



Article

# Regeneration of *Pinus sibirica* Du Tour in the Mountain Tundra of the Northern Urals against the Background of Climate Warming

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Abstract: Climate is one of the key drivers of the plant community's structure and trends. However, the regional vegetation-climate features in the ecotone have not yet been sufficiently studied. The aim of the research is to study features of Pinus sibirica Du Tour germination, survival, and growth in the mountain tundra of the Northern Urals against the background of a changing climate. The following research objectives were set: To determine the abundance and age structure of P. sibirica undergrowth on the mountain tundra plateau, identify the features of P. sibirica growth in the mountain tundra, and examine the correlation between the multi-year air temperature pattern, precipitation, and P. sibirica seedling emergence. A detailed study of the Pinus sibirica natural regeneration in the mountain stony shrub-moss-lichen tundra area at an altitude of 1010-1040 m above sea level on the Tri Bugra mountain massif plateau (59°30′ N, 59°15′ E) in the Northern Urals (Russia) has been conducted. The research involved the period between 1965 and 2017. Woody plant undergrowth was considered in 30 plots,  $5 \times 5$  m in size. The first generations were recorded from 1967–1969. The regeneration has become regular since 1978 and its intensity has been increasing since then. Climate warming is driving these processes. Correlation analysis revealed significant relationships between the number of *Pinus sibirica* seedlings and the minimum temperature in August and September of the current year, the minimum temperatures in May, June, and November of the previous year, the maximum temperatures in May and August of the current year, and precipitation in March of both the current and previous years. However, the young tree growth rate remains low to date (the height at an age of 45-50 years is approximately  $114 \pm 8.8$  cm). At the same time, its open crowns are rare single lateral shoots. The length of the side shoots exceeds its height by 4-5 times, and the length of the lateral roots exceeds its height by 1.2-1.5 times. This is an indicator of the extreme conditions for this tree species. With the current rates of climate warming and the Pinus sibirica tree growth trends, the revealed relationships allow for the prediction that in 20-25 years, the mountain tundra in the studied Northern Urals plateau could develop underground-closed forest communities with a certain forest relationship. The research results are of theoretical importance for clarifying the forest-tundra ecotone concept. From a practical point of view, the revealed relationship can be used to predict the trend in forest ecosystem formation in the mountain forest-tundra ecotone.

**Keywords:** Siberian stone pine; *Pinus sibirica*; mountain tundra; ecotone; climate change; temperature driver



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### 1. Introduction

The climate change problem is one of the most frequently discussed topics in the modern scientific literature, since ecosystem biodiversity, stability, and ecological functions are predicted to face major changes as a result of global climate changes across all continents [1,2], increasing risks for the regional and global environmental crises and a loss of favorable habitat for humans [3]. Climate change can also exacerbate the effect of

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other factors on vegetation, as is the case with man-made pollution [4,5]. In this regard, the climate-vegetation problem is recognized as one of the most urgent in ecology and biogeography [1,2,6–11].

Forest vegetation climatogenic pattern is most clearly observed in ecotones, extreme climatic environment for plants: Southern [1,2,12], northern [6,13,14], and mountainous areas [15,16]. It is established that treelines pass through the isotherm with a mean growing season temperature of 6–8 °C [15,17], which is why the temperature factor is crucial for woody plant survival. In this respect, numerous studies are devoted to studying the impact of air temperature on woody plant growth in extreme ecotone environments [15,18,19]. The impact on treeline sensitivity produced by topographic structures [19,20], winter snow pack [19,21], soil moisture [20], the wind regime [16], the chemical composition of rocks [16], seed production and dissemination [16], damages reindeer and mouse-like rodents inflict on trees [16], and anthropogenic factors [19,20,22] has also been studied. However, despite numerous studies, some fundamental theoretical and terminological issues have not yet been resolved.

The treeline (a row of trees of a certain size prevailing in the area) lies across a rather large ecotone between forest and low-stature alpine vegetation [23]. At the same time, the ecotone shows significant changes in the woody plant morphology and structure and plant community density. These features are still understudied [14,24].

