Climate Warming Impacts on Distributions of Scots Pine (*Pinus sylvestris* L.) Seed Zones and Seed Mass across Russia in the 21st Century

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Abstract: Research highlights: We investigated bioclimatic relationships between Scots pine seed mass and seed zones/climatypes across its range in Russia using extensive published data to predict seed zones and seed mass distributions in a changing climate and to reveal ecological and genetic components in the seed mass variation using our 40-year common garden trial data. Introduction: seed productivity issues of the major Siberian conifers in Asian Russia become especially relevant nowadays in order to compensate for significant forest losses due to various disturbances during the 20th and current centuries. Our goals were to construct bioclimatic models that predict the seed mass of major Siberian conifers (Scots pine, one of the major Siberian conifers) in a warming climate during the current century. Methods: Multi-year seed mass data were derived from the literature and were collected during field work. Climate data (January and July data and annual precipitation) were derived from published reference books on climate and climatic websites. Our multiple regression bioclimatic models were constructed based on the climatic indices of growing degree days > 5 °C, negative degree days < 0 °C, and annual moisture index, which were calculated from January and July temperatures and annual precipitation for both contemporary and future climates. The future 2080 (2070–2100) January and July temperatures and annual precipitation anomalies were derived from the ensemble of twenty CMIP5 (the Coupled Model Intercomparison Project, Phase 5) global circulation models (GCMs) and two scenarios using a mild RCP (Representative Concentration Pathway) 2.6 scenario and an extreme RCP 8.5 scenario. Results: Site climate explained about 70% of the seed mass variation across the Scots pine range. Genetic components explained 30% of the seed mass variation, as per the results from our common garden experiment in south central Siberia. Seed mass varied within 3.5 g (min) and 10.5 g (max) with the mean 6.1 g (n = 1150) across Russia. Our bioclimatic seed mass model predicted that a July temperature elevated by 1 °C increased seed mass by 0.56 g, and a January temperature elevated by 5 °C increased seed mass by 0.43 g. The seed mass would increase from 1 g to 4 g in the moderate RCP 2.6 and the extreme RCP 8.5 climates, respectively. Predicted seed zones with heavier seed would shift northwards in a warming climate. However, the permafrost border would halt this shifting due to slower permafrost thawing; thus, our predicted potential for Scots pine seed zones and seed mass would not be realized in the permafrost zone in a warmed climate. Our common garden experiment in central Siberia showed that trees of northerly origins produced lighter seeds than local trees but heavier ones than the trees at the original site. Trees of southerly origins produced heavier seeds than local trees but lighter seeds than the trees at the original site. Conclusions: The findings from this study could serve as blueprints for predicting new landscapes with climatic optima for *Pinus sylvestris* to produce better quality seeds to adjust to a warming climate.

Keywords: scots pine seed mass and seed zones; a provenance trial; bioclimatic models; an ensemble of general circulation models; RCP 2.6 and RCP 8.5 scenarios; Russia
1. Introduction

Forest restoration is a key issue in world forestry. Climate change, numerous wildfires, massive damage by fungi, pathogens, insects, and clear-cutting have resulted in a significant reduction of forest lands, the loss of valuable tree species populations, and a decline in tree species biodiversity and productivity. Forest regeneration and restoration in Russia has become especially urgent since the end of the 19th century and during the 20th century, which has been caused by intensive clear-cutting for enlarged wood requirements. To compensate for forest land losses that are both natural and man-made, restoration became a principal issue in both theoretical and applied forestry research. In this regard, research directed to improve measures for restoring forest land losses, and, in particular, the seed productivity of conifers, which are the main boreal trees in Russia, has become especially relevant nowadays.

