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Are There Differences in the Response of Natural Stand and Plantation Biomass to Changes in Temperature and Precipitation? A Case for Two-needled Pines in Eurasia

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Abstract: A comparative discussion of the advantages and disadvantages of natural stands and plantations, including in terms of their productivity and stability, began from the moment of the first forest plantings and continues to this day. In the context of the progressive replacement of natural forests by plantations due to deforestation, the question of how will change the carbon storage capacity of forest cover when replacing natural forests with artificial ones in a changing climate becomes extremely relevant. This article presents the first attempt to answer this question at the transcontinental level on a special case for two-needled pine trees (subgenus Pinus L.). The research was carried out using the database compiled by the authors on the single-tree biomass structure of forest-forming species of Eurasia, in particular, data of 1880 and 1967 of natural and plantation trees, respectively. Multi-factor regression models are calculated after combining the matrix of initial data on the structure of tree biomass with the mean January temperature and mean annual precipitation, and their adequacy indices allow us to consider them reproducible. It is found that the aboveground and stem biomass of equal-sized and equal-aged natural and plantation trees increases as the January temperature and precipitation rise. This pattern is only partially valid for the branches biomass, and it has a specific character for the foliage one. The biomass of all components of plantation trees is higher than that of natural trees, but the percent of this excess varies among different components and depends on the level of January temperatures, but does not depend at all on the level of annual precipitation. A number of uncertainties that arose during the modeling process, as well as the preliminary nature of the obtained regularities, are noted.

Key words: two-needled pine trees; natural stands and plantations; regression models; biomass equations; mean January temperature; annual precipitation

1 Introduction

Current climate change make it increasingly important to assess the response of forest cover biomass to this change,

which in turn determines the possibility of climate stabilization by reducing atmospheric CO₂. The planet's natural forests are slowly decreasing by 6–13 million ha annually and

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are often replaced by artificial ones that continue to grow (Niskanen, 2000; FAO, 2006; Kirilenko and Sedjo, 2007; Brockerhoff et al., 2008; Pawson et al., 2013; Mackey, 2014). It is necessary to know how this substitution can affect the change in the biomass structure of the latter under the influence of climate shifts and, accordingly, their carbon-depositing capacity and resilience to climate change (Stegen et al., 2011; Pawson et al., 2013; Dymond et al., 2016).

Today, in the face of increasing anthropogenic pressure and climate change, it is important to know all the advantages and disadvantages of both natural stands and plantations in terms of biological productivity and their ability to mitigate climate change. Discussions related to production advantages of natural and artificial forests began from the time of the first forest plantings and continue to this day. Numerous studies prove the presence of higher production indices of plantations in comparison with natural stands. (Rubtsov et al., 1976; Stage et al., 1988; Gabeev, 1990; Danchenko et al., 1991; Chernov, 2001; Antonov, 2007; Lugansky and Shipitsina, 2008; Merzlenko, 2017; Usoltsev et al., 2017). Nevertheless, there are evidences of greater biological productivity of plantations only at the young age (Zolotukhin, 1966; Makarenko and Biryukova, 1982; Jordan and Farnworth, 1982; Polyakov et al., 1986; Romanov et al., 2014) and even of greater biological productivity of natural forests compared to planted forests in Southeast China (Liu et al., 2016). Climate change exacerbates this uncertainty, and a comparative analysis of possible changes in the biomass of natural stands and plantations as a result of climate shifts becomes even more relevant.

