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Patterns for *Populus* spp. Stand Biomass in Gradients of Winter Temperature and Precipitation of Eurasia

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Abstract: Based on a generated database of 413 sample plots, with definitions of stand biomass of the genus *Populus* spp. in Eurasia, from France to Japan and southern China, statistically significant changes in the structure of forest stand biomass were found, with shifts in winter temperatures and average annual precipitation. When analyzing the reaction of the structure of the biomass of the genus *Populus* to temperature and precipitation in their transcontinental gradients, a clearly expressed positive relationship of all components of the biomass with the temperature in January is visible. Their relationship with precipitation is less clear; in warm climate zones, when precipitation increases, the biomass of all wood components decreases intensively, and in cold climate zones, this decrease is less pronounced. The foliage biomass does not increase when precipitation decreases, as is typical for wood components, but decreases. This can be explained by the specifics of the functioning of the assimilation apparatus, namely its transpiration activity when warming, and the corresponding increase in transpiration, which requires an increase in the influx of assimilates into the foliage, and the desiccation of the climate that reduces this influx of assimilates. Comparison of the obtained patterns with previously published results for other species from Eurasia showed partial or complete discrepancies, the causes of which require special physiological studies. The results obtained can be useful in the management of biosphere functions of forests, which is important in the implementation of climate stabilization measures, as well as in the validation of the results of simulation experiments to assess the carbon-deposition capacity of forests.

Keywords: genus *Populus* spp.; regression models; stand biomass; biomass structure; climate change; average January temperature; average annual precipitation

1. Introduction

Active human economic activity has led to significant global changes in the functioning of the biosphere, and the observed climate warming has had a significant impact on the vegetation cover of the planet [1,2]. If earlier, the problems of assessing climate impacts on vegetation had a regional character [3], then in recent decades it has become clear that the problem has reached a global, general planetary level, and largely determines the future fate of human civilization [4,5]. Mapping the distribution of net primary production (NPP) over the surface of the planet, by extrapolating empirical NPP data obtained from forest sample plots to large areas of biomes [6,7] or to latitude gradients [8,9] does not allow for making any predictions of changes in the climate-NPP system. The same can be said about the common planetary patterns of distribution of NPP harvest data by gradients of average temperatures and precipitation [10].

Due to current climate changes, priority is given to changing the biomass and NPP of forest ecosystems under the influence of average temperatures and precipitation. Similar studies are performed at both a regional [11–13] and transcontinental [14,15] levels. Their implementation, especially in the latter case, is one of the problems that constitute the subject of biogeography [16]. The forest, as we know, is a geographical phenomenon [17], and in view of the topic indicated in the title of this work, it is important for us to identify the geographical aspects of the biomass of forest ecosystems, i.e., to make a choice in favor of those geographical characteristics that determine the distribution of forest biomass on the territory of a particular continent.

However, 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) equations, in which the dependent variable of the previous equation is included as one of the independent variables of the subsequent one [18]. This approach provides a multivariate conditionality of factors that provide flexibility and universality of the regression system describing the dynamics of biomass of stands.

To account for the geographical effect in this recursive system, each equation of the system must be supplemented with corresponding regressors. One possible option is to introduce dummy variables [18] that encode the regional affiliation of the harvest data [11,18,19] as one of the methods for model harmonization [20]. The disadvantage of such equations is that they only take into account the geographical shifts of the desired variables by the value of the interception term. It is assumed that the regression coefficients in such cases are unchanged by region, which is not true. The second option is to include indices of natural zoning and continentality of climate in the equations of the system [21], using the basis that changes in vegetation cover occur both in the latitudinal direction due to changes in the PhAR [22], and in the meridional direction due to changes in the continentality of climate [23]. Therefore, models of the phytomass of trees and plantings have been developed, including their mass-forming indices as independent variables, as well as indices of natural zoning and climate continentality [21]. However, such models do not provide an answer to the question of in which direction the biomass structure of a particular tree species may change with the expected change in air temperature or annual precipitation. 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 [24]. It is assumed that orography, soil water balance, PhAR, and climate continentality are indirectly reflected in the territorial features of temperatures and precipitation.

Studies of forest stand biomass at the transcontinental level, performed for five species from Eurasia, showed that changes in their biomass due to temperatures and precipitation are species-specific, i.e., they differ between species in the total biomass [25]. 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, a particular species adapted to changing environmental conditions, forming a series of vicariate species within the genus [26,27]. 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, *Populus tremula* vs. *P. trichocarpa* vs. *P. pruinosa* are derived from regional climatic features.

