**ORIGINAL PAPER**

# The principle of space-for-time substitution in predicting *Picea* spp. biomass change under climate shifts

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## Abstract

Although forest ecosystems play an essential role in climate stabilization, current climatic shifts might cause striking changes in their biological productivity, which, in turn, affects the biosphere function of forests. Studies of the relationship between the biomass of trees and stands and hydrothermal indicators (temperature and precipitation) have usually been carried out at local or regional levels. It is still unknown how climate changes affect tree and stand biomass along transcontinental gradients. Therefore, the goals of this study were (a) to test if the law of the limiting factor holds for tree and stand biomass of *Picea* spp. at the transcontinental level of Eurasia in relation to temperature and precipitation, and (b) to apply the principle of space-for-time substitution to document the use of the derived tree and stand biomass climate-sensitive models for predicting temporal biomass changes. The results revealed that at a tree level spruce aboveground biomass increased with a temperature increase in moisture-rich regions, whereas in moisture–deficient regions it was reduced. Similarly, precipitation reduction at a constant average January temperature caused a reduction in aboveground biomass in warm regions, while in cold regions its increase was revealed. At a stand level, we also revealed an increase in biomass with increased precipitation amount in warm regions. The study suggested that the principle of space-for-time substitution was clearly manifested on biomass quantity of spruce at both individual tree and forest stand levels.

**Key words:** spruce genus; tree and stand biomass; temperature; precipitation; limiting factor; space-for-time substitution

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## 1. Introduction

The Earth's climate system is gradually losing its stationarity, and climatic excesses are becoming more frequent (Aubin et al. 2018; Dent 2021). The current climatic shifts cause changes in forest areas (Emanuel et al. 1985; Kobak & Kondrasheva 1992; Saraiva et al. 2021). The importance of taking future climate shifts into account when dealing with the spread and health of *Picea abies* was recently shown in the Czech Republic (Čermák et al. 2021). Climate change changes forest biological productivity too, which, in turn, will very probably affect the biosphere function of forest cover. Thus, modern science is faced with the necessity of simultaneous analyses of two interrelated processes, but there is no answer to the question of which of them is primary.

Functional biogeography presumes that the adaptation of vegetation to environment is reflected in plant properties (Reichstein et al. 2014). Forest biomass plays an integral part in sustainable development (Müller et al. 2015), and has been used as one of the main indicators in climate research (Bojinski et al. 2014). Many global vegetation models have applied the optimality theory to model adaptive plant reactions to changing conditions (Rosen 1967; Korzukhin & Semevsky 1992).

The efforts of numerous researchers of forest ecosystems of the second half of the 20th and the beginning of the 21st centuries have accumulated a lot of empirical material on the biomass of forest stands and their trees. These were compiled in the latest version of the database on the biomass of forest-forming species of Eurasia that includes the data from 7,500 sample forest stands (Usolt-

sev 2010) and of about 15,000 trees (Usoltsev 2020). This empirical material was collected by representatives of different areas of forest sciences with different target settings and corresponding methodological specifications. A part of this material was obtained during the implementation of the International Biological Program in 1960s and 1970s following the unified methodology. However, a significant part of the data was obtained from small-scale studies, which are distributed very unevenly across regions.

Uncertainties in the results of modelling the productivity of stands may be the result of incorrect methods of establishing sample plots and taking model trees on them. Liepa (1985) notes such inaccuracies as harvesting model trees without accounting for their cenotic position in the canopy, low representativeness of sample plots within the study region and incorrect selection of impact factors (independent variables). There is some uncertainty in the use of allometric biomass models developed on the basis of pure stands to predict the biomass of trees in mixed stands (and vice versa) that can lead to a significant bias (Dutcă et al. 2018). Large uncertainties are associated with currently existing Net Primary Productivity (NPP) data (Usoltsev 2007a), mainly with root NPP that may be underestimated two to five times (Usoltsev 2018). Biomass data from destructive measurements of trees and stands can be distorted by errors in the conversion of both biomass from the level of a sample to a tree and a stand, and in the conversions of taxation indicators from a tree to a stand level. As an example, we can cite the work (Schulze et al. 1995), in which the calculated characteristics of the average diameter, average height and volume stock of the stands were underestimated by 8 to 20%, 4 to 44% and 1 to 97%, respectively. After the compiler of the database had addressed the German authors, corrections were made, and in the mentioned database (Usoltsev 2001), the corrected values were included. It is not possible to account for similar errors in numerous "gray" Soviet and Russian publications, which make up the largest part of the Eurasian database. The danger of such distortions and errors in the source databases is obvious. Having calculated the biomass model, which includes the dendrometric characteristics of a tree or a stand as independent variables, we get a residual variance, which is explained by both climatic variables and errors in calculations and other uncertainties. These errors and uncertainties can distort the contribution of climate variables to the explanation of biomass variability. It follows from the above that the effectiveness of any attempt to analyze and synthesize existing databases to obtain generalizing patterns may be significantly limited by their qualitative level (Utkin 2004), especially if this analysis has a comparative species-specific base.

Due to the predominance of complex multi-species stands over simple mono-species ones, unified allometric dependences of tree biomass on diameter at breast height have become widespread when assessing tree biomass.

It is concluded that generic equations that do not give significant biases under local conditions can be used to estimate the aboveground biomass of trees (Pastor et al. 1984; Singh 1986; Feller 1992; West et al. 1999; Mugasha et al. 2012). However, recent studies have found that generic allometric models derived from destructively sampled tree data within Eurasia give unacceptable biases of both signs in ecoregions. The mentioned biases ranged from +95 to −52% for larch (*Larix* spp.; Usoltsev et al. 2017a), from +311 to −99% for spruce (*Picea* spp.; Usoltsev et al. 2017b), from +316 to −68% for fir (*Abies* spp.), from +94 to −92% for two-needled pines and from +34 to −56% for five-needled pines (*Pinus* spp.; Usoltsev et al. 2017c), which excludes any possibility of their use at regional levels. These biases are regionally confined, and it can be assumed that they differ due to specific climatic conditions. The differences in soil conditions do not contradict this since soil zoning is also partly related to climatic factors (Dokuchaev 1948; Rukhovich et al. 2019).