Recently, a comparative analysis of the accuracy of different methods for determining the biological productivity of some tree species was fulfilled, and it was shown 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. A climate-sensitive aboveground biomass model led to higher prediction accuracy of tree biomass than those without climatic variables for three larch species (Fu et al., 2017). In the study of the sensitivity of the allometric models for aboveground and underground biomass of larches in China to changes in hydrothermal conditions, it was revealed that the increase in mean annual temperature by 1 °C leads to an increase in aboveground biomass of trees at 0.87% and reduce underground one at 2.26%, and the increase in average annual precipitation by 100 mm causes a decrease in aboveground and underground biomass at 1.52% and 1.09% respectively (Zeng et al., 2017). In such studies, the task is to extract the climatic component (climate signals) from the residual dispersion of a model calculated. To made climatic factors to be predominant and "recoverable" from this "information noise", it is necessary to take into account in the model, in addition to the stem diameter and height, also tree age, which is a factor determining the structure of tree biomass too (Nikitin, 1965; Usoltsev, 1972; Tsel'niker, 1994; Vanninen et al., 1996; Bond-Lamberty et al., 2002; Fatemi et al., 2011; Genet et al., 2011; Ochał et al., 2013; Qiu et al., 2018), as well as climate sensitivity (Carrer and Urbinati, 2004; Yu et al., 2008).

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; Fu et al., 2017; Zeng et al., 2017). The implementation of our intention is encouraged by the result of Rodriguez-Vallejo and Navarro-Cerrillo (2019) showed that climatic variables (temperature and precipitation), as well as site and soil conditions cause differences in the forest decline processes between natural and planted stands.

In our study, the first attempt is made to compare the changes in the component composition of tree biomass of two-needled pines of natural and artificial origin by trans-Eurasian hydrothermal gradients.

2 Material and methods

A unique Eurasian database of harvest data on single-tree biomass compiled by Usoltsev (2016) was used to achieve this goal. From the mentioned database the data for the subgenus *Pinus* L. aboveground biomass in a number of 3847 sample trees, including 1880 and 1967 for natural and artificial origin respectively, were taken (Table 1). There were only 370 definitions for root biomass in the database. The subgenus *Pinus* L. is mainly represented by the Scots pine (*Pinus sylvestris* L.) (86% of the total data) and in a smaller number by species *P. tabuliformis* Carr., *P. massoniana* Lamb., *P. densiflora* S. et Z., *P. thunbergii* Parl.

The joint analysis of different species is caused by the impossibility of growing the same tree species throughout Eurasia, as a result of which their areas within the genus are confined to certain ecoregions. These are substitutive or vicariate species that arose in cases of geologically long-standing separation of a once-continuous area under influence of climate traits (Tolmachev, 1962) or as a result of climate-related morphogenesis (Chernyshev, 1974).

Each sample plot on which tree biomass estimating was performed is positioned relatively to the isolines of the mean January temperature and relatively to the isolines of mean annual precipitation (Fig. 1 and Fig. 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 taken from World Weather Maps (2007) is preferable as of the most informative climatic factors.

Table 1 Distribution of the 3847 sample trees by species, countries, regions, and mensuration indices

Regions	Species of the subgenus <i>Pinus</i> L.	Ages (yr)	DBH (cm)	Heights (m)	Sample No.		
Natural stand							
West Europe	P. sylvestris L.	11-100	1.4-53.1	2.3-32.0	19		
Scandinavia	P. sylvestris L.	9-212	1.9-42.0	3.3-32.4	117		
The Ukraine and Byelorussia	P. sylvestris L.	24–186	1.5-54.6	1.6–36.6	205		
European Russia	P. sylvestris L.	10-207	0.9-54.0	2.2-30.2	514		
Turgay deflection	n <i>P. sylvestris</i> L.	13–110	0.3-47.8	1.4-27.4	411		
Central Siberia	P. sylvestris L.	4-430	0.5-65.6	1.6-28.8	587		
China	P. sylvestris L.	100	18.0	19.0	1		
	P.massoniana Lamb.	20	8.0-22.3	10.4–16.5	5 8		
Japan	P. densiflora S. et Z.	49–120	9.2-60.9	14.1–35.7	11		
	P. thunbergii Parl.	22-33	9.0-24.3	9.5–16.6	7		
Sub-total					1880		
Plantations							
West and Central P sylvestris I 7–50 0.5–36.5.1.4–21.0.77							