*Pinus sylvestris* L. (Scots pine) is one of the main forest-forming tree species that covers 16.2% of the forest lands of Russia (14% within the former Soviet Union), covering about two thirds of northern Eurasia. The reproductive activity of Scots pine across its geographic range, specifically, at the north, is of the foremost interest of forest scientists. The first studies on pine fruiting were accomplished from the end of the 19th century to the mid-20th century (1890–1955) in Scandinavia (Norway, Sweden, Finland), northern Karelia, and the Cola Peninsula (within Russia). In the second half of the 20th century, studies extended their research in Russia to deepen our knowledge of Scots pine cone and seed dynamics, factors controlling seed mass, and quality. Scots pine history research, distribution geography, genetics, and polymorphism were published in detail in monographs [1–5].

Seed mass is one of the indicators of seed quality. Seed mass is a variable trait that depends on a complex combination of ecological and geographical factors and is a stable tree population feature that exposes an inherited evolutionary-adaptive nature of a species.

Quantitative and qualitative biogeography relationships between seed mass and site environmental variables have been studied around the world. As a rule, the environmental variables that were studied were geographical latitude, longitude, and elevation (as an indirect heat measure); monthly temperature (mean, max, min), growing-degree days, or negative degree days (as a direct heat measure); or many other variables. Moles et al. (2003) [6] discovered that latitude explained 21% of the seed mass of 2706 plant species variation globally, with a significant seed mass decrease along the latitudinal direction, increasing to the Pole Circle. Scots pine experiment results in the Sierra Nevada, Spain, suggested that the relationship between the seed mass of the maternal trees and the relative growth rate of their seedlings was controversial; thus, it was not a direct causal [7]. Liu et al. (2013) [8] studied the seed mass of three major forest-forming tree species within their ranges across Canada: black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), and jack pine (*Pinus banksiana* Lamb), depending on their geography (latitude, longitude, and elevation) and 96 climatic variables. Climatic variables explained 34, 14, and 29% of the seed mass variation in black spruce, white spruce, and jack pine, respectively. Himanen et al. (2016) [9] noted the possible impact of different ripening years on spruce seed mass through a different spruce seed moth activities. Freire et al. (2019) [10] discussed the complex connections between climate and the morphological characteristics of *Pinus pinea* L. and its seed production. The important influence of humidity characteristics on the seed yield of *P. pinea* in its Turkish native habitats was stated [11]. The abiotic influence of nutrient and water stress on Mediterranean pine (*Pinus pinaster* Ait) was studied in pine populations of various origins [12]. The authors explored the effect of seed mass on seedling traits such as germination, survival, growth, and biomass partitioning [13]. Populations from more stressful sites were found to produce smaller seeds.

Cherepnin (1980) [3] conducted intensive research regarding the relationship between seed mass and climate in Russia. He collected data on the seed mass and germination of some 1100 provenances from forest units and specialized forest seed stations over the former USSR. He then related part of the data to regional heat variables (growing degree
days above 10 °C) and found that the determination coefficients (e.g., Kazakhstan, the European part of Russia) were as high as 0.8. In the 1970s, common garden trials were started all over the Soviet Union [4,14,15]. Trees tested in some of these provenance trials reached the fruiting age and became seed sources for studying the relationship between seed mass and climatic conditions at these test sites.

This study’s goals are 1. to construct a bioclimatic regression model that relates *P. sylvestris* seed mass to habitat climatic variables across Russia to predict this integral indicator of the seed quality in a changing climate by the end of the century; 2. to relate Scots pine seed mass with its seed zones/climatypes across its range at present and future; 3. to reveal how ecological and genetic factors are partitioned to impact seed mass using our common garden trial data.

## 2. Data and Methods

### 2.1. Seed Mass Data

There are three databases of seed mass and environmental variables (geography, climate, soil) that were created for the bioclimatic modeling of *P. sylvestris* seed mass across the former Soviet Union. The first database included multi-year seed mass data collated by Cherepnin [3] from regularly collected and measured by many forestry units of the All-Union Forestry Agency. This study chose 166 signature sites with seed mass (mass of 1000 seeds) from [3] and assigned geographic coordinates (Figure 1) and multi-year means of climatic variables for each site from a close weather station within a 30 km radius on plains and calculated climate variables based on lapse rates in mountains. In Russian forestry practices, tree and shrub seed mass is measured based on the instructions of the State Standardization System (GOST in Russian, #13056.4-67). In particular, Scots pine seeds are harvested under the clearcutting of mature trees of 100–120 years old. All of the seeds are mixed, and two portions of 500 seeds are selected, weighted, averaged, and calculated for 1000 seed. This method is statistically significant and is used in various countries: all former Soviet Union countries, Eastern European countries, Turkey, Scandinavia, Mongolia, etc. [16–18].