Eurasia is the largest continental area on Earth, located primarily in the Northern and Eastern Hemispheres, it is bordered by the Atlantic Ocean to the west, the Pacific Ocean to the east, the Arctic Ocean to the north, and by Africa, the Mediterranean Sea, and the Indian Ocean to the south. Eurasia covers around 55,000,000 square kilometers (21,000,000 sq mi), or around 36.2% of the Earth's total land area. The landmass contains well over 5 billion people, equating to approximately 70% of the human population. The unique size and complexity of the natural conditions differentiate Eurasia from the rest of continents. No continent has such an original history of paleogeographic development. Structural differences are reflected in the features of the morphological structure. In the territory of Eurasia there are the highest mountain systems, vast highlands, plateaus, and plains. Climatic and landscape conditions are no less diverse. Here you can trace all the geographical zones that are characteristic of the land of the globe from the icy deserts in the North to the humid equatorial forests in the South [28].

In our work, we made the first attempt to study transcontinental trends in the structure of biomass of the genus *Populus* spp., formed under the influence of geographically distributed temperatures and precipitation in the territory of Eurasia. Across the Northern Hemisphere, this genus plays a disproportionately important role in promoting biodiversity and sequestering carbon. It is illustrative of efforts to move beyond single-species conservation worldwide. The genus *Populus* is valued for many reasons, but one highlights their potential as key contributors to regional and global biodiversity [29]. A tremendous need for paper, cardboard, and board materials open almost unlimited opportunities for the economic use of this genus' wood. By density and cellulose content, poplar wood does not come up short compared to the coniferous species. Despite the slightly shorter wood fiber of poplar in comparison to spruce, modern technologies make the first class production of paper, cardboard, and wood board materials out of this "disgraced" species possible. Today, however, the genus *Populus* is an example of a particularly evident disparity, between the potential organic matter production in plantations, and its actual implementation in the boreal natural forests [30].

2. Objects of Research

To analyze geographical patterns of biomass distribution in Eurasian forests formed by stands of the genus *Populus* spp., from the author's database of eight thousand sample plots [31], the materials of 413 determinations with the data of the biomass structure were used. These biomass data were presented in different components (stems, branches, foliage, and roots). The distribution of sample plots with biomass data of the genus *Populus* spp. on the map-scheme of Eurasia is shown in Figure 1, and according to tree species and countries, in Table 1.

Figure 1. Allocation of sample plots with biomass (t/ha) determinations of 413 *Populus* forest stands in the territory of Eurasia.

Table 1. Distribution of plots with determinations of Populus biomass (t/ha) by species and countries.

Species	Botanical Name	Country	Plot Quantity
Quaking aspen	*Populus tremula* L.	Russia, Ukraine, Kazakhstan, Estonia, Belarus	188
David's aspen	*P. davidiana* Dode	China, Japan	129
Californian poplar	*P. trichocarpa* Torr. & A.Gray ex Hook.	France, Austria, Belgium, Netherlands	37
Poplar larrity	*P. laurifolia* Ledeb.	Russia	12
White poplar	*P. alba* Ledeb.	Russia, Kazakhstan	10
Poplar «Robusta»	*Populus × euroamericana*	Ukraine	10
Asiatic poplar	*P. euphratica Olivier*	China	9
Hybrid	*Populus hybrid*	Japan	8
Poplar berry-bearing	*P. deltoids* W. Bartram ex Humphry Marshall	China	6
Black poplar	*P. nigra* L.	Russia	2
Bahala poplar	*Populus × bachelieri* Solemacher	Bulgaria	1
Ploomy poplar	*P. pruinosa* Schrenk	Tajikistan	1
	Total		413

3. Methods

As the plots for estimating biomass of forest stands were usually established in typical 'background' habitats, which were representative in relation to this type of plant communities, one can make on their basis a preliminary geographical analysis of biomass gradients of *Populus* forests. For an analytical description of the geographic distribution patterns of the biomass productivity of forest cover, one must choose the geographical characteristics of the territory of Eurasia that can be expressed by quantity and measure.

The actual values of the biomass of 413 stands of the genus *Populus* (see Figure 1), based on the known coordinates of the sample plots established, we superimposed on the maps of winter (January) temperatures and average annual precipitation distribution [32], and related them to the isolines of the mentioned indices on the maps. In our case, the schematic map of the isolines of mean January temperature, rather than that of the mean annual temperature, was used. With an inter-annual time step, the predominant influence of summer temperature is quite normal [33]. However, against the background of long-term climatic shifts for decades, the prevailing influence is acquired by winter temperatures [34,35]. For example, Toromani and Bojaxhi [36] write: "Earlier studies has shown that phytosynthesis is possible for *Abies alba* in winter, where high temperatures could play an important role in improving carbohydrate storage and growth at following year. For species grown under a Mediterranen climate high temperatures and low precipitation during growing season may cause water stress, which is the main limiting factor for tree growth".