Plantations						
West and Central	P. sylvestris L.	7–50	0.5-36.5 1.4-21.0	77		
Europe						
Scandinavia	P. sylvestris L.	5-143	1.2-37.1 2.1-25.6	196		
The Ukraine and Byelorussia	P. sylvestris L.	8–90	2.1-42.9 2.2-34.7	1010		
European Russia	P. sylvestris L.	6–78	1.5-30.1 1.8-32.6	160		
Turgay deflection	nP. sylvestris L.	9-50	0.4-21.7 1.4-16.2	215		
Central Siberia	P. sylvestris L.	10-73	2.0-36.0 2.4-21.6	170		
Iraq	P. halepensis Mill.	24	15.8 7.4	1		
China	P. tabuliformis Carr.	17–25	4.0-12.0 3.3-10.8	8		
Japan	P. densiflora S. et Z.	3-53	1.7-39.1 2.0-18.7	108		
	P. thunbergii Parl.	5-34	4.6–11.4 4.7–7.6	12		
Sub-total				1967		

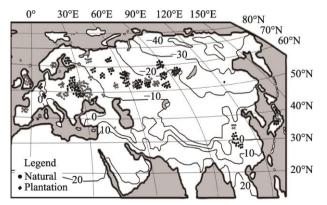


Fig. 1 Distribution of sample plots, where 1880 and 1967 trees of natural (rings) and plantation (squares) origin correspondingly have been harvested, on the map of the mean January temperature ($^{\circ}$ C).

(World Weather Maps 2007. https://store.mapsofworld. com/image/cache/data/map2014/currents-and-temperature-jan-enlarge-900x700.jpg).

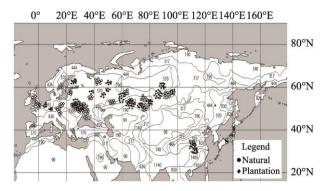


Fig. 2 Distribution of sample plots, where 1880 and 1967 trees of natural (rings) and plantation (squares) origin correspondingly have been harvested, on the map of the mean annual precipitation (mm).

(World Weather Maps 2007. http://www.mapmost.com/ world-precipitation -map/free-world-precipitation-map/).

It was found that when estimating stem biomass growth by using the annual ring width, the greatest contribution to explaining its variability being made by summer temperature accounting for from 16% of the total dispersion (Berner et al., 2013) to 50% of the residual one (Bouriaud et al., 2005). Moreover, the specificity of the relationship (positive or negative) of stand biomass depends on what intra-annual temperature was taken as a predictor: it is established by Khan et al. (2019) that this relationship is positive with the maximum intra-annual temperature and negative with the minimum and average annual temperature. With an inter-annual time step, the predominant influence of summer temperature is quite normal (Zubairov et al., 2018). But against the background of long-term climatic shifts for decades, the prevailing influence is acquired by winter temperatures (Morley et al., 2017), having in mind that winter temperatures in the Northern hemisphere are increased faster than summer ones during the 20th century (Emanuel et al., 1985; Folland et al., 2001; Laing and Binyamin, 2013; Felton et al., 2016). 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.

The final structure of the model includes only those mass-forming indices that are statistically significant for all biomass components, and it has the form (Usoltsev et al., 2019):

$$\ln P_{i} = a_{0i} + a_{1i} \ln A + a_{2i} \ln D + a_{3i} \ln H + a_{4i} (\ln D) \times (\ln H) + a_{5i} B + a_{6i} B \ln A + a_{7i} B [\ln \ln(T + 40)] + a_{8i} [\ln \ln(T + 40)] + a_{9i} \ln PR + a_{10i} B \ln PR + a_{11i} [\ln \ln(T + 40)] \times \ln PR$$

1. Principle of the second of the s

where P_i is biomass of i^{th} component, kg; A is tree age, yr; D

is stem diameter at breast height, cm; H is tree height, m; i is the index of biomass component: stem over bark (P_s) , foliage (P_f) , branches (P_b) and aboveground (P_a) ; B is the binary variable that coordinates the biomass values of natural pines (B=0) and pine plantations (B=1); T is mean January temperature, C; PR is mean annual precipitation, mm. 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+40.