Despite the importance of seedlings for understanding the treeline shift, the main focus of the research is on adult trees. This is due to the limitations of GIS technologies in the recognition of seedlings of woody plants [14–16]. Therefore, young generations of woody plants are still the least studied. However, indicators of seedlings and undergrowth (young trees) (number, growth, vitality, age structure, confinement to the substrate, and cover of crowns and root systems) are the most informative for identifying the expansion of the range and forest ecosystem formation in the mountain forest–tundra ecotone.

Our research is aimed at investigating the features of seed germination, seedling survival, and *Pinus sibirica* Du Tour young tree growth in the mountain tundra of the Northern Urals. It was important for us to test the hypothesis that climatic factors influence *Pinus sibirica* regeneration.

To achieve this aim, a number of research objectives were to be solved: Determine the abundance and age structure of *P. sibirica* undergrowth on the mountain tundra plateau, identify the features of *P. sibirica* growth in the mountain tundra, and examine the correlation between the multi-year air temperature pattern, precipitation, and *P. sibirica* seedling emergence.

Our research is based on long-term observations of the *Pinus sibirica* regeneration at the upper limit of its distribution in the extremely little-studied mountain tundra of the Northern Urals (Russia). We paid special attention to obtaining representative data on the number, height, and age of young Siberian pine trees, as well as the relationship between the characteristics of the crowns and roots. The conclusions were obtained on the basis of correlation and regression analyses.

### 2. Materials and Methods

# 2.1. Study Area

The Ural Mountains are located between the East European and West Siberian plains. The mountains are an obstacle for humid air blowing from the west, and this is a barrier that directly affects the climate. The Urals are a watershed of two large water basins: The Volga-Kama and the Ob. The Ural Mountains stretch across 2500 km from north to south, 40–150 km from east to west, and are divided into Southern, Middle, Northern, Nether-Polar, and Polar Ural.

Soil and water resource protection is an important ecosystem service provided by coniferous forests in the Ural Mountains. Of particular importance are the ecosystem services that preserve moisture in the case of insufficient soil moisture on steep mountain

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slopes. Moisture is preserved by reducing snowmelt and water runoff rates. Under the same conditions, the protection of the soil from erosion is of great importance [25].

The research was conducted in the highlands of the Northern Urals. Global glaciation, the period of which ended 10 Kya, influenced the current appearance of these mountains [26]. The average mountain height is 500–700 m above sea level, with some peaks reaching 960–1300 m above sea level (the highest peak reaches up to 1560 m above sea level). Annual precipitation ranges from 600 to 1000 mm. The average annual humidity is 74%. In summer, the mountains' relative humidity is 5–7% higher than in the adjacent plains. Snow cover ranges from 70 to 130 cm in the mountains, and ranges between 30 and 50 cm in the foothills. The trend this follows is the depth of the snow cover increases by 17–18 cm with each 100 m rise in elevation. Currently, there is no glaciation, although snow persists in some places throughout the year.

The studies were carried out in the mountain stony shrub-moss-lichen tundra belt [27] at an altitude of 1010–1040 m above sea level on the Tri Bugra mountain massif plateau (an altitude of 1060 m above sea level 59°30′ N, 59°15′ E) in the southern part of the main watershed of the Northern Urals (Sverdlovsk region) (Figure 1).

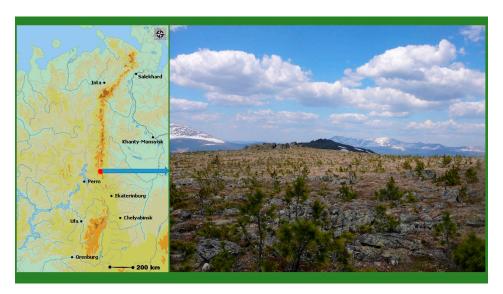


Figure 1. Study area. Source: Ural map [28], photo taken by the authors.

The plateau soil horizon is 5–15 cm thick (up to 20 cm in some places), with the underlying large stony monolith-shaped rock formation. Rock formations occupy 17.1% of the total sample area surface. The average growing season is 80–100 days. The average daily temperature above  $0\,^{\circ}\text{C}$  does not exceed 140–180 days. The snowless period lasts for 130–150 days. Autumn frosts are observed from September 7, while spring frosts continue until June 6. At the same time, freezing temperatures may be reached in June and even July [27]. These trends are representative of the entire research period (1967–2017).