It is of interest what will happen to our biota when the temperature changes, for example, by 1 °C, and when the annual precipitation changes, for example, by 20 or 100 mm. Uncovering these kinds of phenomena is interesting not only for the scientific community, but also important for the humankind existence. Previously published models of tree biomass, the so-called "climate-sensitive models", provide a partial answer to such questions, but they are presented in single studies and at regional levels. The allometric model of biomass, derived by Zeng et al. (2017), which includes a tree size together with air temperature and precipitation as independent variables, indicated that warming by 1 °C leads to an increase in aboveground biomass of trees by 0.9% and a decrease in belowground biomass by 2.3%, and an increase in precipitation by 100 mm causes a decrease in aboveground and belowground biomass by 1.5 and 1.1%, respectively. Another study from European forests (Forrester et al. 2017) did not reveal any statistically significant effect of temperature and precipitation on tree biomass. The reasons may be in the insufficiently wide range of temperature and precipitation variations within Europe, the analysis of species groups, the introduction of many correlating variables and their cumulative effects into the model, as well as the use of meta-data obtained by tabulating allometric models (Glass 1976) instead of biomass indicators estimated by harvest method at sample plots. According to Stegen et al. (2011), climate characteristics explain a small, and in many cases a statistically insignificant share of the variability of forest biomass. However, this contradicts the long-established fact that the structure, functions, and productivity of forests have geographical and, consequently, climatic conditionalities (Paterson 1956).

In the allometric models sensitive to climate (Zeng et al. 2017; Fu et al. 2017), the prediction of changes in tree biomass due to climate shifts is performed using the

principle of "space-for-time substitution". It means that modern patterns observed in spatial gradients may be used to understand and model the same patterns and processes in time gradients that are currently not observable (Blois et al. 2013). Method of space-for-time substitution has been applied prevailingly in geomorphology (Huang et al. 2019), landscape studies (Ghosh & Wildi 2007), biodiversity modelling to predict the impact of climate change on species distribution, species abundance and changes in species composition (Currie 2001; Guisan & Thuiller 2005; Ferrier & Guisan, 2006; Elith & Leathwick 2009; Fitzpatrick et al. 2011; Blois et al. 2013; Horrocks et al. 2020; Costa et al. 2021), in predicting successional vegetation dynamics (Ricklefs 1987; Smolonogov 1995; Miyanishi & Johnson 2007), in the development of stand yield tables based on surveys at temporary sample plots (Anuchin 1952; Poryazov et al. 2004). The success of the application of the theory of space-for-time substitution in plant ecology depends on the extent to which the environmental conditions that determine the properties of plants along territorial gradients correspond to future environmental conditions that determine the properties of plants in time gradient. It is expected that at the current rate of climate change, populations of tree species will find themselves in climatic conditions beyond those to which they are adapted, which will threaten their health conditions, sustainability and viability (McKenney et al. 2011; Thuiller et al. 2005; Čermák et al. 2021). To assess the ability of species to survive within their current ranges, studies aimed at assessing their environmental vulnerability to climate change have been conducted in recent years (Aubin et al. 2018; Belote et al. 2018; Foden et al. 2019; Seidl et al. 2018; Wade et al. 2017; Leštianska et al. 2015, 2020a, b; Čermák et al. 2021). It has been documented that different species, even of the same genus, may have contradictory adaptive abilities. For example, of the two North American species of the *Picea* genus, *Picea glauca* demonstrates a greater adaptive ability than *Picea rubens* (Royer-Tardif et al. 2021).

An increase of temperature by almost 2 °C in Alaska over the past 50 years correlates with the substantial declines in white spruce tree growth (McGuire 2010). Nevertheless, Rößiger et al. (2019) consider it unreasonable to simply extrapolate current changes in the state of spruce forests for the foreseeable future, since it is not known whether these trends are only related to climate shifts. For the conditions of Europe, there are contradictory results of the influence of weather factors on the growth of spruce (*Picea abies*) stands: on the one hand, the range of variation in the width of the annual ring as a reaction to precipitation increases with age (Holmsgaard 1955; cit. according to Fiedler 1978), and later the opposite result was obtained, namely, the lack of precipitation affects the decrease in growth to a greater extent in young spruce forests compared to mature ones due to the superficial root system in young trees (Fiedler 1978). Both low winter temperatures and summer droughts caused

a decrease in the radial growth of spruce forests in the east of Germany, especially a sharp decrease in growth is observed when two extreme values of weather factors are simultaneously affected (Fiedler 1978). In the Moscow region in Russia, a simultaneous decrease in precipitation by 40% and an increase in annual temperature by 60% relative to the average values over the past 50 years caused the death of natural immature *Picea abies* trees in the amount of 25 to 43% in 1938 (Timofeev 1939). This indicates that climate stress exceeds species' compensating mechanisms (Anderegg et al. 2019).

Later, for the conditions of Germany, it was found that the main factor affecting the growth of spruce is summer precipitation, especially in June. Since the 1950s, this influence has almost disappeared at all sites. Since then, the main climatic signal of spruce growth is the sensitivity to the drought of the previous summer. It is concluded that spruce probably reached its climatically determined limit at the southern border of distribution in boreal forests. The growth and viability of forest tree species is mainly affected by an increase in the frequency of extreme weather conditions (Grundmann 2009).

The dependence of the radial growth of European spruce, Scots pine, and European beech trees on climate and soil water balance was studied using data from 24 sample plots in Saxony (Germany) for the period from 1951 to 2006 (Röhle et al. 2010). For each tree species, the relation of growth with 30 independent variables characterizing precipitation, air temperature, and soil water balance for different months was analyzed, which explained from 50 to 57% of the total variability of growth. By combining the obtained models with climate forecast data, it was shown that environmental conditions for spruce become more unfavourable over time, which leads to a gradual decrease in growth (Röhle et al. 2010). In total, in Central Europe, Norway spruce is a species with the most unpredictable response to a warmer and drier climate in the future (Bošela et al. 2019). According to the principle of the limiting factor, the growth rate of plants is limited by a factor that is at a minimum or excess in relation to its needs (Liebig 1840; Shelford 1913; Molchanov 1971; Rosenberg et al. 2016). At the polar limit of birch distribution in Siberia, the limiting factor is temperature, but as moving south, the warmth deficit diminished, and the impact of moisture deficiency increases. At the same time, the replacement of the limiting factor occurs in the subzone of the middle taiga (Fonti 2020). A replacement of the limiting factor is also possible with its rapid change, when ecosystems move from an optimal state (Korzukhin & Semevsky 1992) to a non-stationary one, to a state of stress (Odum 1975; 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 & Anderson 2020).