Along with the three main mass-forming variables i.e. tree age A, diameter D and height H of a tree, the product of two variables ($\ln D$ and $\ln H$) is introduced as an additional predictor, the need for which was shown earlier (Usoltsev et al., 2019). When we introduce only one binary variable B into equation (1), this means that the 3-D surface (temperature-precipitation-biomass) in X-Y-Z coordinates shifts between natural and artificial trees only along the Z axis by the value of the regression coefficient at the binary variable B. According to our assumption, the biomass of trees in natural stands and plantations reacts differently to changes in the age (Zolotukhin, 1966; Jordan and Farnworth, 1982; Makarenko

and Biryukova, 1982; Polyakov et al., 1986; Romanov et al., 2014) and climate variables (Rodriguez-Vallejo and Navarro Cerrillo, 2019). In order to take these differences into account in the designed model, in equation (1), along with B, we introduce the synergisms $B(\ln A)$, $B[\ln(T+40)]$ and $B(\ln PR)$ as independent variables. To account for the simultaneous effects of temperature and precipitation, the synergism $[\ln(T+40)] \times (\ln PR)$ is introduced in equation (1) as another independent variable.

3 Results

The regression coefficients of the multiple regression equation (1) are calculated using the Statgraphics software (see http://www.statgraphics.com/ for more information) and then are shown in Table 2 after the correction for logarithmic transformation by Baskerville (1972) and anti-log transforming procedure. The synergisms $B(\ln A)$ and $B(\ln PR)$ as independent variables were not statistically significant. All regression coefficients at mass-forming variables of equations (1) are characterized by the significance level of 0.05 and better, and the resulting equations are reproducible.

Table 2 Characteristics of regression model (1) calculated

P_i	Regression model calculated	$adjR^2$	SE
P_s	$P_s = 2.014 \times 10^{-3} + A^{0.1525} + D^{1.5284} + H^{0.4322} + D^{0.1398(\ln H)} + e^{-0.1448B} + (T+40)^{0.0526B} + (T+40)^{0.6901} + PR^{0.4292} + (T+40)^{-0.1046(\ln PR)}$	0.987	1.24
P_f	$P_f = 7.842 \times 10^{-5} + A^{-0.4624} + D^{2.4422} + H^{-1.2824} + D^{0.1571(\ln H)} + e^{1.3265B} + (T+40)^{-0.3345B} + (T+40)^{2.1870} + PR^{1.4287} + (T+40)^{-0.3918(\ln PR)}$	0.900	1.61
P_b	$P_b = 6.524 \times 10^{-6} + A^{-0.1796} + D^{2.8848} + H^{-1.6954} + D^{0.1995(\ln H)} + e^{0.1512B} + (T+40)^{-0.0343B} + (T+40)^{2.4966} + PR^{1.5638} + (T+40)^{-0.4007(\ln PR)}$	0.926	1.66
P_a	$P_a = 2.218 \times 10^{-4} + A^{0.0407} + D^{1.7700} + H^{-0.1235} + D^{0.1778(\ln H)} + e^{0.2536B} + (T + 40)^{-0.0629B} + (T + 40)^{1.6918} + PR^{1.0370} + (T + 40)^{-0.2635(\ln PR)}$	0.986	1.24

Note: P_s , P_f , P_b , P_a mean biomass of stem over bark, needle, branches and aboveground, respectively; The abbreviation adj \mathbb{R}^2 is a coefficient of determination adjusted for the number of parameters; SE is equation standard error.

The results of tabulating the equation (1) represent a rather cumbersome table. We took from it the calculated data of component biomass for the age of 50 years, *D* equal to 14 cm and *H* equal to 13 m and built 3D-graphs of their dependence on temperature and precipitation (Fig. 3).