![Figure 1](image-url)

**Figure 1.** The distribution of 42 *P. sylvestris* provenances across Russia (green points) that were used in our common garden trial in the test site of the Boguchany settlement (blue circle), central Siberia. All 166 provenances (green and red points) were used to construct our bioclimatic seed mass model.

To analyze and identify the partial impacts of site climates and genetic traits on seed mass, the second database was composed based on the seed mass of trees from 82 Scots pine provenances of the former Soviet Union tested in two common garden trials on loamy and sandy soils near the Boguchany settlement, which is located in the southern taiga zone of the near-Angara Central Siberian Plateau, Siberia, in 1976–1977. The seeds were collected
in 1974 so that the climatic variables (monthly temperatures of the warmest and coldest months, annual precipitation) of this year and the provenance geography coordinates and multi-year climate means were included in this database. Regular measurements of tree growth in height and diameter, stem volume, needle morphology, cone and seed productivity, and resistance to fungi and pathogens were regularly conducted for about 40 years. Study results were published by Kuzmina and Kuzmin from 1978 to 2020 (see the References section) [19–24].

The third seed mass database was designed from the seed mass measurements of 25–35-year-old trees (the second class in the Russian age classification) of 42 Scots pine provenances from the common garden trial near the Boguchany settlement, central Siberia. The seeds of 5–10 randomly selected trees from various provenances were collected and weighed in 1999, 2000, 2001, 2002, 2003, and 2010 to determine the influence of a Scots pine original provenance (a genetic trait) on seed mass in the introduction site and to determine the influence of the climatic conditions on the seed mass of various provenances in the introduction site (an ecological trait).

2.2. Climate Data

The climatic variables included mean January and July temperatures, and annual precipitation levels were derived from climatic websites (Supplementary 2) and were calculated. The climatic indices included: growing degree days >5 °C, GDD_5; negative degree days < 0 °C, NDD; and annual moisture index, AMI, calculated as the ratio of GDD_5/annual precipitation. The future 2080 (for 2070–2100) climate variables such as January and July temperatures and annual precipitation were calculated as sums of climatic means for the basic period (1960–90) and their mean anomalies for 2070–2100. Anomalies were calculated as anomaly means derived from the ensemble of twenty general circulation models, GCMs, of the CMIP5 from the IPCC Data Distribution Centre (Supplementary 2), and two scenarios using a mild climate (RCP 2.6 scenario) and an extreme climate (RCP 8.5 scenario); anomalies were interpolated on a 0.25° resolution grid. The future climate variables for the January and July temperatures and the annual precipitation were employed to calculate the resultant climatic indices at the end of the century.

Additionally, the current permafrost border position was explicitly included in the analyses as a factor controlling the Scots pine distribution across Russia. The northern and northeastern border of Scots pine distribution across Russia is limited by the southern permafrost border. However, Scots pine may break through further north up, to 70° N, along the broad valleys of the big Siberian rivers, the Yenisei and the Lena, in eastern Siberia, where a deeper active layer thaws in the summer, allowing for Scots pine to succeed [25]. The permafrost border distribution across Russia was calculated using growing GDD_5, NDD, and annual precipitation (R^2 = 0.78), as was also the case with our bioclimatic Siberian vegetation model [26,27]. Seed mass was predicted within the potential _P. sylvestris_ range and was overlapped with the permafrost border to separate actual and non-realized (north-eastwards of the border) seed zones in both contemporary and future climates.