More detailed monthly climatic characteristics are given in Table 1. Data are obtained from WorldClim version 2.1. The estimated period was 1970–2000 [29].

**Table 1.** Climatic data for the studied mountain stony shrub-moss-lichen tundra of the Northern Urals (WorldClim version 2.1 climate data for 1970–2000 [29].

Variable	Jan.	Feb.	Mar.	Apr.	May.	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Average temperature (°C)	-16.3	-13.7	-5.2	1.9	8.6	14.7	17.1	13.5	8.2	0.6	-8.1	-13.3
Minimum temperature (°C)	-20.3	-18.3	-10.2	-3.2	2.8	8.7	11.4	8.5	3.8	-2.6	-11.5	-17.0
Maximum temperature (°C)	-12.3	-9.2	-0.1	7.0	14.4	20.3	22.7	18.6	12.6	3.8	-4.8	-9.5
Precipitation (mm)	33	23	24	38	51	67	96	83	64	48	41	35
Solar radiation (kJ $m^{-2}$ day <sup>-1</sup> )	1870	4489	9525	14,507	19,140	21,625	19,326	13,912	8343	4160	20,581	1240

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The climatic needs for plant species reflect the bioclimatic variables derived from the monthly temperature and rainfall values and represent annual trends. These are often used in species distribution modeling and related ecological modeling approaches [29–32]. Nineteen bioclimatic variables are presented in Table 2.

**Table 2.** Bioclimatic variables for the studied mountain stony shrub-moss-lichen tundra of the Northern Urals (WorldClim version 2.1 climate data for 1970–2000 [29].

Bioclimatic Variables	Description	Value
BIO1	Annual Mean Temperature	0.67
BIO2	Mean Diurnal Range (Mean of monthly (max temp-min temp))	9.31
BIO3	Isothermality (BIO2/BIO7) (×100)	21.66
BIO4	Temperature Seasonality (standard deviation $\times$ 100)	1189.55
BIO5	Max Temperature of Warmest Month	22.71
BIO6	Min Temperature of Coldest Month	-20.28
BIO7	Temperature Annual Range (BIO5-BIO6)	42.99
BIO8	Mean Temperature of Wettest Quarter	15.12
BIO9	Mean Temperature of Driest Quarter	-11.73
BIO10	Mean Temperature of Warmest Quarter	15.12
BIO11	Mean Temperature of Coldest Quarter	-14.43
BIO12	Annual Precipitation	603
BIO13	Precipitation of Wettest Month	96
BIO14	Precipitation of Driest Month	23
BIO15	Precipitation Seasonality (Coefficient of Variation)	44.95
BIO16	Precipitation of Wettest Quarter	246
BIO17	Precipitation of Driest Quarter	80
BIO18	Precipitation of Warmest Quarter	246
BIO19	Precipitation of Coldest Quarter	91

### 2.2. Research Subjects

The research subject is *Pinus sibirica* undergrowth (young trees). *Pinus sibirica* (Siberian cedar, Siberian stone pine) (Pinaceae Family) is a tree up to 35–40 m tall with a 1.8 m trunk diameter. The crown of the trees is wide and thick and oval in shape. The leaves are 6–13 cm long and 0.8–1.2 mm wide, are joined five in a fascicle, and may not fall from branches for up to 4 years. Needles are used as a vitamin and anti-scurvy agent. Buds are ovoid-conical without resin [33]. Seed cones are isolated or grouped in whorls of 2–3, resinous, 7–12 cm long, and 6–8 cm wide. The seed cones turn dark brown when ripe. The seeds are large and have a length of 10–14 mm and a width of 5–7 mm [34]. Seeds consist of up to 50% oil [33]. Under optimal conditions, seed bearing in *Pinus sibirica* is noted to start from the age of 20. The maximum seed productivity was revealed at the age of 160 years, which can last up to 400 years [35]. Dense and light wood is an excellent ornamental material.