Since the number of trees with measured underground biomass is 7 times less than the number of trees that have a component composition of above-ground biomass, we risk getting fake patterns that logically contradict (do not correspond) to the patterns shown in Fig. 3. It is known that relative (dimensionless) indices are more unified than absolute values (Detlaf and Detlaf, 1982), and are characterized by genetically determined stability (Lyr et al., 1967). Therefore, we will try to use the regression method to explain the variability of the ratio of underground to aboveground biomass (*R/S* as root: shoot ratio), rather than the absolute values of underground tree biomass. Initially, the structure of the model (1) is adopted for the analysis of the *R/S* ratio. But, as

expected, most of the regressors of the model (1) were not statistically significant, and the equation is finally obtained.

$$R/S = 1.562D^{-0.1949} \times (T+40)^{-0.4666}$$

 $(R^2 = 0.153; SE = 1.54)$ (2)

where R and S are underground and aboveground biomass, respectively. The graphical interpretation of equation (2) is shown in Fig. 4. Equation (2) is characterized by a fairly low coefficient of determination, since it is known that the closer the relationship between two factors, the less their relationship is explained by known determining factors (Usoltsev, 1985). However, the Student's criteria determining the significance of the regression coefficients of the model (2) are quite high and are 6.9 and 5.9, which is more than 2.0. We can see that as we move from warm to cold zones, the absolute value of the R/S ratio for thin trees (DBH = 8 cm) increases from 0.17 to 0.26, and for thick

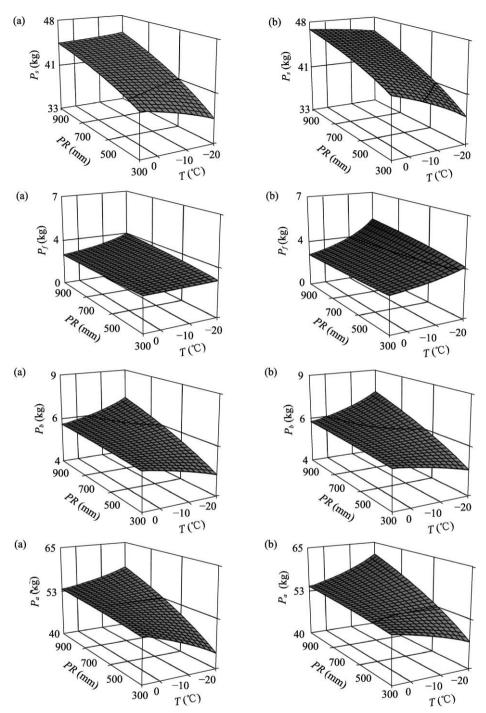


Fig. 3 Dependence of pine tree biomass in natural stands (a) and plantations (b) upon the mean January temperature (7) and mean annual precipitation (*PR*)

Note: P_s , P_f , P_b and P_a are dry biomass in kg of stem, foliage, branches and aboveground, respectively.

trees (DBH=32 cm) from 0.13 to 0.20, but in percentage terms it does not depend on the tree thickness and increases by 48%.

4 Discussion

When analyzing the 3D-surfaces shown in Fig. 3, we will distinguish two stages: In the first of them, we note the patterns common to trees in natural stands and cultures (we

will call them natural and plantation trees, respectively), and then, when considering in detail, we establish what and how differ the resulting patterns between natural and plantation trees.

(1) With regard to stem biomass, we see that it increases with increasing precipitation in all temperature zones, as well as with increasing temperatures in areas of insufficient moisture. But as we move to areas of sufficient moisture,

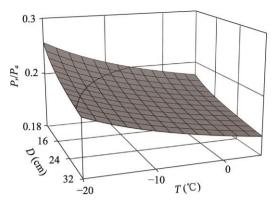


Fig. 4 Changes of the theoretical *R/S* ratio of natural stands and plantations in relation to tree stem diameter under different mean January temperature (*T*).

the last trend is modified.

- (2) The biomass of needles and branches increases in cold zones as precipitation increases, as well as in areas of sufficient moisture as the temperature decreases. But as we move to areas of insufficient moisture and warm regions, these trends change.
- (3) Aboveground biomass sums up component-specific patterns in itself, amplifying the coincident ones and neutralizing (compensating) the contradictory ones. In cold areas there is significant increase with increasing precipitation, but in the transition to the warm zone this trend disappears. In moisture-rich regions, the biomass increases as the temperature decreases, but in water-deficient regions, the pattern changes to the opposite trend.