2.3. _P. sylvestris_ Range and Seed Zones across Russia

Climatic envelopes of the _P. sylvestris_ range were subdivided into seed zones/climatypes using the results of Rehfeldt et al. [28–30]. These results were based on common garden studies that had been established across the former Soviet Union. The differential performance of populations reflects the adaptive differences that have accrued from natural selection in the climate of the provenance where the seeds originated. The results of such studies can be used in defining a climatype as the climatic space occupied by a group of populations whose individuals are adapted to the same or a similar climate. The analyses of Rehfeldt et al. [28–30] used published data across the former Soviet Union within 46–86° N and 24–150° E on the height and survival of 313 populations of _P. sylvestris_ that had been planted on 36 sites. These data were used to develop transfer functions that predicted
12-year height and survival from the difference in climate between the provenance of a population and the planting site. The functions were based on a Weibull model. There were three transfer functions driven by GDD$_5$, NDD, and AMI that were developed for *P. sylvestris* growth and survival. The transfer distances were ±240 degrees for GDD$_5$, ±575 degrees for NDD, and ±0.6 units for AMI, which were applied for Siberia [31]. It follows, therefore, that populations separated by the breadth of these transfer intervals tend to be genetically different for the traits controlling growth and survival. All possible combinations of these classes produced the maximal number of pine seed zones/climatypes 180 (Table 1). However, not all seed zones were realized in current and future climates. Of the 180 potential seed zones, only 39 realized seed zones, which make up more than 1% of the total Scots pine range, were found in both the current and future climates (Table 1), and these zones were used for this study’s analyses. The arrow in Table 1 indicates the realized seed zones and seed mass change along the climatic gradient: from low seed mass in moist climates with extreme cold/long winters and cool/short summers (upper left) to intermediate seed mass in sufficiently moist climates with cool winters and warm summers (middle) to high seed mass in dry climates with warm winters and hot/long summers (lower right).

### Table 1. Climatic limits (GDD5, NDD, and AMI) of 180 potential seed zones (#), 39 realized seed zones (>1% of the total range, bold), and their modeled seed mass (g/1000 seed, italic) in current and CMIP5 RCP2.6 and RCP 8.5 climates in Russia.

| GDD$_5$, °C | AMI | NDD, °C |
|-------------|------|---------|
|             |      | −6000–4850 | −4850–3700 | −3700–2550 | −2550–1400 | −1400–250 | >−250 |
| 600–1080    | 0.6–1.8 | 1 | 3.4–5.9 | 3.9–6.4 | 3 | 4.3–6.8 | 4.8–7.3 | 5.3–7.8 | 6 |
|             | 1.8–3.0 | 7 | 4.1–6.6 | 4.6–7.1 | 9 | 5.0–7.5 | 10 | 11 | 12 |
|             | 3.0–4.2 | 13 | 14 | 15 | 16 | 17 | 18 | |
|             | 4.2–5.4 | 19 | 20 | 21 | 22 | 23 | 24 | |
|             | 5.4–6.6 | 25 | 26 | 27 | 28 | 29 | 30 | |
|             | 6.6–7.0 | 31 | 32 | 33 | 34 | 35 | 36 | |
| 1080–1560   | 0.6–1.8 | 37 | 38 | 39 | 5.7–8.2 | 40 | 6.1–8.6 | 41 | 6.6–9.1 | 42 |
|             | 1.8–3.0 | 43 | 44 | 5.9–8.4 | 45 | 6.4–8.9 | 46 | 6.8–9.3 | 47 | 7.3–9.8 | 48 |
|             | 3.0–4.2 | 49 | 6.1–8.6 | 50 | 6.6–9.1 | 51 | 7.1–9.6 | 52 | 7.5–10.0 | 53 | 54 |
|             | 4.2–5.4 | 55 | 56 | 57 | 58 | 59 | 60 | |
|             | 5.4–6.6 | 61 | 62 | 63 | 64 | 65 | 66 | |
|             | 6.6–7.0 | 67 | 68 | 69 | 70 | 71 | 72 | |
| 1560–2040   | 0.6–1.8 | 73 | 74 | 75 | 76 | 77 | 78 | |
|             | 1.8–3.0 | 79 | 80 | 81 | 7.7–10.2 | 82 | 8.2–10.7 | 83 | 8.6–11.1 | 84 | 9.1–11.2 |
|             | 3.0–4.2 | 85 | 86 | 7.9–10.4 | 87 | 8.4–10.9 | 88 | 8.9–11.4 | 89 | 9.3–11.8 | 90 |
|             | 4.2–5.4 | 91 | 92 | 93 | 9.1–11.6 | 94 | 95 | 96 | |
|             | 5.4–6.6 | 97 | 98 | 99 | 100 | 101 | 102 | |
|             | 6.6–7.0 | 103 | 104 | 105 | 106 | 107 | 108 | |
2.4. Experiments with Seed Mass during the Common Garden Trial at the Test Site