When using the database of tree biomass of 28 woody and shrub species of Eurasia formed by the authors, transcontinental allometric biomass models of two types

were developed (Usoltsev et al. 2019c). The first type of model includes crown width and tree height as independent variables, while the second type uses data about tree height and stem diameter at breast height as predictors. It was found that the explanatory power of the first model type for foliage, branches and roots was lower compared to the second one, but the difference between them was not significant. For stem and aboveground biomass, the explanatory power of the first model type was 4% lower, and this difference was statistically significant. However, the lower explanatory ability of the first model type is compensated by the possibility of obtaining numerous measurements by repeated flights over the same area, which is not comparable to ground-based surveys. This allows to assessing the change in the carbon pool of forests at some area during a specific period.

Based on the findings from previous works and our knowledge, the tasks of this study were formulated as follows:

– to prove the effect of the law of the limiting factor at the transcontinental level when modelling changes

in the biomass of trees and stands of *Picea* spp. on the territory of Eurasia in relation to geographically determined indices of temperatures and precipitation;

– to identify the patterns of changes in tree and stand aboveground biomass and stand NPP due to temperature and precipitation;

– to find out whether the derived climate-sensitive models of tree and stand biomass can be applied to predict biomass changes along temporal gradients using the principle of space-for-time substitution.

## 2. Material and methods

Our analyses were based on the previously compiled Eurasian biomass database comprising data about 15,300 sample trees of different species (Usoltsev 2020) and 7,500 sample forest stands of different species (Usoltsev 2010), out of which approximately 1,380 trees and 900 stands represented *Picea* spp. (Fig. 1, 2, Tables 1 and 2).

**Table 1.** Spruce species included in the analysis of aboveground tree biomass at levels of trees (kg) and stands (t per ha) and representation of countries.

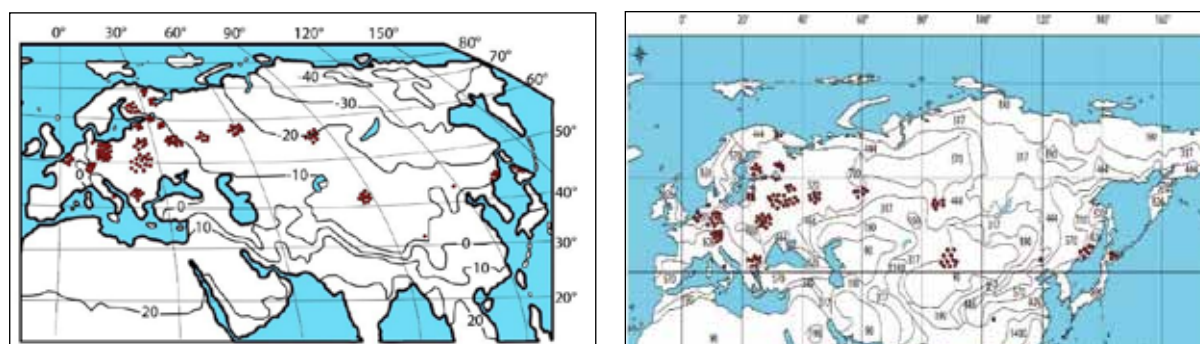| Tree level | | |
|---|---|---|
| Species | Country | Number of sample trees |
| *Picea abies* (L.) H. Karst. | Belarus, Belgium, Czech Republic, Finland, Germany, Latvia, Russia, Sweden, Switzerland, Ukraine | 1011 |
| *P. obovata* Ledeb. | Russia | 342 |
| *P. schrenkiana* F. & C. A. Mey. | China | 15 |
| *P. jezoensis* (S. & Z.) Carrièr | Japan, Russia | 8 |
| *P. purpurea* Masters | China | 2 |
| *P. koraiensis* Nakai | China | 1 |
| *P. glehnii* F. Schmidt | Japan | 1 |
| Total | | 1380 |
| Stand level | | |
| Species | Country | Number of sample plots |
| *Picea abies* (L.) H. Karst. | Austria, Belarus, Belgium, Bulgaria, Czech Republic, Denmark, Estonia, Finland, France, Germany, Italy, Latvia, Lithuania, Norway, Russia, Slovakia, Sweden, Ukraine | 486 |
| *P. obovata* L. | Russia | 144 |
| *P. jezoensis* (S. & Z.) Carrièr | China, Russia | 190 |
| *P. schrenkiana* F. & C.A. Mey. | China, Kazakhstan | 58 |
| *P. sitchensis* (Bong.) Carrière | Great Britain, Ireland | 12 |
| *P. purpurea* Masters | China | 4 |
| *P. orientalis* Link | Georgia, Russia | 4 |
| *P. koraiensis* Nakai | Japan | 2 |
| Total | | 900 |



**Fig. 1.** Spatial distribution of 1,380 single tree data on aboveground (the sum of stems, branches and foliage) biomass of *Picea* spp. overlapped with the mean January temperature in ºC (left) and mean annual precipitation total in mm (right) (means calculated for the period from 1997 to 2007) (sources: https://store.mapsofworld.com/image/cache/data/map_2014/currents-and-temperature-jan-enlarge-900×700.jpg for the left map and https://www.eldoradoweather.com/climate/world-maps/world-annual-precip-map.html for the right map, see also World Weather Maps, 2007).
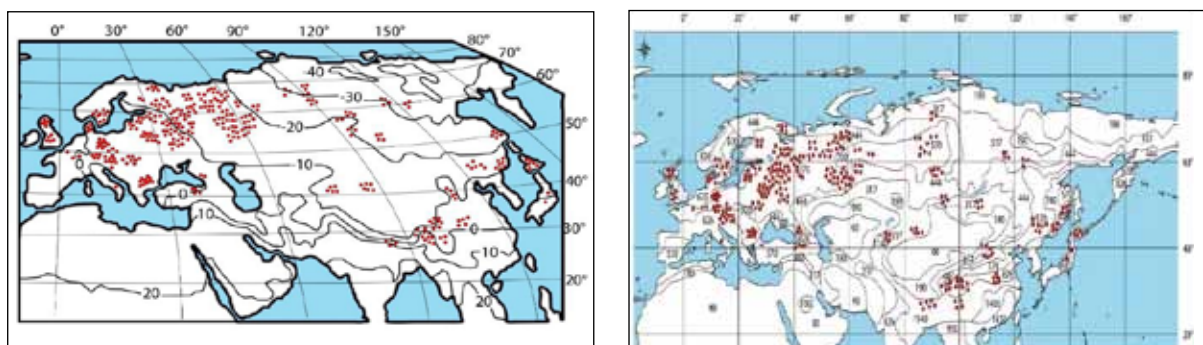
**Fig. 2.** Spatial distribution of 900 *Picea* spp. forests with biomass data obtained from destructive sampling overlapped with the mean January temperature in ºC (left) and mean annual precipitation expressed in mm (right) (sources: https://store.mapsof-world.com/image/cache/data/map_2014/currents-and-temperature-jan-enlarge-900×700.jpg, see also World Weather Maps, 2007).