Turning to the analysis of differences in the biomass trends of natural and plantation trees according to the second stage, it should be noted that, judging by the structure of the calculated equation (1), these differences are related only to changes in temperatures, but not precipitation, since the synergism $B(\ln PR)$ was not statistically significant. Our assumption of different age dynamics of the tree biomass of natural and artificial stands is also not confirmed, since the predictor $B(\ln A)$ is not statistically significant. The biomass of all components of plantation trees is higher than that of natural ones, but the percentage of this excess is different for all components and changes at different rates in relation to changes in temperature. Changes in the excess of biomass components of plantation trees above natural ones are shown in Table 3.

We can see that as we move from cold zones to warm ones, the excess of plantation tree biomass over natural ones increases from 1.3% to 5.3% for stem biomass, decreases from 27.7% to 5.9% for foliage biomass, as well as from 4.8% to 2.1% and from 6.3% to 1.5% for branches and aboveground biomass respectively, regardless of the precipitation level.

However, the most interesting question is how much the structure of forest biomass will change with an assumed temperature deviation, for example, by 1 °C and with a

Table 3 Changes in the excess percentage (%) of different components biomass of plantation trees above natural ones due to changes in January temperature

Biomass component	Mean temperature in January (°C)						
	-20	-16	-12	-8	-4	0	4
Stems	1.3	2.2	3.0	3.7	4.3	4.8	5.3
Foliage	27.7	23.1	19.1	15.4	12.0	8.8	5.9
Branches	4.8	4.2	3.6	3.2	2.8	2.5	2.1
Aboveground	6.3	5.2	4.3	3.5	2.8	2.1	1.5

deviation of precipitation from the usual norm, for example, by 100 mm per year. The constructed model gives the answer to such question in relation to forest trees. To do this, we take the first derivative of our 3-Dimensional surfaces (Fig. 3), and not analytically, but graphically, i.e. we take off the biomass difference interval (Δ , %%) corresponding to temperature interval 1 °C and precipitation interval 100 mm directly from the graphs or from the corresponding tables, and get the answer in the form of 3-Dimensional surfaces divided into plus and minus areas that correspond to the increase or decrease in the biomass of trees having the age of 50 years, DBH of 14 cm and height of 13 m.

In this case, the differences between the biomass of natural and plantation trees become more obvious (Fig. 5).

- (1) If the stem biomass of plantation trees increases when the temperature grows by $1\,^{\circ}\text{C}$ over the entire precipitation range from 300 to 900 mm (the entire 3D surface is located above the zero plane), then the biomass of natural trees only in the range from 300 to 700 mm (located above the zero plane), and in the range from 700 to 900 mm it decreases (located below the zero plane).
- (2) The foliage biomass in this case decreases over the entire range of precipitation from 300 to 900 mm, both in natural and plantation trees (the entire surface is located below the zero plane), but the percentage of decline in the latter is clearly greater than in the former.
- (3) In terms of changing the branch biomass when the temperature assumes to increase by 1 $^{\circ}$ C, natural and plantation trees do not differ much and show an increase in the precipitation range from 300 to 500 mm and a decrease in the range from 500 to 900 mm.
- (4) When the temperature increases by 1 $^{\circ}$ C, there is also a slight difference between natural and plantation trees in the change of aboveground biomass: the former increase in the precipitation range from 300 to 600 mm, and the latter in the range from 300 to 500 mm only.