We defined a genetic component in the seed mass as the difference between the local and a j-provenance seed mass in a certain year of measurements (1999–2003 and 2010) at the Boguchany test site. This difference in seed mass indicates the genetic component of the provenance traits because trees grown from the provenances and local seeds presently grow in the same environmental conditions.

We defined an ecological component in the seed mass as the difference between the seed mass of a j-provenance collected in 1974 in the original provenance and a j-provenance seed mass in a certain year of measurements (1999–2003 and 2010) at the Boguchany test site, and we then related these differences to the climatic conditions of the corresponding years for 1999–2003 and 2010.

2.5. Mapping Seed Zones and Seed Mass across Russia

Finally, the seed zones of Scots pine were mapped for Russia by coupling the climate maps of GDD$_5$, NDD, and AMI for the contemporary climate and the climates predicted by an ensemble of twenty GCMs for 2070–2100 with our seed zone and seed mass bioclimatic models. Multiple regression bioclimatic models of seed mass were constructed to simulate seed mass based on climatic indices using STATISTICA v. 8.0, and the seed mass distributions in the present and future climates were mapped using raster software TerrSet v. 18.21.

3. Results

3.1. Bioclimatic Models of P. sylvestris Seed Mass

There are two bioclimatic models (Equations (1) and (2)) that are linear multiple regressions that relate to Scots pine seed mass (M) for the January ($T_1$) and July ($T_7$) temperatures and for the annual precipitation ($R_{\text{mm}}$) (Equation (1)) and for the annual moisture index (AMI), growing degree days (GDD$_5$), and Negative degree days (NDD) (Equation (2)) that were constructed:

$$M = -1.35 + 0.085 T_1 + 0.557 T_7 - 0.0021 R_{\text{mm}}$$

$$N = 166, R^2_{\text{adj}} = 0.61, \text{Std. Err.} = 0.72, p < 0.00000;$$

Equation (1)
\[ M = 3.9 + 0.59 \text{AMI} + 0.00042 \text{NDD} + 0.00274 \text{GDD}_5 \]

\[ N = 166; R^2_{\text{adj}} = 0.68; \text{Std. Err.} = 0.65, p < 0.00000; \]

Both bioclimatic seed mass models showed reasonable results over the Russian territory. A July temperature elevated by 1 °C increased the seed mass by 0.56 g, and a January temperature elevated by 5 °C increased the seed mass by 0.43 g (Figure 2). Coupled with climatic layers of AMI, GDD$_5$, and NDD, the model resulted in the Scots pine seed mass distribution maps across Russia in contemporary and future climates (Figure 3). Our modeled seed mass map is good visual agreement with a real seed mass distribution map by Cherepnin [3].

The two maps of the seed mass distribution in future climates (Figure 3) showed that the seed mass would increase by 1 g under the moderate RCP 2.6 and to 4 g under the extreme RCP 8.5, in which the July temperatures were predicted to increase by 1.5–2.0 and 4.0–6.0 °C, respectively, and in which the January temperatures were predicted to elevate by 3.0–4.0 and 8.0–12.0 °C, respectively; the annual precipitation was expected to increase by 30–70 up to 60–100 mm accordingly. As expected, seed mass decreased along the southwest to the northeast, with a declining temperature gradient and increasing climate severity and continentality along with the decreasing of the active layer depth, which is a crucial factor for Scots pine survival and distribution in interior northern Asia.

