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CHANGES IN FOLIAGE BIOMASS OF THE GENERA *LARIX* AND *PINUS* ALONG GRADIENTS OF TEMPERATURE AND PRECIPITATION IN EURASIA

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Abstract

Forest ecosystems are an essential part of the global carbon cycle and constitute a large fraction of the storage of terrestrial carbon. However, climate change may induce shifts in temperature and precipitation. These changes in temperature and precipitation have pronounced consequences for forest growth and carbon sequestration potential. This study addressed the comparative analysis of foliage biomass in the deciduous genus *Larix* spp. and the evergreen subgenus *Pinus* spp. in gradients of annual precipitation and winter temperature. The database for modeling involved 400 and 2,110 sample plots for Larch and Pine, respectively. Pine had reduced foliage biomass in dry conditions; however, an increase in foliage biomass was observed in moist conditions. On the contrary, regardless of conditions, *Larix* accumulated more foliage biomass. Interestingly, precipitation (100mm) increased Pine tree foliage biomass in warm regions. This positive trend of precipitation was observed for Larch in warm regions. We argue that these responses are related to the differences in physiology. In winter, Larch carries out only respiration. We discuss that these responses are due to the different status of tree needles in these two species. Understanding tree genera responses to rising temperature and shifts in precipitation regimes will enable us to improve predictions of the carbon storage potential in Eurasian forests.

Key words: *Pinus; Larix*; Biomass; Eurasia; Equations.

Introduction

Numerous studies have demonstrated the inevitable effect of climate change in recent decades. Such studies have addressed the possible negative impacts on vegetation and human health (Behrensmeyer, 2006; Lenton *et al*., 2019; Malhi *et al*., 2020). Indeed, climate change is a severe environmental problem and affects biological and non-biological systems worldwide (Malhi *et al.*, 2020). Forest ecosystems constitute an integral component of the global carbon cycle as they store significant amounts of carbon above- and belowground (Ripple *et al.*, 2019). Eurasian forests, and particularly boreal forests, play a vital role in the global sequestration and storage of C forests (Usoltsev, 2007). Eurasian forests account for 70% of total C storage in forests (Myneni *et al.,* 2001). Eurasia constitutes 36.2% of the global terrestrial area, harbors high plant biodiversity, and provides vital ecosystem services (Addison & Greiner, 2016; Zhou *et al.,* 2017). In particular, 5,283 species are native to the Eurasia region (Hu & Li, 2015). It clearly demonstrates the significance of Eurasian forests.

Scientific data suggests that Eurasia has experienced an increase in temperature (Serreze *et al.,* 2000), and high temperature indeed depicted a negative impact on the Eurasian forests. For instance, a significant shift in tree lines has been attributed to high temperature, and reduced cone and seed production were reported in *Larix sibirica* and *Pinus slyvestris* in Eurasia (Kharuk *et al.,* 2007). This shows the importance of changing temperature patterns for tree species composition, phenology, and forest structure in Eurasia (Kharuk *et al.*, 2007).

Forest landscape model (FLM), simulations of forest cover excluding species identity composition showed that moderate increase in temperature (+3°C) resulted in high photosynthesis activity; however, less biomass was observed. Interestingly, an increase of 6°C reduced biomass production and photosynthesis. On the contrary, increasing precipitation tends to increase photosynthesis and biomass (Gustafson *et al.,* 2017). While using a biomass data set of more than 6,200 forest plots from 61 countries across a mean annual temperature gradient of, i.e., 40°C, it was found that average annual temperature better predicts tree biomass allocation to plant organs than soil moisture (Reich *et al*., 2014). Notably, the study by Reich *et al*., (2014) showed that the proportion of belowground part (roots) increases whereas the proportion of foliage decreases towards colder climates. This result supports the hypotheses about forest tree adaptability to survive against temperature (Reich *et al.*, 2014). At the level of forest communities (phytocenoses), numerous studies of biomass structure are related to climate variables (Poudel *et al.*, 2011; Stegen *et al.*, 2011; Gustafson *et al.*, 2017; Sperry *et al.*, 2019). Nonetheless, these studies did not provide substantial explanations about the impact of temperature and precipitation even within a single region. In particular, the effects of temperature and precipitation on forest biomass production along Trans-Eurasian climatic gradients are unknown because of fragmentary regional information (Stegen *et al.*, 2011; Forrester *et al.*, 2017; Fu *et al.*, 2017).