The data on the biomass of trees were obtained using the destructive method on sample plots. Before felling the tree, the crown radii were measured in four perpendicular directions from the stem base, and the average diameter of the crown was calculated. After felling the tree, the length of the tree and the diameter of the stem at breast height were measured, and its age was determined by counting the number of annual rings on the stump. The procedure for destructive determination of the biomass of sample trees on the territory of Russia was described earlier (Usoltsev 1990). The matrix of biomass data was explained by dendrometric characteristics and two climatic variables: mean January temperature (Fig. 1) and annual precipitation total (Fig. 2) taken from World Weather Maps (2007) that represented the period from 1997 to 2007. The use of the winter temperature instead of the annual average was justified earlier (Usoltsev et al. 2019a).

For the purposes of the study, data were analysed and models were derived at levels of individual trees and stands. In turn, each of these levels was studied using two models. At the tree level, the models were based on the data about $H$, $Dcr$ and $D$. The first model included the crown width and tree height as independent variables in the model, while the second model used stem diameter at breast height, and tree height (Chave et al. 2005). It is still unknown how the two models for *Picea* spp. single trees will be sensitive to changes in climate variables. However, for *Quercus* spp. trees it was found that the contribution

of climatic variables to the explanation of the variability of the biomass varies from 11 to 28%, depending on the structure of the model, namely, on the number and combination of dendrometric (morphological) variables (Usoltsev et al. 2020a).

Similarly, two models were constructed for the stand level, the first one for stand biomass, and the second one for stand NPP. Although biomass and NPP are determined using the same structural and dendrometric stand characteristics (Keeling & Phillips 2007), the contributions of climate variables to explain the variability of biomass and NPP in one case and in the other one may differ significantly. For example, in models for stands of *Quercus* spp. these contributions were 22 and 16%, respectively (Usoltsev et al. 2020b).

The data on the biomass of trees and stands obtained from destructive sampling (Tables 1 and 2) were processed using Statgraphics-19 software (http://www.statgraphics.com/). We performed a multiple regression analysis to explain the variability in biomass data. In order to reduce the length of the article, and to make it clear for readers, the patterns are given here only for the total aboveground biomass (sum of stems, branches, and foliage). In fact, the patterns based on separate tree components (stem, foliage, branches) are very similar to that of the aboveground biomass. The justifications of model structures were given earlier (see Usoltsev et al. 2019a, b; Usoltsev et al. 2020b for more details).

**Table 2.** Statistical characteristics of *Picea* spp. samples in Eurasia used to derive models

| Statistics[a] | Tree characteristic[b] | | | | Stand characteristic[c] | | | |
|---|---|---|---|---|---|---|---|---|
| | H [m] | D [cm] | Dcr [m] | $P_{tree}$ [kg] | A [years] | N [1,000 per ha] | $P_{stand}$ [t ha⁻¹] | $Z_{stand}$ [t ha⁻¹ per year] |
| Mean | 13.8 | 15.7 | 2.7 | 168.1 | 84 | 2.7 | 155.7 | 127.5 |
| Min | 0.43 | 0.5 | 0.25 | 0.011 | 3 | 0.13 | 0.04 | 0.003 |
| Max | 44.8 | 98.2 | 10.9 | 5089.0 | 317 | 281 | 574 | 528 |
| SD | 9.3 | 13.0 | 1.5 | 413.0 | 51.7 | 12.4 | 98.8 | 85.3 |
| CV [%] | 67.6 | 82.8 | 55.8 | 245.7 | 61.3 | 48.0 | 63.5 | 66.9 |
| N | 1,380 | 1,380 | 970 | 1,380 | 900 | 900 | 900 | 350 |

[a] Mean is mean value; Min is minimum value; Max is maximum value; SD is standard deviation; CV is coefficient of variation; n is number of observations. [b] H is tree height (m); D is stem diameter at breast height (cm); Dcr is crown width (m); $P_{tree}$ is aboveground tree biomass (sum of stem, branches, and foliage) in dry weight (kg). [c] A is a stand age (years); N is tree number (1,000 individuals per ha); $P_{stand}$ is the aboveground stand biomass (the sum of stems, branches and foliage) in dry weight (t per ha); $Z_{stand}$ is the aboveground net primary production (NPP; t per ha and year). The NPP was determined on the sample plots using the destructive method by measuring the annual increase in biomass of stems, branches and foliage of sample trees, followed by their calculation per 1 ha according to the tree data accounting on sample plots (Usoltsev 2007b).

## 3. Results

Regression models sensitive to climate were calculated at four above-mentioned levels:

– a model for estimating aboveground tree biomass using tree height and crown diameter as predictors ($adjR^2 = 0.960$; $SE = 0.44$):

$$\ln P_{tree} = 105.76 + 0.9088(\ln Dcr) + 1.7171(\ln H) - 28.3300[\ln(T+50)] - 17.3923(\ln PR) + 4.6052[\ln(T+50)]\cdot(\ln PR) \qquad [1]$$

– a model for estimating aboveground tree biomass from tree diameter and height ($adjR^2 = 0.984$; $SE = 0.25$):

$$\ln P_{tree} = 42.3950 + 1.1121(\ln D) - 0.4295(\ln H) + 0.3529(\ln D)(\ln H) - 11.4190[\ln(T+50)] - 6.7934(\ln PR) + 1.8182[\ln(T+50)]\cdot(\ln PR) \qquad [2]$$

– a model for the estimation of aboveground stand biomass based on mean stand characteristics ($adjR^2 = 0.717$; $SE = 0.58$):

$$\ln P_{stand} = 13.0570 + 4.0112(\ln A) - 0.0589(\ln A)^3 + 0.9058(\ln N) - 0.1933(\ln A)(\ln N) - 5.5295[\ln(T+50)] - 4.5395(\ln PR) + 1.2305[\ln(T+50)]\cdot(\ln PR) \qquad [3]$$

– a model to estimate aboveground stand NPP ($adjR^2 = 0.674$; $SE = 0.37$):

$$\ln Z_{stand} = 3.7483 + 0.0974(\ln A)(\ln N) + 0.6329(\ln P_{stand}) - 1.4516[\ln(T+50)] - 1.3861(\ln PR) + 0.3896[\ln(T+50)]\cdot(\ln PR) \qquad [4]$$

where $H$ is tree height (m); $D$ is stem diameter at breast height (cm); $Dcr$ is crown width (m); $P$ is aboveground biomass in dry weight (kg), $Z_{stand}$ is aboveground net primary production (t per ha and year), $T$ is mean January temperature in ºC; $PR$ is average annual precipitation total in mm; $adjR^2$ is a coefficient of determination adjusted for the number of parameters; SE – tandard error of the equation.