*Pinus sibirica* extends from west to east from the lower reaches of the Vychegda River to the upper reaches of the Aldan River, which is approximately 4500 km in a straight line. From north to south, the length of the range is approximately 2700 km, from the Igarka River (in the lower reaches of the Yenisei River) to the upper reaches of the Orkhon River in Mongolia. *Pinus sibirica* is characterized by high winter hardiness and can withstand very low winter temperatures (up to -65 °C in Eastern Siberia). The vast abundance of *Pinus sibirica* is explained by its high ecological plasticity. The ecological optimum of this tree species is confined to the low-mountain regions of Western Sayan and Northeastern Altai [36].

*Pinus sibirica* distribution and regeneration depend on fauna diversity. Seeds are food for chipmunks, squirrels, sables, and bears. A special role in *Pinus sibirica* dispersion belongs to the nutcracker (*Nucifraga caryocatactes macrorhynchos* Brehm C. L). This bird lays a store of food for the winter and can carry *Pinus sibirica* seeds at a distance of up to 15 km [37]. In this way, *Pinus sibirica*'s regeneration is unique. Nutcrackers arrange seed caches only in certain conditions, which is generally moss cover appropriate for seed

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germination and seedling survival [38]. Nutcrackers use seed stocks for food and to feed baby birds throughout the winter–autumn–spring period. At the same time, nutcrackers can extract their food stores from under snow up to 60 cm deep. However, some seed caches remain unused, and these seeds germinate in the spring. This feature fundamentally differs *Pinus sibirica* from anemochorous tree species and even from many zoochorous plants. Few seeds of these plants are accidentally dispersed into conditions favorable for germination.

Dark coniferous forests are of great biospheric and ecological importance. Mountain *Pinus sibirica* forests are of particular value due to their important functions to protect soil and water [39]. For us, this tree species is interesting for its ability to spread into the mountain tundra and form the upper tree line.

## 2.3. Sampling Procedures and Data Analysis

# 2.3.1. Pinus sibirica Natural Regeneration Study

The studies were carried out on the basis of proven methods [40]. Environmental conditions, abundance, vitality, age and undergrowth parameters of woody plants, species composition, and projective cover of other vegetation were considered using an example of 30 sample plots  $5 \times 5$  m in size, relatively homogeneously distributed across the mountain stony shrub-moss-lichen tundra. Twenty sample plots were examined in 2014. After that, a follow-up study was carried out in 2018, and 10 more sample plots were added. We placed the sample plots in three parallel rows. The distance between the rows was 300 m. The sample plots in the rows were located 100 m away from each other. All woody plants from seedlings to the largest trees were taken into account in each sample plot. We determined the species, measured the height, diameter of the crown with an accuracy of 1 cm, and diameter of the trunk with an accuracy of 0.2 mm, and determined the age with an accuracy of 1 year.

The undergrowth age was determined by the annual height increment indicators, if applicable (annual height increments are clearly visible and tree tops were not dry). When the accuracy of determining the age using this method was at risk, the young tree was cut down at the soil level. The undergrowth age was determined by the number of annual rings on the cross-section of the stem base, measured using the LinTab-6 instrument (*Pinus* sibirica annual rings are clearly visible and show the age of the tree with accuracy to one year [40]). We could accurately determine the age by using the first method when studying most young trees under the age of 20. Fifty-four P. sibirica undergrowth specimens of various heights (up to 130 cm) and ages (up to 56 years old) were selected as models. The undergrowth was sampled randomly from all over the mountain tundra area under study. The samples included specimens that ranged from seedlings to large trees, with various height-age dependencies. Since there were very few large trees in the studied mountain tundra area, the number of samples in this category was lower than for small undergrowth. In addition to determining the aboveground parameters and age, all roots were dug out for each specimen. Each 5 cm of root length was measured to determine the diameter. The average root system length was identified.

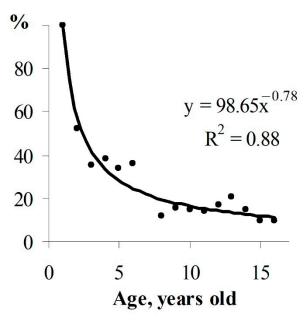
# 2.3.2. Investigation Relationships between the Natural Regeneration of *Pinus sibirica* and the Air Temperature and Precipitation

Historical monthly weather data for 1960–2018 given in WordClim version 2.1 [29] were used to study the relationship between the *Pinus sibirica* natural regeneration and the air temperatures. Climate data and bioclimatic variables were also obtained from WordClim version 2.1 in 2.5 min spatial resolutions [29]. Currently, there is a huge amount of research on the relationship between vegetation and climate based on the use of WordClim data [41–44]. For this reason, this resource was chosen as a source of information.