We should keep in mind that winter temperatures in the Northern Hemisphere have increased faster than summer ones during the 20th century [37–39]. 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.

Then, the compiled matrix of harvest data (Table 2) were subjected to the common regression analysis.

Table 2. A fragment of the original matrix of experimental data *.

A	N	V	P_i						Tm	PRm
			P_s	P_b	P_f	P_a	P_r	P_t		
40	0.790	208	89	5.5	2.40	98.0	21.6	119.6	−7	570
21	0.278	218	99.8	20.7	4.19	129.7	29.2	158.9	−3	570
12	12.54	62.5	34.8	4.45	1.91	41.2	15.0	56.2	−13	290
22	4.550	30	16.1	4.24	0.80	21.1	6.0	27.1	−13	290
49	0.650	284	113	22.5	3.07	138.6	57.0	195.6	−20	317
41	0.526	192	76.0	22.2	2.40	100.6	55.0	155.6	−18	250
78	0.518	200	88.83	28.37	4.99	127.7	38.79	166.5	−15	570
45	0.500	105	49.62	10.92	4.52	67.56	8.58	76.14	−26	570
78	0.666	185	103.1	45.44	8.75	163.9	37.8	201.7	−15	570
27	2.935	142	84.29	17.56	7.01	114.0	42.73	156.7	−9	820
68	1.244	223	102.4	22.44	7.43	138.5	51.47	190.0	−15	570
25	4.066	122	73.51	11.31	5.89	95.04	36.6	131.6	−15	570
40	1.062	224	99.81	32.82	7.69	146.6	45.47	192.1	−15	570
34	1.595	182	95.77	13.15	7.91	122.6	52.18	174.8	−10	444
50	1.510	163	75.11	22.44	6.21	108.4	34.26	142.7	−25	444
28	7.32	129	73.0	11.40	2.00	89.93	17.2	107.1	−15	570
37	2.913	153	86.65	18.56	6.27	116.7	41.79	158.5	−15	570
69	0.811	284	110.9	17.20	7.62	142.2	56.36	198.6	−26	444
58	1.188	124	61.47	16.79	3.66	85.63	27.24	112.9	−26	444
79	0.403	163	68.75	18.91	3.66	95.43	29.6	125.0	−26	444
38	4.255	121	73.56	11.79	6.19	95.95	38.21	134.2	−15	570
68	1.822	234	117.3	30.29	7.23	162.0	54.8	216.8	−26	444
29	2.000	61	34.42	16.31	2.77	55.88	16.57	72.45	−5	826
39	2.774	62	37.92	8.72	3.00	58.27	9.41	67.68	−5	826

* *A* = stand age, y; *V* = stem volume, m³/ha; *N* = tree density, 1000/ha; *i* = index of biomass component: total wood storey (*t*), aboveground wood storey (*a*), underground wood storey, or roots (*r*), stem over the bark (*s*), foliage (*f*), and branches (*b*); *PRm* = mean annual precipitation, mm; *Tm* = mean January temperature, °C.

The basic principles of modelling and the results obtained by means of regression analysis should have an ecologic-geographical interpretation. The biological productivity of forests is dependent on climatic factors, but only as a first approximation, since there are ontogenetic, cenotic, edaphic, and other levels of its variability. Therefore, we included in the regression equations the independent variables explaining the variability of the dependent variable, expressing not only with climatic parameters but also with forest age, tree density, and stem volume.

As the mean January temperature in the northern part of Eurasia has negative values, the corresponding independent variable was modified to the form $(Tm + 50)$. Then, the technique of multiple regression analysis (http://www.statgraphics.com/for more information), according to three blocks of recursive equations, was used: two blocks of mass-forming indices, N and V, and a single block of biomass P_i (arrows show the sequence of calculations)

$$\ln N = a_0 + a_1(\ln A) + a_2[\ln (Tm + 50)] + a_3(\ln PRm); \tag{1}$$

$$\ln V = a_0 + a_1(\ln A) + a_2(\ln N) + a_3 [\ln (Tm + 50)] + a_4(\ln PRm); \tag{2}$$

$$\ln P_i = a_0 + a_1(\ln A) + a_2(\ln V) + a_3(\ln N) + a_4[\ln(Tm + 50)] + a_5(\ln PRm) \tag{3}$$

4. Results and Discussion

The results of the calculation of Equations (1)–(3) are listed in the Table 3. Only the variables that are significant at the level of probability of P_{95} and above are showed in this table. The equations were tabulated in the sequence illustrated by the arrows. The results of tabulating the models in the sequence of Equations (1)–(3) present the rather cumbersome table. We took from it the values of the component composition of the biomass of the *Populus* forests of the age of 50 years and built 3D-graphs of their dependence upon temperature and precipitation (Figure 2).