When annual precipitation assumes to be increased by 100 mm at constant January temperatures, the biomass of stems, branches and aboveground increases in all temperature zones, and the foliage biomass only in the range of temperature zones from -20 °C to -2 °C, and the same for

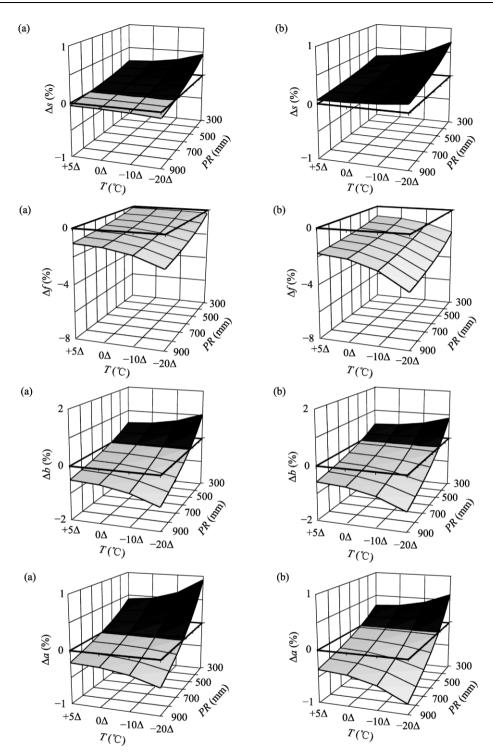


Fig. 5 Change of tree biomass of natural stands (a) and plantations (b) when temperature assumes to be increased by 1 $^{\circ}$ C due to the expected climate change at different territorial levels of temperature and precipitation

Note: Symbols Δs , Δf , Δb and Δa on the ordinate axes mean the change (±%) of biomass of stems, foliage, branches and aboveground, respectively, with the temperature increase by 1 $^{\circ}$ C and at the constant precipitation.

both natural and plantation trees (Fig. 6).

The similar modification of Fig. 4 for the R/S ratio is shown in Fig. 7. If the overall decrease in R/S ratio during the transition from cold to warm zones was 48%, then the decrease in R/S ratio "at the point", i.e. when shifting in the

same direction by 1 $^{\circ}$ C, was from –2.3% to –1.0%, regardless of the thickness of tree stems and their origin.

It is known, the solution of each new problem and the corresponding removal of the associated uncertainty generates several new ones. In our case, some uncertainties have

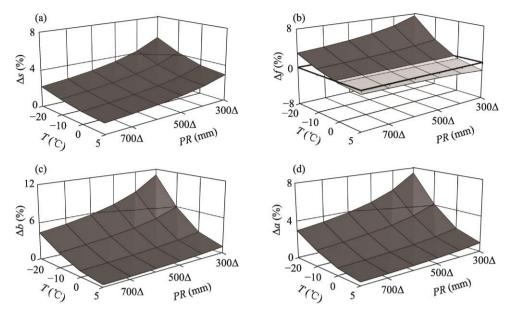


Fig. 6 Change of tree biomass of natural stands and plantations when precipitation assumes to be increased by 100 mm due to the expected climate change at different territorial levels of temperature and precipitation

Note: The symbols Δs , Δf , Δb and Δa along the ordinate axes represent the change (±%) of biomass of stems, foliage, branches and aboveground, respectively, with precipitation increase by 100 mm and at the constant mean temperatures of January.

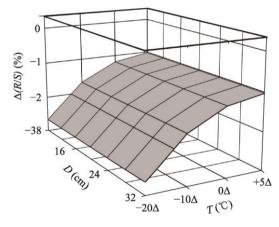


Fig. 7 Change of R/S ratio of natural stands and plantations when temperature assumes to be increased by 1 $^{\circ}$ C due to the expected climate change at different territorial levels of temperature

arisen too:

(1) The patterns of biomass amount change under assumed changed climatic conditions (Fig. 5 and Fig. 6) are hypothetical. They reflect long-term adaptive responses of forest stands to regional climatic conditions and do not take into account rapid trends of current environmental changes, which place serious constraints on the ability of forests to adapt to new climatic conditions (Givnish, 2002; Alcamo et al., 2007; Berner et al., 2013; Schaphoff et al., 2016; Spathelf et al., 2018; Vasseur et al., 2018; DeLeo et al., 2020; Denney and Anderson, 2020). The law of limiting factors (Liebig, 1840; Shelford, 1913) works well in stationary conditions. With a rapid change in limiting factors (such as

air temperature or precipitation), forest ecosystems are in a transitional (non-stationary) state, in which some factors that were still not significant may come to the fore, and the end result may be determined by other limiting factors (Odum, 1975).