Contradictory results were recorded in the forest ecosystem of Russia and Siberia (Lapenis *et al.*, 2005); interestingly, authors showed a decline in foliage biomass, but this negative pattern was not observed in the belowground parts. Moreover, a different trend was reported in different forest types. For instance, high and low net primary production was observed in temperate and boreal forests, respectively. Normalized difference vegetation index (NDVI) had different zonal trends, but importantly it had negative trends, and these patterns could not be explained clearly (Paquette *et al.*, 2018).

Foliage efficiency is one of the crucial parameters to understand forest production. It is defined as the net primary production value per unit mass of foliage (Usoltsev *et al.*, 2018). The foliage efficiency of any given tree genera varies due to several factors. Among them, temperature and precipitation determine the foliage efficiency. Besides these climatic factors, morphology and tree ages are taken into consideration to predict the foliage biomass of any given tree (Usoltsev *et al*., 2018).

Liebig's Law of the minimum has been applied to forest ecosystems (Molchanov, 1971; Stine, 2019). According to this law, "resistance limit for any organism may be regarded as limiting factors (Bobrov, 1978). For instance, temperature and precipitation could determine biomass in tree species. It is essential to mention that low biomass values were reported due to decreasing temperature and precipitation (Stine, 2019).

In our study, we focus on the *Larix* spp. (deciduous) and *Pinus* spp. (evergreen) as the primary biomass forming dominant tree species that contribute significantly to C storage in Eurasia (Kharuk *et al.*, 2007; Pfadenhauer & Klotzli, 2020). Species of the genus *Larix* are dominant in Northern Eurasia due to continuous permafrost, low annual precipitation, thin snow cover, early-summer drought, and cold winter temperatures (Tchebakova *et al.*, 2005; Herzschuh, 2019). At present, 15-19 species of the genus *Larix* are documented for the Northern Hemisphere, including 13-14 main species along Northern Eurasia and three hybrid species. Apparently, only the *Larix* genus, among other forest-forming species, is represented by a variety of species, i.e. *L. decidua* Mill., *L. sukaczewii* N. Dyl., *L. sibirica* Ledeb., *L. czekanovskii* Turcz., *L. gmelinii* Rupr., and *L. cajanderi* Mayr (Borisov, 1967).

We assessed foliage biomass response against temperature and precipitation. Our results will improve our understanding of tree genera responses to changing temperature and precipitation regimes. In addition to this, the present result may aid in predicting the C storage potential of Eurasian forests.

Materials and Methods

We selected and processed pure stands harvest data from the previous database to study the impact of temperature and precipitation on *Larix* and *Pinus* in Eurasia. Our forest biomass data consisted of four hundred and 2,110 samples for *Larix* and *Pinus, respectively.* Larix spp. is presented by eight species, and a majority of *Pinus* species are dominated by *Pinus sylvestris* L. (Sokolov *et al.*, 1977; Bobrov, 1978). As we can see in Figure 1, the distribution of these genera is uniform within the habitats on the territory of Eurasia.

Availability of schematic maps of rainfall distribution and average January temperatures for the period from 1996 to 2006 on the territory of Eurasia allowed us to combine the harvest data and the available coordinates of the experimental sites (World Weather Maps, 2007). This temperature, precipitation, and biomass data were subjected to correlation and regression analysis. We show a fragment of a numerical matrix (Table 1) for the explanatory purpose. We preferred the average temperature of January since it changes in the planetary biota most intensively than the average annual one (Morley *et al*., 2017). The seasonality of solar radiation changes allowed us to select one of two different levels of average temperatures – winter or summer. The seasonality of rainfall in most of the territory of Eurasia is not expressed to the same extent; therefore, we selected the average annual data.

