall peninsula (South West UK). *PLoS*

ONE, 13 (2): 1–18. e0191021.

Laing J., & Binyamin J. (2013). Climate change effect on winter temperature and precipi-tation of Yellowknife, Northwest Territories, Canada from 1943 to 2011. *Am. J. Clim. Change*, 2: 275-283.

Lapenis A., Shvidenko A., Shepaschenko D., Nilsson S., & Aiyyer A. (2005). Acclimation of Russian forests to recent changes in climate. *Global Change Biol*., 11: 2090-2102.

Liu L.B., Yang H.M., Xu Y., Guo Y.M., & Ni J. (2016). Forest biomass and net primary productivity in southwestern China: A meta-analysis focusing on environmental driving factors. *Forests*, 7:173. DOI:10.3390/f7080173

Luyssaert S., Inglima I., Jung M. et al. (2007). CO_2 balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biol*., 13: 2509-2537.

Morley J.W., Batt R.D., & Pinsky M.L. (2017). Marine assemblages respond rapidly to winter climate variability. *Global Change Biol.*, 23: 2590–2601.

Odum, E.P. (1975). *Fundamentals of Ecology*. Moscow: “Mir” Publishing. 740 pp. (Translated from: E.P. Odum. Fundamentals of Ecology. The third Edition. Philadelphia-London-Toronto, W.B. Saunders Company, 1971).

Schaphoff S., Reyer Ch.P.O., Schepaschenko D., Gerten D., & Shvidenko A. (2016). Tamm Review: Observed and projected climate change impacts on Russia’s forests and its carbon balance. *Forest Ecol. Manag.*, 361: 432-444. DOI: 10.1016/j.foreco.2015.11.043.

Shvidenko A.Z., Shchepashchenko D.G., Vaganov E.A., & Nilsson S. (2008). Net primary production of forest ecosystems of Russia: A new estimate. *Doklady Earth Sciences*, 421A (6): 1009–1012.

Spathelf P., Stanturf J., Kleine M., Jandl R., Chiatante D., & Bolte A. (2018). Adaptive measures: integrating adaptive forest management and forest landscape restoration. *Ann. For. Sci.*, 75 (2): 55.

Sperry J.S., Venturasa M.D., Todda H.N., Trugmana A.T., Anderegga W.R.L., Wanga Y., & Tai X. (2019). The impact of rising CO2 and acclimation on the response of US forests to global warming. *PNAS USA*, 116 (51): 25734-25744.

Usoltsev V.A. (2004). On the application of regression analysis in forestry problems. *Lesnaya Taksatsiya i Lesoustroistvo (Forest Mensuration and Management)*, 1 (33): 49-55 (Rus.).

Usoltsev V. A. (2007). Some methodological and conceptual uncertainties in estimating the income component of the forest carbon cycle. *Rus. J. Ecol.*, 38 (1):11–10.

Usoltsev V.A. (2020). *Forest biomass and primary production database for Eurasia: CD-version*. The third edition, enlarged. Yekaterinburg: Ural State Forest Engineering University, ISBN 978-5-94984-732-9. DOI: 10.13140/RG.2.2.29991.70568

Usoltsev V.A., Koltunova A.I., Kajimoto T., Osawa A., & Koike T. (2002). Geographical gradients of annual biomass production from larch forests in Northern Eurasia. *Eurasian J. For. Res.*, 5: 55-62.

Usoltsev V.A., & Salnikov A.A. (1998). A new method for estimating the carbon pool of forest ecosystems. *Rus. J. Ecol.*, 29 (1): 3-13.

Usoltsev V.A., Shobairi S.O.R., & Chasovskikh V.P. (2017). Net primary production geography of forest-forming species in climate-induced gradients of Eurasia. *Current World Environ.*, 12 (3): 567-585.

Usoltsev V.A., Voronov M.P., & Chasovskikh V.P. (2011). Net primary production of Ural forests: Methods and results of automated estimating. *Rus. J. Ecol.*, 42 (5): 362–370.

Vasseur F., Exposito-Alonso M., Ayala-Garay O.J., Wang G., Enquist B.J., Vile D., Violle C., & Weigel D. (2018). Adaptive diversification of growth allometry in the plant Arabidopsis thaliana. *PNAS USA*, 115 (13): 3416–3421.

Voronin P.Yu., Konovalov P.V., Bolondinskii V.K., & Kaipiainen L.K. (2004). Chlorophyll index and photosynthetic carbon sequestration in Northern Eurasia forests. *Fiziologia Rasteniy*, (51): 390–395. (in Rus.).

World Weather Maps, 2007. URL: https://www.mapsofworld.com/referrals/weather/ (date of appeal: 15.06.2018).

Xu C., T.A. Kohler T. A., Lenton T. M., Svenning J.-C., & Scheffer M. (2020). Future of the human climate niche. *PNAS USA*, 117(21): 201910114. DOI: 10.1073/pnas.1910114117.

Zamolodchikov D.G. & Utkin A.I. (2000). A system of conversion relations for calculating the net primary production of forest ecosystems from tree stocks. *Lesovedenie*, 6: 54–63.

Zeng W.S. (2017). Developing tree biomass models for eight major tree species in China. In: *Biomass volume estimation and* *valorization for energy*. Chapter 1 / J. S. Tumuluri (ed.). Inтech Publisher: 3-21.

Zheng D., & Zeng W. (2013). Using dummy variable approach to construct segmented aboveground biomass models for larch and oak in northeastern China. *Journal of Beijing Forestry University*, 35 (6): 34-36 (in Chinese with English abstract).

Zhou W.N. (1992). *Phytomass and features of nitrogen and ash elements cycling in the ecosystems of the cherry oak of various phenological varieties in the conditions of the Central Chernozem region*. PhD Thesis. Voronezh, Voronezh Forest Engineering Institute. 23 p. (in Rus.).