Table 3. Characteristics of biomass Equations (1) to (3).

Dependent Variables	Coefficients and Independent Variables						adjR^2 **	SE ***
	a_0 *	$a_1(\ln A)$	$a_2(\ln V)$	$a_3(\ln N)$	$a_5[\ln(Tm + 50)]$	$a_6(\ln PRm)$		
$\ln(N)$	10.7307	−1.2994	-	-	−2.4045	0.4747	0.623	0.74
$\ln(V)$	5.9573	0.3617	-	−0.2589	0.5288	−0.6169	0.534	0.47
$\ln(P_s)$	−1.8923	0.2068	0.9123	0.0646	0.0764	0.0811	0.963	0.17
$\ln(P_b)$	−2.8796	0.2421	0.5520	−0.0537	0.3792	0.0678	0.675	0.44
$\ln(P_f)$	−4.0545	0.0070	0.4127	0.1332	−0.0589	0.5272	0.522	0.38
$\ln(P_r)$	−3.5174	0.0497	0.7113	0.0563	0.2306	0.3533	0.720	0.35
$\ln(P_a)$	−1.2511	0.1782	0.8183	0.0463	0.0984	0.0960	0.955	0.17
$\ln(P_t)$	−1.1022	0.0477	0.7969	0.0486	0.1467	0.1849	0.918	0.18

* The constant corrected for logarithmic retransformation by [40]; ** $adjR^2$ = determination coefficient adjusted for the number of variables; *** SE = standard error of the equations.

When analyzing the reaction of the biomass structure of the genus *Populus* to temperature and precipitation in their transcontinental gradients, a clearly expressed unambiguous positive relationship of all components of the biomass with the average temperature of January is seen. Their relationship with precipitation is less clear; in warm climate zones ($Tm = 0\ °C$), when precipitation increases the biomass of all wood components decreases most intensively, and in cold climate zones ($Tm = -40\ °C$) this decrease is expressed to a much lesser extent.
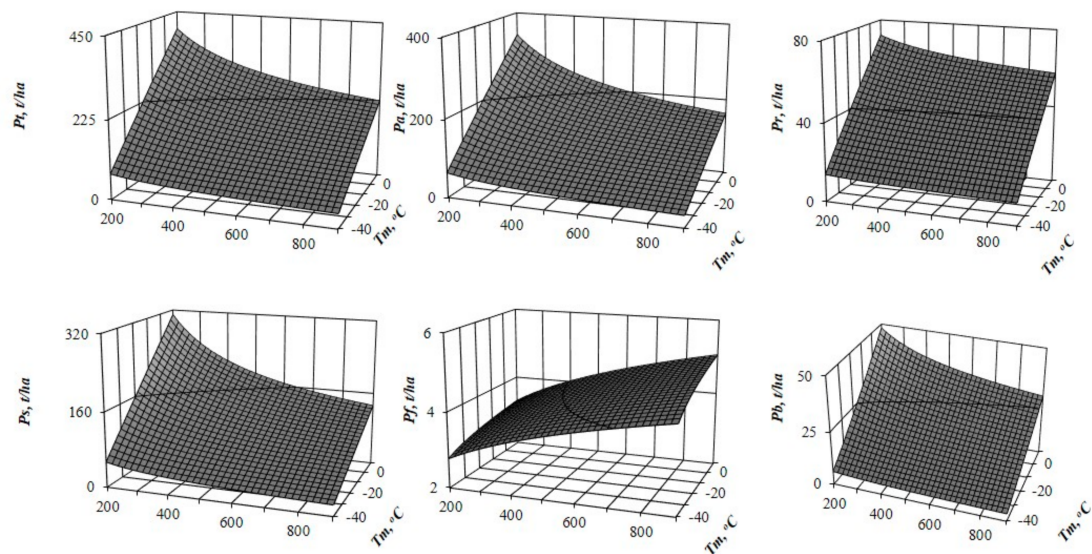
Figure 2. Dependence of *Populus* ecosystems of Eurasia upon the mean January temperature (*Tm*) and mean annual precipitation (*PRm*). Abbreviations: *Pt*, *Pa*, *Ps*, *Pr*, *Pf*, *Pb* are, respectively, biomass of: total wood storey, aboveground, stems (wood and bark), roots, foliage, and branches, t/ha.