Bioclimatic variables are used to reveal general characteristics of the climate in the studied area. The relationship between the monthly precipitation minimum and maximum temperature patterns and the number of *Pinus sibirica* seedlings over the period of 1965 to 2017 were analyzed. The relationship was studied using correlation and regression

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analyses. The number of annual *Pinus sibirica* seedlings was remodeled by building the undergrowth survival curves (Figure 2) [45].



**Figure 2.** Empirical survival curve of the *Pinus sibirica* undergrowth from the initial number of seedlings (%) in the mountain tundra.

### 3. Results

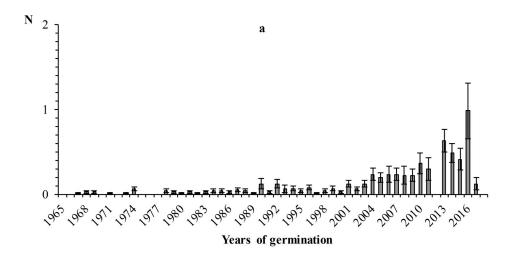
### 3.1. Investigation of the Pinus sibirica Natural Regeneration

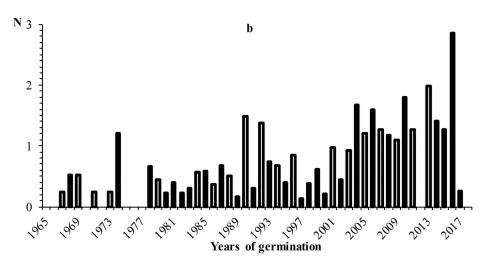
On the one hand, Figure 1 shows a fairly homogeneous young tree distribution over the area, as well as their small-sized, sparse, and sprawling crown. The *Pinus sibirica* undergrowth and seedlings are concentrated on a lichen-moss substrate, represented mainly by *Pleurozium Schreberi* (Brid.) Mitt. (10% cover), and on a moss-lichen substrate with a predominance of *Cladonia* sp. (46.6% cover), as well as on the substrate formed by a dense cover of *Arctostaphylos uva-ursi* (L.) Spreng. (21.4% cover). At the same time, rare *Betula nana* L., *Rosa cinnamomea* L., *Salix* sp. no more than 30 cm in height (12.6% projective cover) and undersized creeping *Vaccinium uliginosum* L., *V. vitis idaea* L., *Empetrum nigrum* L., *Dryas octopetala* L. (45% cover) are not stored by nutcrackers. Undergrowth quantitative research conducted in the studied mountain tundra revealed that *Pinus sibirica* is the dominant species of tree at an age of up to 56 (6.0  $\pm$  0.4 thousand specimens per ha). There are few *Picea obovata* Ledeb. and *Pinus sylvestris* L. specimens not older than 10–15 years.

The analysis of the *Pinus sibirica* undergrowth age structure showed that the seedlings firstly appeared in 1967. Seedlings did not appear every year, and their number was small. Regeneration has become regular since 1978 (Figure 3). An increase in the number of seedlings has also been revealed, starting from 1978 and spanning to the present day.

Figure 1 shows, on the one hand, a fairly uniform distribution over the area of young trees, as well as their small-sized, sparse, and sprawling crown. In the mountain tundra, *P. sibirica* undergrowth aged 7 years old gives single lateral shoots that stand out above their height and the overall shrub tier. Most of the undergrowth has two or more tops (Figure 4). In addition, approximately 20% of the undergrowth is over 20 years old and has dry tops.

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**Figure 3.** Trend in the *Pinus sibirica* regeneration on the mountain tundra plateau: (a) Number of undergrowth (N) (thousand specimens per ha) with an average error  $(\pm m)$ ; (b) remodeled number of seedlings that appeared initially (N), thousand per ha.