The equations [1 – 4] include the logarithm of temperature ($\ln(T+50)$). Since in permafrost areas of Siberia the January temperature may sometimes exceed −50 ºC, the constant of 50 was added to temperature ($T+50$) to enable logarithmic transformation of temperature $T$. Due to the logarithmic transformation, we applied a correction according to Madgwick (1983). Most regression coefficients in all derived models were significant at a level of $p < 0.001$. The exception was model (4), in which climate variables were significant at a level of $p < 0.10$. The low level of significance of climate variables in the model (4) may be due to above-mentioned uncertainties related to methodological diversity of obtaining NPP data from destructive tree sampling, as well as the lower amount of NPP data, 2.6 times less than for stand biomass, as well as their uneven distribution across climatic regions. Note that derived models are valid within the ranges of predictors (Tables 1, 2).

Four-factor models (1 – 4) can be geometrically interpreted in a five-dimensional space (Jensen 1984). However, according to the formulation of the research task, we were interested in identifying the dependence of the biomass of trees and stands on two climatic factors. With this in mind, we presented a geometric interpretation of models (1 – 4) in relation to air temperature and precipitation (Fig. 3) using the average values of the structural explanatory variables ($D, H, A, N$) shown in Tables 1 and 2.

Tables 3 and 4 show the biomass of trees and stands at temperature and precipitation limits, including their confidence intervals (mean value ± standard error of equation). Tabulation of equations [1–4] is performed for the average values of the independent variables presented in Table 2.

In Fig. 3 we can see the change in the calculated biomass and NPP along the gradients of temperatures and precipitation. Based on the above-mentioned principle of space-for-time substitution, we can use the presented models to analyze the reactions of the aboveground bio-

**Table 3.** Aboveground tree biomass (kg) at combinations of January temperature and annual precipitation totals, where a transitional precipitation value represents a spot at which a change in the factor limiting tree biomass occurs.

| Annual precipitation total [mm] | | Average temperature in January [ºC] | | | | |
|---|---|---|---|---|---|---|
| | | 5 | 0 | −10 | −15 | −20 |
| | | Aboveground tree biomass [kg] according to equation [1] (mean ± standard error) | | | | |
| MInimum | 400 | 56.0±18.1 | 61.1±19.7 | 67.4±21.8 | 75.5±24.4 | 86.4±27.9 |
| Transitional | 470 | 65.6±21.3 | 65.5±21.2 | 65.5±21.2 | 65.4±21.1 | 65.4±21.1 |
| Maximum | 800 | 110.3±35.7 | 82.6±26.7 | 59.5±19.2 | 40.8±13.2 | 26.1±8.4 |
| | | According To Equation [2] | | | | |
| Minimum | 400 | 59.2±10.6 | 63.0±11.2 | 67.6±12.1 | 73.3±13.1 | 80.7±14.4 |
| Transitional | 540 | 68.0±12.1 | 67.8±12.1 | 67.6±12.1 | 67.4±12.0 | 67.2±12.0 |
| Maximum | 800 | 81.4±14.5 | 74.7±13.3 | 67.7±12.1 | 60.5±10.8 | 52.9±9.4 |

**Table 4.** Aboveground stand biomass (t per ha) at combinations of average January temperature and annual precipitation totals.

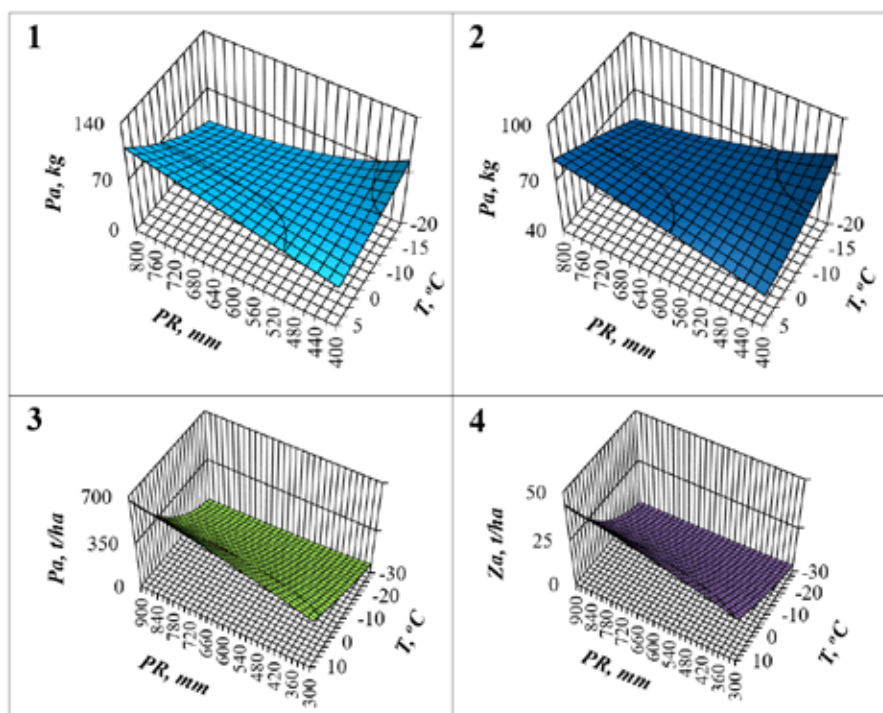| Annual precipitation total [mm] | | Average temperature in January [ºC] | | | | |
|---|---|---|---|---|---|---|
| | | 10 | 0 | −10 | −20 | −30 |
| | | Aboveground stand biomass [t/ha] according to equation [3] (mean ± standard error) | | | | |
| Minimum | 300 | 388.3±169.0 | 296.0±128.8 | 212.3±92.4 | 138.3±60.2 | 75.6±32.9 |
| Maximum | 900 | 671.3±292.2 | 400.0±174.1 | 212.2±92.4 | 93.7±40.8 | 29.6±12.9 |
| | | According To Equation [4] | | | | |
| Minimum | 300 | 24.5±6.7 | 17.9±4.9 | 12.2±3.3 | 7.5±2.0 | 3.7±1.0 |
| Maximum | 900 | 43.6±11.9 | 25.3±6.9 | 12.9±3.5 | 5.5±1.5 | 1.6±0.4 |