It is interesting to compare the obtained patterns of changes in the total biomass of the genus *Populus* with previously published results for other forest-forming species of Eurasia, obtained using a similar methodology [25]. The increase in the total biomass of *Populus* during the transition from cold to warm regions was confirmed earlier for *Larix* spp., *Picea* spp., *Abies* spp., and *Betula* spp. However, the decrease in the total biomass as precipitation increases was confirmed only in larch, whereas in spruce, fir, and birch, the dependence is the opposite of that established for *Populus*. The specific pattern of the change in the total biomass was obtained for two-needled pines *Pinus* L.; its increase during the transition from cold to warm regions was recorded only in regions with heavy precipitation, and with the transition to water-deficit regions, the pattern changes to the opposite. If, in *Populus* and *Larix*, the decrease in total biomass with the transition from water-deficient to moisture-rich regions was observed in all thermal zones, then in two-needled pines (only in cold zones, and with the transition from cold to warm climatic zones) this negative trend changes to the opposite.

We can see that the reaction of foliage biomass with increasing precipitation does not decrease, as is typical for wood components, but increases (Figure 2). This is consistent with a similar situation observed in Russian Siberia with respect to forest cover [41], where with a warming climate and a simultaneous decrease in precipitation, the share of assimilation mass decreases, and the share of wood components increases. This is explained by the specifics of foliage functioning, namely, its transpiration activity when warming, and a corresponding increase in transpiration requires an increase in the influx of assimilates into the foliage, while the desiccation of the climate reduces this influx of assimilates due to a decrease in transpiration activity. Perhaps this phenomenon demonstrates the future scenario of acclimatization of trees to the ongoing warming and changes in the water balance of territories. However, in Canada's forests, a contradictory result was obtained. If the January temperature and humidity conditions of the growing season had a positive effect on the growth of *Betula papyrifera* Marsh. and the growth of *Picea mariana* Mill., then *Populus tremuloides* Michx. might be the least responsive species [42].

The patterns of biomass-amount change, under assumed changed climatic conditions (Figure 2), are hypothetical. They reflect long-term adaptive responses of forest stands to regional climatic conditions and do not take into account rapid trends of current environmental changes, which place serious constraints on the ability of forests to adapt to new climatic conditions [43–49]. Climate changes are manifested primarily in shifts in the phenology of a particular species, and are determined by the

degree of species-specific phenotypic plasticity [50], which were not taken into account in our work, and require special study.

The law of limiting factors [51] works well in stationary conditions. With a rapid change in limiting factors (such as air temperature or precipitation), forest ecosystems are in a transitional (non-stationary) state, in which some factors that were not significant may come to the fore, and the end result may be determined by other limiting factors [52].

The main pool of biomass harvest data in Eurasia was obtained during the 1970s–1990s, and the climate maps used, cover the period of the late 1990s–early 2000s. Some discrepancy between the two time periods may cause some biases in the results obtained, but for such a small time difference in the used data, the inclusion of compensatory mechanisms or phenological shifts in forest communities is unlikely [47,48].

5. Conclusions

Based on a database of 413 sample plots, with definitions of forest biomass of the genus *Populus* spp. in Eurasia, in the territory from France to the South of China and Japan, a statistically significant increase in stem, aboveground, and underground biomass was found with an increase in winter temperatures and a decrease in precipitation, especially in warm climate regions. In contrast to the woody components of biomass, the mass of foliage, while increasing with warming, simultaneously decreases with a decrease in precipitation, which is due to the specifics of the functioning of foliage, namely, its transpiration activity.

Comparison of the results obtained for *Populus* showed that the regularities of *Populus* are repeated only in *Larix*, and in other species, only partially. In our work, we can only state the species-specificity of the reaction of various Eurasian species to changes in temperature and precipitation, but explaining this specificity at the level of physiological processes is the task of the future.

The results obtained can be useful in the management of biosphere functions of forests, which is important in the implementation of climate stabilization measures, as well as in the validation of the results of simulation experiments to assess the carbon-deposition capacity of forests. They also provide a preliminary idea of possible shifts in forest biological productivity indicators under the influence of climate change.

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