*P. sibirica* model specimens were combined into four age groups with the corresponding average parameter values obtained as a result of age determination (Table 3). The table clearly shows that *P. sibirica* grows very slowly in the mountain tundra and reaches only 114 cm in height by the age of fifty, on average. The relationship between age and height for the studied young trees is shown in Figure 5. The maximum height values account for 13 cm at 5 years, 24 cm at 10 years, 60 cm at 20 years, 93 cm at 30 years, and 188 at the age of 37–50.

**Table 3.** Model specimen average parameters for *Pinus sibirica* undergrowth by age group (the N value is 54).

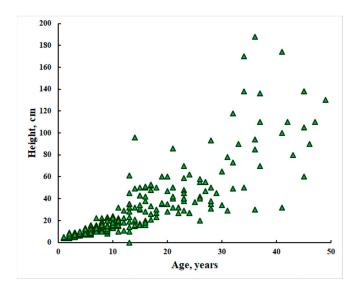
Undergrowth Age, Years Old	7–10	12–20	25–35	45–56
Undergrowth height, cm	$15 \pm 0.5$	$32 \pm 1.9$	$56 \pm 5.1$	$114 \pm 8.8$
Crown diameter, cm	12	24	38	65
Roots length, cm	$25\pm2$	$50 \pm 5$	$95 \pm 9$	$125\pm15$
Soil nutrition area, m <sup>2</sup>	0.2	0.78	2.83	4.91

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**Figure 4.** *P. sibirica* growth characteristics common to the mountain tundra. The tree in the picture is 18 years old and 30 cm in height. The tree crown diameter is 20 cm. The photo was taken by the authors in 2014; photo taken by the authors.

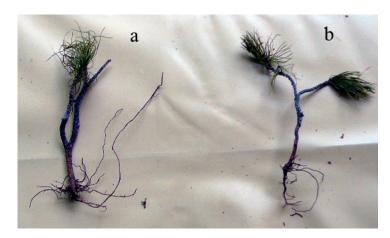
The following maximum values of the root length were determined in model specimens in the corresponding age groups: 40 cm at the age of 9 years and a height of 18 cm; 130 cm at the age of 18 and 80 cm high; 140 cm at the age of 35 and 80 cm high; and 180 cm at the age of 56 years 125 cm high. From an early age, the undergrowth root system goes beyond the crown projection, while under the canopy and on the felling, this occurs by the age of 40 [46].



**Figure 5.** The relationship between age and height for the studied undergrowth of *Pinus sibirica* (the N value is 579).

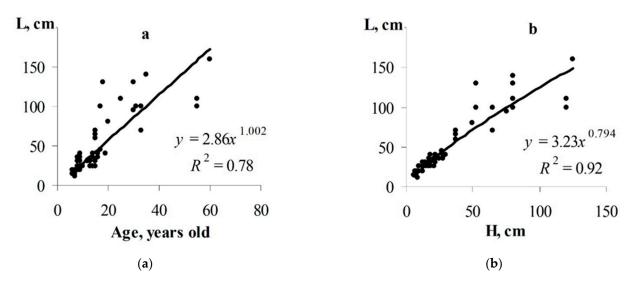
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At the same time, its crowns consist of rare single lateral shoots. Thus, in the mountain tundra environment, the root system of the *Pinus sibirica* undergrowth grows more intensively than its aboveground parts. This pattern is clearly demonstrated in Figure 6. The length of the lateral roots exceeds its height by 1.2–1.5 times, and the length of the side shoots—by 4–5 times. At the same time, undergrowth of a similar height can belong to different age groups.



**Figure 6.** Samples of *Pinus sibirica* undergrowth: (a) Aged 10, 17 cm in height, average root length is 38 cm; (b) aged 12, 17 cm in height, average root length is 35 cm; photo taken by the authors.

Special studies were conducted to identify the relationship between the root length of the *Pinus sibirica* undergrowth and its height and age. Regression analysis revealed a close ( $R^2 = 0.78$ ) positive and almost linear relationship between the average root system length of the undergrowth and its age (Figure 7a), and an even closer ( $R^2 = 0.92$ ) relationship with its height (Figure 7b).



**Figure 7.** Relationship between the root length of the *Pinus sibirica* undergrowth and its age (**a**) and height (**b**).