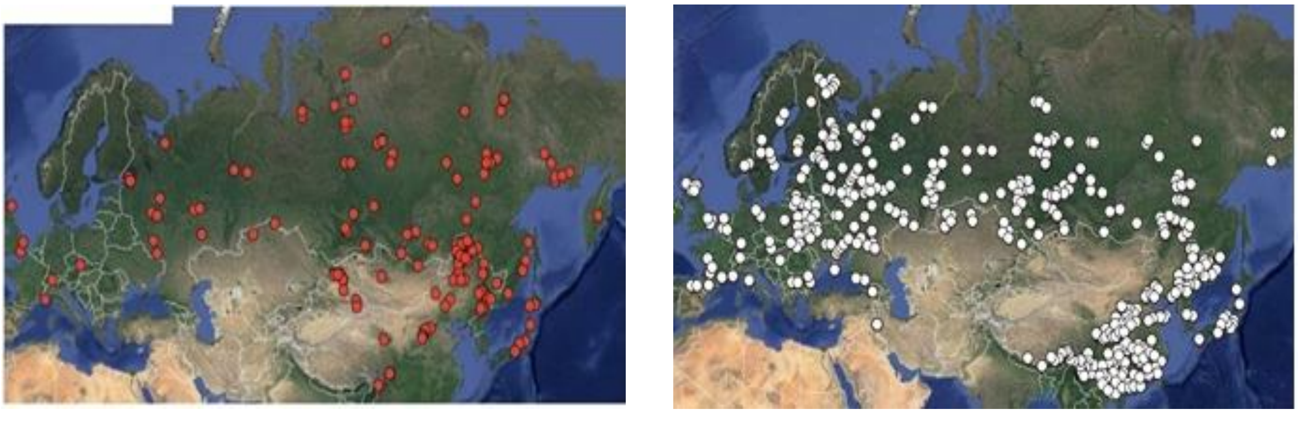

Fig. 1. Position of *Larix* (left) and *Pinus* (right) harvest data.

Table 1. A Part of the experimental database.

Larch stands						Pine stands					
Stand age	**Tree density**	**Stem volume**	**Foliage biomass**	**Mean January temperature**	**Mean annual precipitation**	**Stand age**	**Tree density**	**Volume**	**Foliage biomass**	**Tm**	**PRm**
13	1.36	27	4	10	826	20	2.275	15	1.4	-6	570
20	3.32	135	5.4	10	826	25	3.838	50	2.69	-6	570
20	2.685	215	6.5	10	826	25	4.516	60	1.63	-6	570
172	1.028	378	7.95	-15	317	23	3.640	94	5.06	5	730
177	1.117	522.5	10.06	-15	317	31	2.370	174	8.28	5	730
107	1.775	284.6	6.82	-15	317	35	1.890	210	9.83	5	730
47	2.294	130.4	3.11	-25	444	55	0.760	206	7.24	5	730
50	3.679	152	3.84	-25	444	18	5.189	25	3.10	6	826
59	15.58	153.5	4.3	-25	444	28	3.608	65	4.80	6	826
46	0.588	156	2.34	-10	500	80	0.528	461	5.74	-4	570
62	1.145	202	3.45	-10	500	100	0.349	508	5.73	-4	570
53	1.607	234	3.99	-10	500	120	0.258	528	5.70	-4	570
29	1.990	258	3.31	-10	570	13	82.40	63	7.10	-15	260
11	10.00	92	15.1	-10	570	20	44.43	126	7.17	-15	260
11	30.00	98	14.4	-10	570	20	19.76	68	8.10	-15	260
150	0.201	24	0.5	-30	570	22	43.81	142	8.40	-15	260
150	0.232	28	0.5	-30	570	32	19.91	196	6.11	-15	260
150	0.558	29	0.6	-30	570	30	1.475	50	10.54	-10	500
75	1.700	92	2.4	-30	380	26	2.543	59	6.39	-10	500
128	1.683	415	9	-30	380	25	1.533	84	7.62	-10	500
118	0.860	111	2.6	-30	380	35	2.104	217	7.00	-5	980
90	0.465	13	0.5	-39	317	28	0.542	162	7.51	0	1300
32	1.025	31	1.3	-39	317	32	0.546	199	9.63	0	1300
44	3.040	60	0.8	-39	317	28	0.540	167	7.77	0	1300
200	2.235	176	2.34	-35	250	50	0.101	264	10.8	10	1140
200	2.104	141	2.4	-35	250	50	0.389	214	9.24	10	1140
22	10.00	27.1	1.51	-35	250	110	0.091	326	13.0	10	1140
15	6.875	0.6	0.25	-30	444	100	0.661	144	2.70	-12	444
50	3.100	11.3	1.47	-30	444	210	0.722	190	1.6	-12	444
50	5.850	131	7.23	-30	444	25	1.329	88	5.2	-5	570
160	0.286	80	1.5	-30	500	29	1.707	169	6.6	-5	570
140	0.237	57	1.1	-30	500	18	36.93	93.2	6.3	0	890