Figure 2. The dependence of Scots pine seed mass on latitude and longitude (a); GDD$_5$ and NDD (b); the dependence of GDD$_5$ on latitude (c); the dependence of NDD on longitude (d).
Figure 3. Distributions of potential seed zones (Left) and seed mass (Right) across Russia in contemporary climate (Upper) and future RCP 2.6 (Middle) and RCP 8.5 (Lower) climates by 2080. The white line is the permafrost border that divides the realized (below the border) and non-realized (above the border) seed zones with the corresponding seed mass. Seed zone legend see Table 1.

3.2. Distribution of *P. sylvestris* Seed Zones in a Warming Climate by 2080

Of the 180 potential seed zones in the climatic envelope of *P. sylvestris*, most were small: 39 seed zones, with areas >1% accounting for 90–92% of the species’ envelope over Russia in both the present and future climates; 141 potential seed zones accounted for the remaining <10% of the envelope. Of these 39 large seed zones, 24 were found at present and 19 and 21 were found in the RCP 2.6 and RCP 8.5 climates, respectively. Some zones occurred in the present and two future climates; some zones did not (Tables 1 and 2).
Table 2. Scots pine seed zone coverage (%, >5% of the total range in bold) of various seed mass grades (the prevailing grade, % of a seed zone, is in bold) in contemporary and future climates in Russia.

| Seed Zone | Seed Mass Grades | Seed Zone, % of Each Mass Grade | Current Climate | Scenario RCP 2.6 | Scenario RCP 8.5 |
|-----------|-----------------|---------------------------------|-----------------|-----------------|-----------------|
|           | % of Total Area  | Seed Zone, % of Each Mass Grade |                 |                 |                 |
|           | <2   2–4 4–6 6–8 8–10 10–12 | 2–4 4–6 6–8 8–10 10–12 | 2–4 4–6 6–8 8–10 10–12 | 6–8 8–10 10–12 >12 | 6–8 8–10 10–12 >12 |
| 1         | 52.9 47.1 | 3.36 | 6.75 96.6 3.4 | 5.43 |
| 2         | 16.9 82.3 0.8 | 7.78 51.8 48.2 | 4.59 |
| 3         | 2.1 87.9 10.0 | 6.53 3.4 96.6 | 1.24 |
| 4         | 39.6 60.4 | 9.8 90.2 | 1.99 |
| 5         | 12.8 87.2 | 1.87 2.36 62.4 37.6 | 4.61 |
| 6         | 1.8 87.6 10.6 | 2.29 88.2 11.8 | 2.60 |
| 7         | 36.0 64.0 | 1.89 | 1.88 98.7 1.3 | 3.29 98.9 1.2 | 1.22 |
| 8         | 28.1 71.9 | 1.89 | 1.88 98.7 1.3 | 3.29 98.9 1.2 | 1.22 |
| 9         | 0.6 99.4 | 2.29 | 2.29 88.2 11.8 | 2.60 |
| 10        | 100 | 1.74 | 1.74 | 1.74 |
| 11        | 28.8 71.2 | 5.97 | 100 | 3.01 97.4 2.6 | 2.17 |
| 12        | 0.4 98.8 0.7 | 13.06 89.2 10.8 | 11.10 68.7 31.3 | 5.43 |
| 13        | 76.3 23.7 | 11.29 | 11.29 35.3 64.7 | 15.66 |
| 14        | 24.5 75.5 | 3.74 | 3.74 16.7 83.3 | 8.14 |
| 15        | 50.9 49.1 | 3.19 | 3.19 | 3.19 |
| 16        | 3.9 96.1 | 2.47 | 2.47 82.5 17.5 | 3.36 |
| 17        | 80.2 19.8 | 2.25 | 2.25 19.6 80.4 | 2.07 |
| 18        | 4.8 95.2 | 1.74 | 1.74 | 1.74 |
| 19        | 30.8 69.2 | 1.08 | 1.08 100 | 1.17 100 | 4.97 |
| 20        | 100 | 1.15 | 1.15 97.4 2.6 | 8.21 78.9 21.1 | 12.08 |
### Table 2. Cont.