3.2. Relationship between Pinus sibirica Natural Regeneration and Air Temperature and Precipitation

The results of the correlation analysis are shown in Table 4. Historical monthly weather data for 1965–2017, given in WordClim version 2.1., were used, and data obtained in the course of research on the number of *Pinus sibirica* seedlings for the same time period were applied.

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an.	Feb.	Mar.	Apr.	Mav.	Iun.	Iul.	Aug.	Sep.	Oct.	Nov.	Dec.	-
t	undra and	air temp	erature a	and preci	pitation.							
]	T <b>able 4.</b> Co	rrelation	coefficie	ents betw	een the n	umber o	of the Pini	ıs sibirica	seedling	s in the r	nountaiı	ı

	Jan.	Feb.	Mar.	Apr.	May.	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Current year												
Minimum temperature	0.067	0.249	0.097	0.022	0.224	0.136	0.116	0.353 *	0.295 *	0.199	0.014	0.091
Maximum temperature	0.001	0.227	0.019	-0.089	0.281 *	0.057	0.118	0.287 *	0.070	0.083	-0.069	0.046
Precipitation	0.108	0.024	0.282 *	0.186	0.00	0.042	-0.09	-0.142	0.106	0.060	0.082	0.049
Previous year												
Minimum temperature	0.164	0.248	0.231	0.136	0.508 *	0.462 *	-0.05	0.183	0.020	0.249	0.276 *	0.006
Maximum temperature	0.156	0.048	0.117	0.062	0.128	0.022	0.026	0.217	-0.028	0.137	0.189	0.124
Precipitation	-0.054	-0.138	0.281 *	0.031	-0.066	0.070	0.049	0.208	-0.040	0.180	-0.039	0.226

<sup>\*</sup> The given correlations are significant at the level of p < 0.05.

These trends do not appear to show a strong correlation. We assume that this is due to many factors and the synergistic effect they produce, which distorts the relationship ratio. The relationship between climate and *Pinus sibirica* regeneration is complicated by the influence of *Nucifraga caryocatactes macrorhynchos*, the abundance of which also depends on many factors. Therefore, we accept correlation coefficients that are significant at the level of 0.05 as sufficient to consider the factors significant for *Pinus sibirica* regeneration.

Significant correlation between the number of the *Pinus sibirica* seedlings and the minimum temperature in August and September of the current year, the minimum temperatures in May, June, and November of the previous year, the maximum temperatures in May and August of the current year, and precipitation in March of both the current and previous years was revealed. The multi-year trend in temperature and precipitation pattern for these months is shown in Figure 8. This figure clearly shows a warming trend. However, the warming intensity varies for different months. For example, the maximum temperatures in September and November practically did not change during the studied period. At the same time, minimum temperatures for the same months varied, and September and November became warmer in general. The long-term trend in the March precipitation increase is also clearly visible.

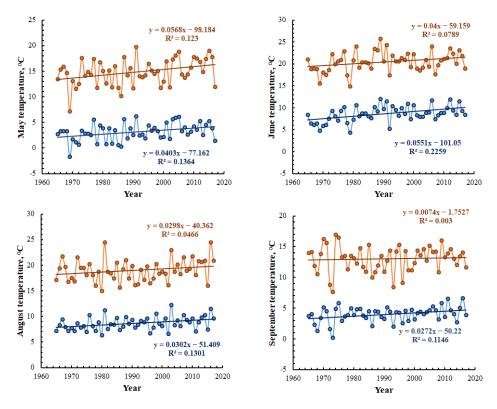
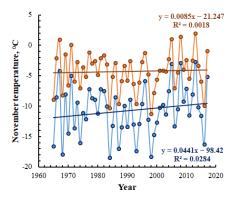
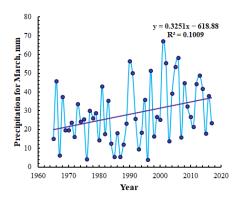


Figure 8. Cont.

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**Figure 8.** Multi-year monthly trend in temperature and precipitation pattern for which statistically significant relationship was found: The upper and lower lines show the corresponding maximum and minimum patterns.