Tm = mean January temperature (°C) ; *PRm* = mean annual precipitation (mm)

The biomass of tree species is dependent on morphology and tree age (Usoltsev, 2007). To model the changes in biomass of specific species in relative challenging. Nonetheless, the logarithmic transformation of equations may overcome this challenging task (Baskerville, 1972; Stahl *et al.*, 2012). We used a system of equations, as suggested previously (Moore, 1917). After transformation, we got 50 M and 40 M for *Larix* and *Pinus*. Notation of variables in equations is described in Table 1. First, the structure of the main equation is assumed.

$$\ln Pf = f\ \{\ln A,\ \ln V,\ \ln N,\ (\ln A)(\ln N),\ \ln(Tm\text{+M}),\ \ln PRm,\ [\ln(Tm\text{+M})]\cdot(\ln PRm)\} \qquad (1)$$

It is important to mention that we can only incorporate or insert tree age. But they can be obtained by calculating using our database. This idea is implemented by calculating two related equations:

$$\ln N = f\ \{\ln A,\ \ln(Tm\text{+M}),\ \ln PRm,\ [\ln(Tm\text{+M})]\cdot(\ln PRm)\} \qquad (2)$$

$$\ln V = f\ [\ln A,\ \ln N,\ (\ln A)(\ln N),\ \ln(Tm\text{+M}),\ \ln PRm,\ [\ln(Tm\text{+M})]\cdot(\ln PRm)\} \qquad (3)$$

Correlation and regression analyses were carried out in Statgraphics (Statgraphics, 1988).

Results and Discussion

The results of equations 1, 2, 3 are shown in Table 2. Differences in Larch and Pine biomass responses against climatic factors (temperature and precipitation) are described (Table 2). The slopes of independent variables for temperature, rainfall, and their joint impact in the foliage biomass were +3,390, +1,783, and -0,524 for Larch -3,614, -1,684 and +0,555 for Pine, suggesting a common trend for the foliage biomass of Larch and Pine, respectively. Larch and Pine significant regressions were calculated at the probability level of 0.999. T-test results indicated +3.71, +3.29, and -3.54 for Larch foliage. On the other hand, Pine foliage values were -6.20, -5.31, and +6.03. Independent variables contribution to tree foliage biomass were highlighted in Table 3. Our biomass variable results explained 75% and 78% variations in foliar biomass of *Larix* and *Pinus*. Stem volume accounted for 39% and 47% of explained variance in *Larix* and *Pinus*. Temperature and precipitation (climate variables) explained 25% and 22% of the foliage biomass variability in *Larix*, and *Pinus* respectively.