| Seed Zone | Seed Mass Grades | Scenario RCP 2.6 | Scenario RCP 8.5 |
|-----------|------------------|-----------------|-----------------|
|           | % of Each Mass | Seed Zone, % of | Seed Zone, % of | Seed Zone, % of | Seed Zone, % of |
|           | Grade | Total Area | Mass Grade | Total Area | Mass Grade |
| <2 | 2–4 | 4–6 | 6–8 | 8–10 | 10–12 | 2–4 | 4–6 | 6–8 | 8–10 | 10–12 | 6–8 | 8–10 | 10–12 | >12 |
| 83 | 98.8 | 1.2 | 1.18 | 76.5 | 23.5 | 9.22 | 26.5 | 73.5 | 7.79 |
| 84 | 10.3 | 89.7 | 4.62 |
| 86 | 100 | 123 |
| 87 | 80.1 | 19.9 | 7.27 |
| 88 | 92.6 | 7.4 | 2.25 | 55.6 | 44.4 | 3.97 | 35.9 | 64.1 | 3.52 |
| 89 | 0.6 | 99.4 | 2.35 | 19.8 | 80.2 | 1.21 |
| 93 | 4.5 | 95.5 | 4.38 |
| 118 | 100 | 7.34 |
| 119 | 93.8 | 6.2 | 4.06 |
| 120 | 100 | 3.13 |
| 124 | 92.4 | 7.6 | 1.29 | 70.7 | 29.3 | 12.88 |
| 125 | 9.0 | 91.0 | 1.71 |
| 126 | 18.3 | 81.7 | 1.30 | 100 | 2.15 |
| 131 | 55.1 | 44.9 | 1.08 | 100 | 1.16 |
| 137 | 100 | 1.05 |
| 167 | 100 | 0.98 |
Not all potential seed zones could be realized in both contemporary and future climates because of impossible climate combinations and the occurrence of permafrost, e.g., extremely cold winters (lowest NDD) never intermix with extremely hot (high GDD) and dry (high AMI) summers (Table 1). The climate gradient along which the seed zones were distributed started from the permafrost border in interior north Asia, which varied from being extremely cold in the winter and moderately warm and sufficiently moist in the summer in the extreme continental climate in the interior Asian continent, to being moderately warm in the summer and cold in winter and sufficiently moist in the moderate climate of Eastern Europe and west central Siberia, to the hot and dry climates at the southern border of the Scots pine range in Eurasia. Northeast of the permafrost border, Scots pine can only survive in specific geomorphology that allows for active layer depth (ALD) thawing at 1.5–2 m during the summer [26].

As the climate becomes warmer in the RCP 2.6 scenario, 2/3 (16) of the seed zones would remain, and 1/3 (8) would be lost compared to the present. In the much warmer RCP 8.5 climate, the picture is the opposite: 17 out of 24 contemporary seed zones would be lost, as the climate for which they are best suited disappears, but 14 novel seed zones should appear in association with the appearance of climates currently not found in Russia that will cover about 1/2 of the Scots pine range. Only 1/3 of the lands within the climatic envelope of today would remain, but they would change their geographic position, shifting northeastwards along the leading climate change gradient direction (Figure 3). The seven largest (each >5% of the total range) seed zones that currently dominate >60% of the Scots pine forests in Russia are expected to be reduced to 6% of their contemporary distributions in the extreme RCP 8.5 climate (Table 2 and Figure 3). On the other hand, of the seven largest seed zones expected in the future, three would be absent, three would be minor (each ~1%), and one would be twice as large as the present. The moderate RCP 2.6 scenario performs a transition climate between the contemporary and the extreme RCP 8.5 climate. Of the seven largest seed zones that occur nowadays, six will be present in the RCP 2.6 climate. However, their size will be smaller in cold climates and larger in warm climates. Compared to the extreme RCP 8.5 climate, sizes of the largest seed zones in the moderate RCP 2.6 climate will be larger in warm climates and smaller (or be absent) in hot climates (Table 2).