### 4. Discussion

The primary reason for the absolute dominance of *Pinus sibirica* in the woody plant undergrowth on the mountain tundra plateau is that thin-billed nutcrackers create forage food stores by carrying their seeds over considerable distances from their source trees. In turn, most seeds of the anemochory tree species growing at a distance of up to 1 km are not likely to reach the mountain tundra. Certainly, nutcrackers have always brought *Pinus sibirica* seeds into the mountain tundra, which is known for the open types of substrate the birds prefer to create food stores [47]. However, the emerging seedlings are likely to not have survived in the previously harsh conditions of the mountain tundra.

The results of our research have shown that the survival and, consequently, further growth and development of *Pinus sibirica*, are due to climate warming. This conclusion is in good agreement with the results of research (including other tree species) on the Polar Urals [16,48], the Khibiny Massif (Kola Peninsula) [49], the western Putorana Plateau [48,49] in the Southern Rockies (region of northern New Mexico and southern Colorado) [50], in the Himalayas [51], and in the southern European range (the Pyrenees) [52]. The obtained results complement the meta-analysis of annual tree line shift rates at 143 sites from 38 published studies [53] and clarify the impact temperature and precipitation have on *Pinus sibirica* regeneration. This is a certain combination of thermal and hydrological factors that drives treeline shift rates across the Northern Hemisphere [53]. The combination may include temperatures in early summer and precipitation in early winter [48,49], temperature–moisture correlations throughout the year [50], winter precipitation only (high snow depth) [14], and winter temperatures [54]. Our research shows the greatest correlation between Pinus sibirica regeneration and the maximum temperatures in May and June of the previous year. Regarding the precipitation factor, only precipitation in March (both current and previous years) seems to be significant.

Generally, despite the fact that global warming is one of the main modern threats to biosphere stability, climate warming has a positive effect on the woody vegetation germination in the mountain tundra. We also fully agree with the results of Hoffrén's research with co-authors [52], the essence of which was to identify the positive impact of any tree canopy not only on the spatial diversity of microclimatic metrics but also on their refugial capacity. Undoubtedly, the revealed tree canopy formation will have a positive effect on the microclimate and protection of soil from erosion, strengthening water protection functions and spreading other plant species into the mountain tundra.

Currently, GIS technologies and methods for recognizing woody plants are actively developing, and new approaches and methods are being used for research; at the same time, labor-intensive and difficult-to-access plot-based data acquire special value for predictive estimates, since there is still little data on regional and landscape features [55–57]. In this regard, the results obtained in the course of the study will be highly relevant.

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#### 5. Conclusions

Thus, a detailed study of the *Pinus sibirica* natural regeneration in the area of the mountain stony shrub-moss-lichen tundra at an altitude of 1010-1040 m above sea level on the Tri Bugra mountain massif plateau of the Northern Urals showed the regular regeneration of this tree species. The first small-scale tree generations were recorded in 1967–1969. Regeneration has become regular since 1978; since then, its intensity has only been increasing. Climate warming is driving these processes. The correlation analysis revealed a significant relationship between the number of Pinus sibirica seedlings and the minimum temperature in August and September of the current year, the minimum temperatures in May, June, and November of the previous year, the maximum temperatures in May and August of the current year, and the precipitation in March of both the current and previous years. However, the young tree growth rate remains low to date (the height at an age of 45–50 is approximately  $114 \pm 8.8$  cm). At the same time, its open crowns consist of rare single lateral shoots. The length of the side shoots exceeds its height by 4–5 times, and the length of the lateral roots exceeds its height by 1.2–1.5 times. This is an indicator of the extreme conditions for this tree species. Regarding the current climate warming and *Pinus sibirica* tree growth trends, the revealed relationship allows for the prediction that, over 20-25 years, the mountain tundra in the studied Northern Urals plateau could develop a mosaic formation of primary underground-closed forest communities with characteristic forest relationships, and communities with multiple root system interweaving over 40-50 years. The research results are of theoretical importance for clarifying the forest-tundra ecotone concept. From a practical point of view, the revealed relationship can be used to predict the trends in forest ecosystem formation in the mountain forest-tundra ecotone. The research will also be useful for conducting global research on the tree line shift in the Northern Hemisphere.

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