Table 2. Model results for the effects of forest stand factors and climatic indices on foliage biomass of *Larix* and *Pinus*.

ln(*Y*)[1]	a_0[2]	ln*A*	ln*V*	ln*N*	(ln*A*)·(ln*N*)	Ln (*Tm*+M)	ln*PRm*	[ln(*Tm*+M)]·(ln*PRm*)	adjR[2(3)]	SE[4]
					Larix					
ln(*N*)	0.9264	-0.9330	-	-	-	1.6526	0.8802	-0.3648	0.436	0.73
ln(*V*)	-14.4847	0.7836	-	-1.1206	0.3384	5.7240	1.6297	-0.6172	0.562	0.61
ln(*Pf*)	-12.5131	-0.1977	0.6214	0.9387	-0.1866	3.3906	1.7836	-0.5349	0.638	0.45
					Pinus					
ln(*N*)	2.8168	-1.0696	-	-	-	1.9165	0.5011	-0.3577	0.566	0.72
ln(*V*)	16.4304	0.7200	-	-0.7996	0.2065	-3.3579	-2.5007	0.6225	0.472	0.69
ln(*Pf*)	11.8492	-0.3495	0.4313	0.1311	-0.0289	-3.6140	-1.6842	0.5555	0.424	0.36

[1]Dependent variables; [2]logarithmic retransformation [(3)]*adjR*^{2} adjusted R squared; [(4)]*SE* – standard error of the equations

Table 3. Contribution of independent variables of equations (1).

ln(*Y*)	Independent variables								
	ln*A*(I)	ln*V* (II)	ln*N* (III)	(ln*A*)·(ln*N*) (IV)	I+II+III+IV	ln(*Tm*+M) (V)	ln*PRm* (VI)	[ln(*Tm*+M)]·(ln*PRm*) (VII)	V+VI+VII
					Larix				
ln(*Pf*)	8.7	39.1	14.6	12.3	74.7	8.9	7.9	8.5	25.3
					Pinus				
ln(*Pf*)	22.4	47.3	4.3	3.6	77.6	7.9	6.8	7.7	22.4

Foliage biomass of Larch and Pine showed statistically significant transcontinental trends along gradients of temperature and precipitation. 3-D graphs clearly showed a dependence of foliage biomass on temperature and precipitation (Fig. 2) with clear differences between Larch and Pine, respectively.

The central theme in forest ecology is to study foliage biomass responses against air temperature deviation by one °C and precipitation by 100 mm per year. Our constructed model answered such a question concerning Larch and Pine stands. We showed different foliage biomass responses of *Larix* (Fig. 2a) and *Pinus* (Fig. 2b). The tree stands age was 100 years for both genera, i.e., *Larix* and *Pinus.*

Different eco-regions differ in temperature and precipitation. Temperature change also occurs regionally. In addition to the change in temperature, annual precipitation change occurs. In Fig. 3, we indicated an increase in precipitation by 100 mm at various territorial levels. Such an increase in precipitation was designated as 200Δ (300Δ) ... 800Δ (900Δ). *Larix* and *Pinus* foliage biomass (Δ, %) responded differently to an increase of 1°C in different eco-regions (Fig. 3). Furthermore, a decrease in foliage biomass was observed in the insufficient moist region (PRm = 300-400 mm) (Fig. 3b). On the contrary, temperature and precipitation depicted a positive impact on leaf biomass in the *Larix* (Fig. 3a). The percentage of increase in biomass was also reported from warm regions to cold ones (Tm = -40°C).

High precipitation induced the changes in *Pinus* foliage biomass (Fig. 4b). Increased foliage biomass was observed in warm areas (0°C to 10°C), with an increase in precipitation of 100 mm; however, this trend changed to negative in cold areas (-20°C to -30°C). Interestingly, *Larix* accumulated more biomass in foliage in cold regions (Tm= -40°C), as evident in Fig. 4a.