(2) A disadvantage of the database used in this study is the uneven spatial distribution and different representation of sampling sites and natural and plantation trees over Eurasia (Fig. 1 and Fig. 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.

(3) In equation (1), three mass-determining factors (*A*, *D*, and *H*) take upon himself the main share of the explained variance: for the masses of stems, needles, branches, and aboveground 94%, 86%, 91%, and 87%, respectively. Climate variables and differences between natural and plantation trees account for only 6% to 13% of the variability. The structure of these "residual" variables is highly variable and heterogeneous. In addition to the already noted uneven filling the initial data matrix, there are discrepancies between the age periods of mapping (Fig. 1 and Fig. 2) and calendar ages of different biomass components, between the large step of temperature and precipitation isolines on the maps and local topography features, as well as local soil differences, despite the fact that the soil zoning reflects the action of climatic factors (Dokuchaev, 1948; Rukhovich et al., 2019).

Taking into account the stated methodological and conceptual uncertainties, the results presented in this study provide a solution to the problem only in the first approximation and should be considered as preliminary ones and having not so much factual as methodological significance. They can be modified if the biomass database will be enlarged by additional data, mainly site-specific and stand-specific characteristics as well as by more advanced and correct methodologies.

5 Conclusions

When using the database compiled for natural and plantation single-trees, it is found that the aboveground and stem biomass of equal-sized and equal-aged natural and plantation trees increases as the January temperature and annual precipitation rise. This pattern is only partially valid for the branches biomass, and it has a specific character for the foliage one. The biomass of all components of plantation trees is higher than that of natural trees, but the percent of this excess varies among different components and depends on the level of January temperatures, but does not depend at all on the level of annual precipitation. As one moves from cold zones to warm ones, the excess of plantation tree biomass over natural ones increases from 1.3% to 5.3% for stem biomass, decreases from 28% to 6% for foliage biomass, as well as from 4.8% to 2.1% and from 6.3% to 1.5% for branches and aboveground biomass respectively, regardless of the precipitation level. As one moves from warm to cold zones, the absolute value of the root; shoot (R/S)ratio for thin trees (DBH = 8 cm) increases from 0.17 to 0.26, and for thick trees (DBH = 32 cm) from 0.13 to 0.20, but in percentage terms it does not depend on the stem thickness and increases by 48%. The results presented can be accounted for as the first approximation only.

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天然林和人工林生物量对温度和降水变化的响应是否存在差异?以欧亚大陆两针松为例

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摘 要:对天然林和人工林在生产力和稳定性方面的比较研究一直是森林生态学的重要研究内容之一。森林砍伐导致人工林逐步取代了天然林,在此背景下,研究全球气候变化下森林碳储存能力的变化就显得非常重要。本文在跨大陆水平上以两针松(Pinus L.)为例首次回答了这个问题。本文使用作者收集的有关欧亚大陆森林的单树生物量结构数据库,对 1880 株天然林林木和 1967 株人工林林木的数据进行了相关研究。基于林木生物量结构的原始数据、一月平均温度和年平均降水量等,采用多元回归模型,研究了温度与降水对森林生物量的影响。结果发现,随着一月温度和降水量的增加,同等规模和同等树龄的天然林和人工林地上和茎生物量均有所增加,但这种关系仅对枝条部分的生物量有效,而对树叶生物量的影响应具体问题具体分析;同时,人工林的所有组成部分的生物量均高于天然林树种的生物量,但在林木的不同组成部分之间这种差别的程度有所不同,并且主要取决于一月的温度水平,而与年降水量关系不大。当然,在建模的各个环节都存在许多不确定性,本文的结论只是对影响林木生物量的气候因素的初步认识。

关键词:两针松;天然林分和人工林;回归模型;生物量方程;一月平均温度;年降水量