**Fig. 3.** Aboveground biomass and NPP in relation to the average January temperature (*T; ºC*) and annual precipitation total (*PR; mm*): *1* – according to the tree-level model [eq. 1]; *2* – according to the tree-level model [eq. 2]; *3* – according to the stand-level model [eq. 3] designed to assess aboveground stand biomass; *4* – according to the stand-level model [eq. 4] designed to estimate stand aboveground NPP.
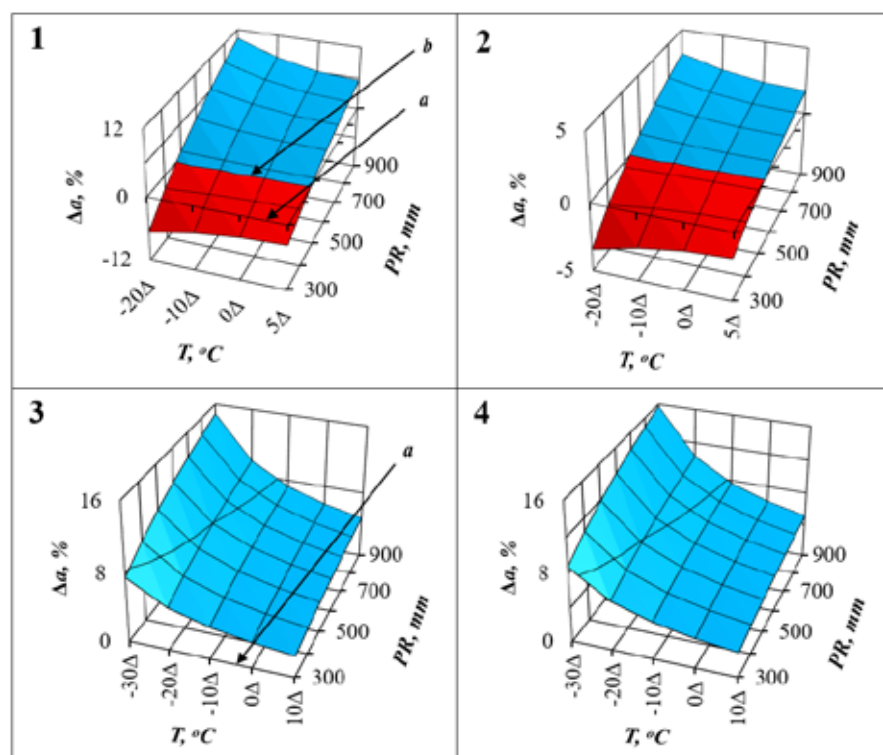


**Fig. 4.** The relative change in the aboveground tree and stand biomass and NPP under the increase in temperature (T) by 1 ºC (Δ) due to the climate change with regard to actual values of temperature and precipitation (PR). Here −20Δ = 20+1 ºC. Graph numbers refer to models (1)–(4). (*a*) – represents the plane with no change in biomass under the assumed temperature increase by 1 ºC; (*b*) – is the border line between positive and negative changes in biomass under temperature increase by 1 ºC. Colours indicate an increase (blue) and a decrease (red) of aboveground biomass or NPP in comparison to the reference climate.

mass of trees and stands to changes in temperature or precipitation. Here we examined the impact of temperature increase by 1 °C and annual precipitation reduction by 20 mm. First derivatives of the models (3) and (4) represent biomass changes under the specified change of temperature or precipitation (Figs. 4 and 5). In Figure 4, it is assumed that precipitation changes only geographically, while the on-site temperature increased by 1 °C (Δ) denoted as −30Δ to +10Δ. Similarly, in Figure 5 the January temperature changes only geographically, and precipitation is reduced by 20 mm designated as −300Δ to −900Δ.

later all the trees died due to periodic droughts (Protasov 1952).

Liepa (1980) connects the concept of optimum with the active period of the exposure to a factor: "The concept of the active period is connected with the concept of the optimum of the ecological factor. Each factor has its characteristic optimum of impact, at which the system's needs for this factor are fully satisfied and the process under study proceeds most successfully. The optimum is a certain zone of the factor level, below which the system lacks a factor, and at a level above this zone, the factor has an inhibitory effect" (p. 110–111). In other words,
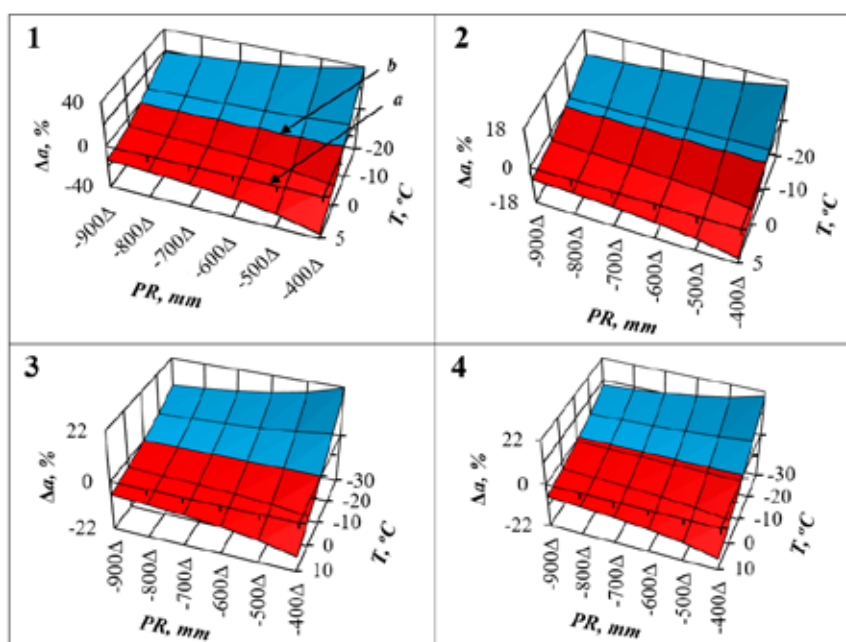


**Fig. 5.** Relative changes in the aboveground tree and stand biomass and NPP under the reduced precipitation (PR) by 20 mm due to the climate change with regard to the actual values of temperature (T) and precipitation. Here −900Δ = 900–20 mm. Graph numbers refet to derived models (1)–(4) and the numbers shown in Fig. 3; (*a*) – represents the plane with no change in biomass under the assumed precipitation reduction by 20 mm; (*b*) – is the border line between positive and negative changes in biomass under the precipitation decrease by 100 mm. Colours indicate an increase (blue) and a decrease (red) of aboveground biomass or NPP.