Pine forests increased foliage biomass with increasing temperature, but only in a relative high precipitation area (PRm = 900 mm). The opposite trend was found in (PRm=300) (Fig. 2b). Interestingly, *Pine* tree species accumulated more foliage biomass due to high rainfall, and this pattern was observed in cold areas (Tm = -30°C). However, negative results were obtained in warm zones (Tm= 10°C). Scientific data obtained previously in Siberia (Glebov & Litvinenko, 1976) validated our current findings. In Siberia, maximum temperature and precipitation showed positive impacts on above ground parts, i.e., stem. However, low temperature and high precipitation decreased stem biomass by 4-9%. Nonetheless, an increase in radial growth was observed in the high-temperature range at the moderate precipitation level of 600 mm (Glebov & Litvinenko, 1976). This shows the importance of temperature and precipitation in Eurasia. Recent work has also highlighted the significance of temperature and precipitation to determine the biomass of tree species in Eurasia (Usoltsev *et al.,* 2020a, 2020b). Responses of Pine trees (Fig. 2) followed the Liebig-Shelford trend because we noticed a decline in foliar biomass due to minimum precipitation. At the same time, Larch demonstrated the opposite pattern, at least in a warm climate (*Tm* = 0°C) with insufficient moisture (*PRm* = 200 to 300 mm). The explanation for such a pattern is described in the following lines. The distribution of *Larches* and *Pines* is approximately the same (Fig. 1). Since the distribution of Larches and Pines is almost similar, we argue that temperature and precipitation values are identical for these two tree species. Ultimately, model results produced almost similar results for *Larches* and *Pines*. It is worth mentioning that *Pines* biomass was slightly higher than *Larch* stands. Biomass pooled data for *Larches* and *Pines* authenticated the validity of models in our analyses. Furthermore, we did not observe any change in variables (temperature and precipitation). Foliage efficiency (FE) increased in *Pine* but decreased in *Larch* in the same zonal range. This increase and decrease trend was found in the northern belt towards subequatorial areas (Usoltsev *et al.,* 2018). Current modeling results highlighted the physiological differences between the two species. It is evident that evergreen and deciduous species have differences in photosynthetic activity. Evergreen species can prolong the assimilation process even in winter (Wieser, 1997; Usoltsev *et al.,* 2018).

Higher temperatures in the winter season induce increased physiological activities (Photosynthesis) in *Pine* trees (Usoltsev *et al.,* 2018). It is one of the plausible explanations for the high foliage efficiency of *Pines* in northern zones. On the other hand, *Larch* trees had more foliage efficiency (northern temperate to subequatorial zone). Larches perform more respiration and shed leaves; therefore, Larches' foliage efficiency is less (Usoltsev *et al.*, 2018).

The modeling results of this study reported different foliage efficiency and biomass of Larches and Pines. But these differences in foliage efficiency and biomass coincided only in low moisture areas (*PRm* =200 to 300 mm) (Fig. 2a,b); however, in areas of sufficient moisture (*PRm* = 800 to 900mm), these contradictions become less pronounced. Our results represent a change in biomass patterns under assumed climatic conditions. The present findings of the study highlighted the importance of the adaptability of tree species in the Eurasia region. Due to the rise in temperature, the majority of forest tree species are unable to adapt to high temperatures, resulting in the loss of tree species (Schaphoff *et al.,* 2016; Spathelf *et al.,* 2018).

We carried out data analyses in 1970-1990 and used maps to predict the changes in foliage biomass of Larches and Pines in Eurasia. Our results are significant to understand the tree genera responses to climate change in Eurasia. Our work can improve predictions of how forest ecosystems will change at a continental scale under a warming climate. Ultimately, combining large datasets of forest plots with physiological data will be essential to understand better the underlying mechanisms (DeLeo *et al.,* 2020).