## 4. Discussion

For any living organism or community, there is a combination of environmental factors that is optimal for its growth and reproduction. On both sides of this optimum, biological productivity gradually decreases until a deviation from the optimum leads to a lethal result (Ricklefs 1979). Ignoring the fact that the ecological and climatic conditions of the growing area go far beyond their optimum leads to lethal results in forest cultivation. For example, in the conditions of the dry steppe of Northern Kazakhstan (51°10′ N, 71°24′ E; in years 1940–1950 mean January temperature was −18 °C, mean July temperature +20 °C, mean annual temperature +1.4 °C, mean annual precipitation 311 mm), Siberian larch planted on dark-chestnut soils reached a height of 16 m and a stem diameter of 18 cm by the age of 48 years, but

any external factor affecting the ecosystem has a certain range in which its action is most effective.

At the global level, the temperature gradient is known to have an optimum temperature factor near the equator, where the net primary production of forest cover reaches its maximum and decreases to minimum values as we move towards the north and south poles (Anderson et al. 2006; Huston & Wolverton 2009). We see a similar picture in the humidity gradient of the environment: productivity increases in the direction from swamps to optimal humidity conditions and then decreases with the transition to dry environmental conditions (Olenin 1982; Ricklefs 1979; Wilmking et al. 2004; Toromani & Bojaxhi 2010; Berner et al. 2013). Thus, the maximum productivity is observed at an optimal temperature value under the condition of constant humidity and at an opti-

mal humidity value under the condition of constant temperature (Nebe 1966).

A different picture may develop when independent variables are mutually correlated. The mutual correlation requires the introduction of the products of independent variables along with independent variables themselves. For example, when temperature and precipitation were used as independent variables, 48% of the variability of the yield of Canadian hemlock cones was explained. The introduction of additional variables in the form of the product of these variables and their squares increased the coefficient of determination to 79%. This means that the nonlinearity of the factors under consideration accounts for 31% of the total influence of all factors on the formation of the crop of cones (Maurin's et al. 1977). Similarly, Draper and Smith (1966) presented an example when a relationship with a single variable explained 89% of the variability of the dependent variable. The introduction of the product of this independent variable with another independent variable into the model increased the variability explained by the model to 94%. At the same time, the threshold (cutoff) value of the contribution of the new explanatory variable, below which a new independent variable can be ignored, plays a role. Booth et al. (1994) recommend this cutoff value at a level of 10%.

As a result of our construction of models of four levels for the biomass of *Picea* spp., a statistically significant effect of the product of temperatures and precipitation was established, and as a result, we have the same propeller-shaped 2-factor surface for equally sized trees, as well as for stands.

The dependences of the aboveground biomass of trees and stands on temperatures and precipitation show some differences between the patterns at tree (1 and 2, Fig. 3) and stand (3 and 4, Fig. 3) levels. At a tree level, the biomass of equally sized trees increased with the increasing precipitation in warm regions, while in cold regions, the opposite trend was revealed. This trend can be explained by sparser stands in the Kola Peninsula, although the influence of stand density in the model was statistically weak. Since the limiting factor at the tree level changed during the transition from warm to cold regions, Table 3 shows that this change occurs at annual precipitation totals from 470 to 540 mm. This means that we observe the manifestation of the above-mentioned law of the limiting factor (Liebig 1840; Shelford 1913; Molchanov 1971; Rosenberg et al. 2016). At the tree level, the limiting factor in moisture-rich regions is low temperature, while in water-deficient regions it is high temperature. In the temperature range from 5 to −20 °C in moisture-rich conditions, the biomass of equally sized trees decreased from 110 to 26 kg (by 323%) according to equation [1] and from 81 to 53 kg (53%) according to equation [2]. In water-deficient conditions, the biomass of equally sized trees increased from 56 to 86 kg (54%) with the decreasing temperature according to equation [1] and from 59 to 73 kg (37%) according to equation [2] (Table 3).

At a stand level, we also observed an increase of biomass and NPP with precipitation in warm regions, but as the temperature decreased, this increase in aboveground stand biomass was much less pronounced. In moisture-rich regions, we revealed a 21-fold decrease in biomass and a 26-fold decrease in NPP as the temperature decreased from 10 to −30 °C. In water-deficient regions, the decrease in biomass was only 4-fold and the decrease in NPP was 6-fold (Table 4).

We compared the aboveground stand biomass estimated by our model with the data of the project CANIF (Schulze 2000; Scarascia-Mugnozza et al. 2000), during which sample plots were established in a latitudinal gradient from Sweden to Italy. For the north of Europe, the aboveground stand biomass calculated by our model was 112 ±92 t/ha, i.e. from 120 to 304 t/ha, which is consistent with the CANIF project that reported values from 120 to 190 t/ha. Similarly, the aboveground stand biomass for the south of Europe calculated by our model (412 ±179 t/ha, i.e. from 230 to 590 t/ha) coincided with the project data (from 240 to 260 t/ha).

It is known that the results of a local biomass model cannot be extrapolated to the global level, and vice versa (Muukkonen & Mäkipää 2006). Nevertheless, our trans-Eurasian results are to some extent comparable with the local results obtained for Siberian swamp pine forests (Glebov & Litvinenko 1976). According to Glebov and Litvinenko (1976), the annual radial growth decreases from 0.71 to 0.57 mm with an increase in the sum of temperatures above 10 °C from 1600 °C to 2200 °C in the case of annual precipitation total of 400 mm, and increases from 0.65 to 0.74 mm under annual precipitation of 600 mm. In a more productive type of forest, the pattern persists: in the first case, there is a decrease in growth from 1.93 to 1.66 mm, and in the second one, there is an increase from 1.86 to 2.48 mm. This means that with reduced precipitation, the limiting factor is an increase in temperature, and with increased precipitation, the increase is limited by a decrease in temperature. In the conditions of the forest-steppe in the south of Russia, it has long been established that the degree of influence of air temperature on the growth of Scots pine depends only on the conditions of moisture availability (Tolsky 1904; Rubtsov & Ilyin 1956).

A different pattern was obtained from German spruce forests (Nebe 1966), where the dependence of the upper stand height on the annual temperature, adjusted for its coefficient of variability, and on average precipitation for the period from May to August was examined. At high temperatures, no dependence of growth on precipitation was revealed. At low temperatures, an increase in precipitation causes an increase in stand height, while in swamp pine forests of Siberia, there is a decrease in growth under these conditions. At low precipitation sums, the stand height of German spruce forests changes along a bell-shaped curve with an increase in temperature, while at high precipitation totals it increases monotonously with a

positive sign of the first derivative. Naturally, none of the contradictory local trends shown above can be extrapolated to the trans-continental level.

Since changes in temperature and precipitation caused by the greenhouse effect are more frequently accompanied by droughts and floods (Hari et al. 2020; Buras et al. 2020; Schnabel et al. 2021), it would be useful to include the coefficient of temperature variability as an independent variable in addition to the annual temperature, when predicting the productivity of vegetation cover. Accordingly, in relation to another independent variable, it would be possible to use not only annual precipitation, but also precipitation multiplied with the coefficient of variability of annual precipitation. In this way, the catastrophic impact of droughts and floods on the productivity of vegetation cover could be accounted for to some extent.

Fig. 4 shows the change in the aboveground biomass of trees and stands ($\Delta a$, %) under an increase in mean January temperature by 1 °C. It is assumed that precipitation changes only geographically. The revealed general pattern at the Eurasian scale suggests that at a tree level, in moisture-rich climatic zones, an increase in temperature by 1°C under a constant amount of precipitation causes an increase in aboveground tree biomass (blue surface areas in Fig. 4), while in precipitation–deficit zones there is its decrease (red areas in Fig. 4). At a stand level, an increase in temperature by 1 °C causes an increase in biomass and NPP in the whole territory of Eurasia, regardless of the actual territorial temperature and precipitation levels (total blue surface areas in Fig. 4).

Fig. 5 shows the changes in the biomass ($\Delta a$, %) at tree and stand levels under the assumption of annual precipitation reduction by 20 mm. The revealed general transcontinental pattern indicates that in warm climatic zones, a decrease in precipitation by 20 mm causes a decrease in aboveground biomass (red area in Fig. 5), and in cold climatic zones – its increase (blue area in Fig. 5).

Contribution of climatic variables to the explanation of variability of tree biomass and biomass and NPP of stands in models (1) to (4) amounted to 26, 16, 14 and 8%, respectively, and the contribution of structural variables ($D, H, A, N$) was 74, 84, 86 and 92%, respectively. Since the contribution of climate variables is formed "according to the residual principle", i.e. it is extracted from the residual variance formed after the assessment of the contribution of structural variables, the contribution of climatic variables strongly depends on the structure of the model, in particular, on which structural variables and their combinations are included in the model as independent variables (Usoltsev et al. 2020a).

It needs to be considered that the revealed changes in tree and stand biomass under the assumed climatic shifts (Figs. 3, 4 and 5) do not account for the ongoing rapid environmental changes and the ability of forest vegetation to adapt to new climate (Dussarrat et al. 2021), but indicate the responses of forest ecosystems based on the long-term adaptive potential to regional climatic conditions. Although Veloz et al. (2012) pointed out that using the current spatial distribution of species to predict future trajectories of vegetation under changing climate may lead to biased results, the applied approach of space-for-time substitution may at least partially reveal possible temporal trends. The success of such studies depends on the variability of environmental conditions captured by data to cover also the shifts to extreme conditions. Since our models derived for *Picea* genus were based on measurements from a wide range of environmental conditions (Fig. 1 and 2), we were able to examine the changes over a large span of combinations of temperature and precipitation. Other alternatives used in research include studies of species or provenances moved to drier and/or warmer conditions than their original sites (Leštianska et al. 2015, 2020a, 2020b).

When analysing the results, we must keep in mind the presence of significant uncertainties related to the variety of methods for obtaining data on tree biomass, ignoring the social position of trees in the canopy, uneven spatial distribution and hence representation in different climatic regions, the presence of errors in calculations, the above-mentioned uncertainty of space-for-time substitution method, as well as to the inaccurate binding of sample plots to climate maps due to the interpolation procedure, the low resolution of the climate maps used, the discrepancy between the time of obtaining biomass data and the time climate maps represent.

The main pool of our forest biomass data in Eurasia was obtained in the period between 1970s and 1990s, while the used climate data covered the period from the late 1990s to early 2000s. Some discrepancy between the two time periods may cause possible biases in the results obtained, but for such a 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). Geologically formed climates of two neighbouring ecoregions determined not only the separation of one genus into two species or the replacement of one species by another, but also the difference in the morphological structure and biomass of stands. The adaptation of species to different climates of these regions lasted for thousands of years. We extrapolated the territorial climate difference to the currently predicted climate difference (the method of analogies, or of space-for-time substitution).

Further modelling of climate effects on tree and stand biomass would be established on more precise climate data in combination with the most probable scenarios of climate development in specific time horizons. However, such an attempt can strike on a lack of reliable data (sufficiently precise at a local level), especially for the Asian part of the studied transcontinental range. Anyway, under the current conditions, especially as for the limited input data on climate, our study could be understood as a good start as well as an example of methodological approaches

for modelling in this field, since it is pointless to intend the model to an accuracy of 5% if the initial data can be obtained with an error of at least 10% (McLone 1979).

## 5. Conclusions

Our research analysed the dependence of tree and stand biomass on air temperature and precipitation for *Picea* genus along trans-Eurasian climatic gradients. The derived models can be used as decision support tools in the development of global strategies for managing the carbon sequestration capacity of forests. Obviously, our models should be considered tentative, and much more work should be done in this field to improve their explanatory power. Especially, more precise meteorological data should be implemented as input for our modelling. The interpretability of models could also be increased by additional data that would fill the gaps in the current spatial distribution of sampled trees and/or stands.

Anyway, our calculations suggested clear tendencies in aboveground biomass with changing temperature and/or precipitation, and potential modifications in aboveground biomass at both tree and stand levels in *Picea* spp. due to climate change. We suggest that under changing environmental conditions, climate-sensitive models such as those presented here should provide more robust predictions of biomass and potential biomass changes in future. Another possibility for further analyses would be focusing on the most common and wide-spread tree species, for instance Norway spruce. Those would bring knowledge about species-specific biomass reactions to ongoing climate change under specific regional conditions. Such knowledge might be useable also at a local scale in terms of making decisions about forest management adjusted to changing ecological conditions.

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