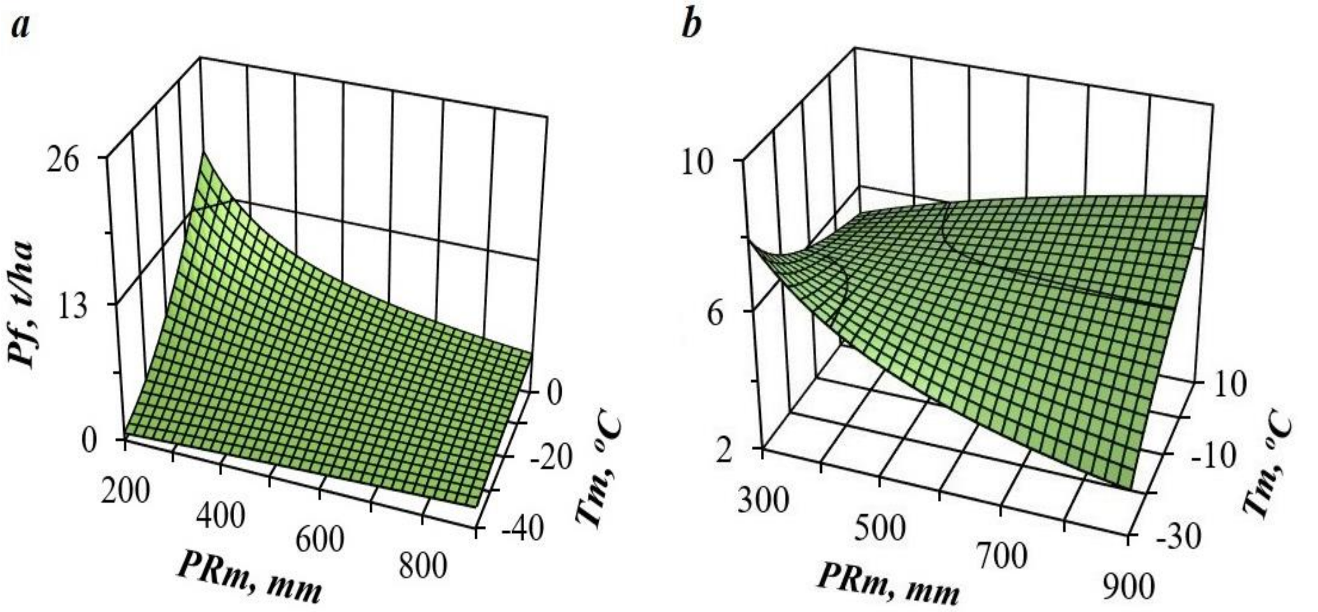

Fig. 2. Larch (a) and Pine (b) foliage biomass (*Pf*) dependence on mean January temperature (Tm), and mean annual precipitation (PRm).

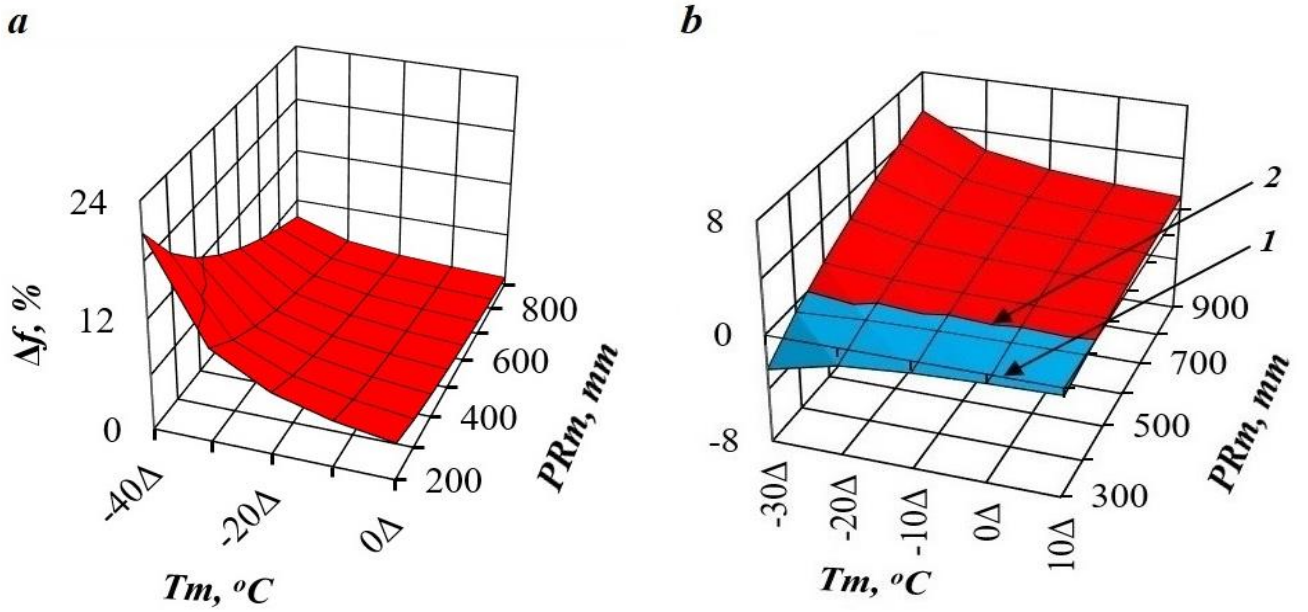

Fig. 3. Model prediction in Larch (a) Pine (b) foliage biomass.

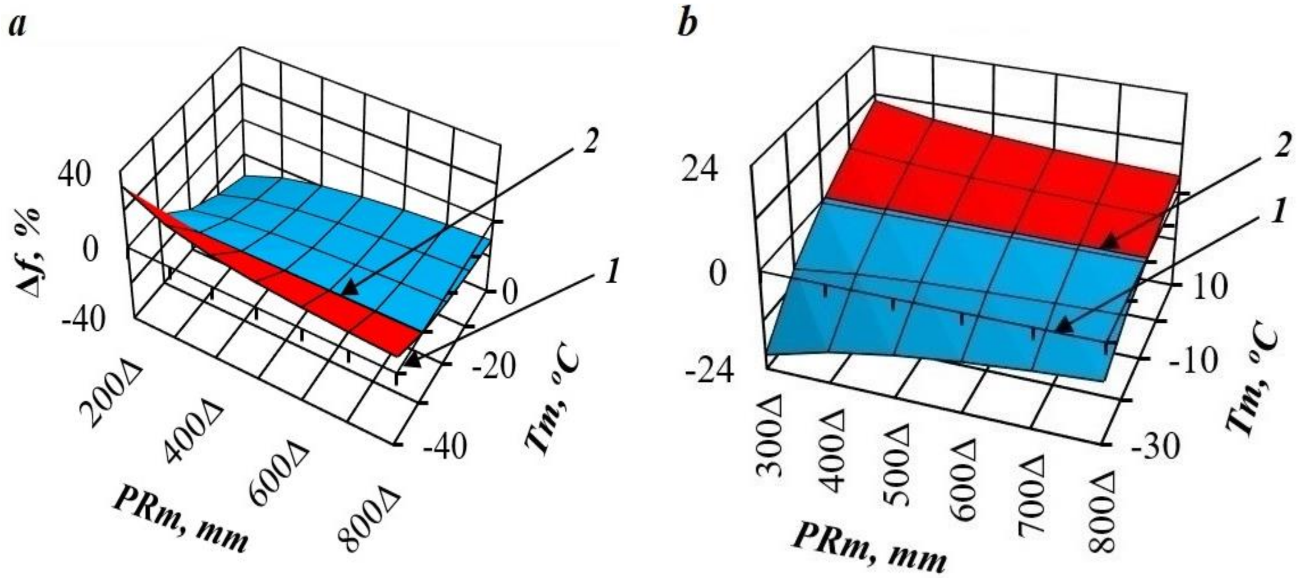

Fig. 4. Model prediction in Larch (a) Pine (b) foliage biomass.

Conclusions

Pine trees accumulated more biomass in warm regions due to increased precipitation by 100 mm. On the contrary, Larch trees had reduced foliage biomass in warm areas. Our model results of Larch and Pine species showed differential foliage biomass responses against temperature and precipitation in Eurasia.

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