3.3. Coupled Seed Zones and Seed Mass Distributions in Contemporary and Future Climates

Seed mass was calculated from Equation (2) for the realized seed zones (Table 1). In one seed zone, the seed mass varied 2–2.5 g/1000 seed. From the 1st seed zone to seed zone #174, the seed mass was predicted to vary from <2 g to 16 g. Below, we analyze the shifting of the largest seed zones (>5% of the total Scots pine range) jointly with their seed mass (Table 2) in contemporary (Figure 4 Left) and future climates (Figure 4 Central and Right).

The future location of climates inhabited by contemporary seed zones is expected to shift geographically. In cool summers (under GDD = < 1080 °C) in forest-tundra, northern, and middle taiga, seed zones ## 2, 3, 4, and 7 with a prevailing seed mass of 2–4 g, were predicted in both the current and future climates. However, they would not be realized in the future because they were predicted to be in the permafrost zone (north of the permafrost border marked by the white line) where Scots pine cannot survive except for in warmer wide floodplains [32]. The warmer seed zones, ## 44, 45, 46, and 47, with a prevailing mass 4–6 g occurring in southern taiga, subtaiga, and forest-steppe (under GDD = 1080–1600 °C) would be realized in the current and the moderate RCP 2.6 climates, wherein the seed mass may reach 8 g. These seed zones were predicted to be south of the permafrost border. However, in the RCP 8.5 climate, these seed zones were predicted to cross the permafrost border so that they would not be suitable for the survival of Scots pines on cold soils with an ALD less than the 1.5 m (Figure 3). The warmer seed zones, ## 81, 82, 83, 84, and 87, would be realized in the southern taiga, subtaiga, and forest-steppe (under GDD = 1600–2000 °C) in the current and future climates, including the extreme RCP 8.5 climate scenario. The prevailing seed mass was predicted to be as high as 6–8 g under the moderate...
scenario RCP 2.6 and 8–12 g under the extreme scenario RCP 8.5. These seed zones were predicted south of the permafrost border where warm soils would be suitable for Scots pine. However, these predictions could only be realized under sufficient moisture conditions at the southern border of the Scots pine range. The warmest seed zones, ##118, 119, 120, 124, and 125, with a high seed mass of 10–12 g and higher would mostly be realized in the dry conditions of the forest-steppe (under GDD5 = 2000–2500 °C) in the extreme RCP 8.5 climate. Small coverage of the warmest seed zones, ##167, 173, 174, with a seed mass greater than 12 g were predicted in hot (under GDD5 > 2500 °C) and dry (AMI > 4.0) steppe habitats that could be suitable for Scots pine only in the permafrost zone, where the melting of the permafrost provides additional water.

| Contemporary climate | RCP 2.6 | RCP 8.5 |
|----------------------|---------|---------|
| Largest seed zones within GDD5 = 600-1080°C |
| Seed zones #: 1 – 2; 2 – 3; 3 – 4; 4 – 7; 5 – other, the white line in the permafrost border |
| Largest seed zones within GDD5 = 1080-1560°C |
| Seed zones #: 1 – 44; 2 – 45; 3 – 46; 4 – 47; 5 – other |
| Largest seed zones within GDD5 = 1560-2040 |
| Seed zones #: 1 – 81; 2 – 82; 3 – 83; 4 – 84; 5 – 87; 6 – other |
| Largest seed zones within GDD5 = 2040-2520 |
| Seed zones #: 1 – 118; 2 – 119; 3 – 120; 4 – 124; 5 – 125; 6 – other |

**Figure 4.** Distributions of large seed zones (>5% of the total seed zone area) across Russia in contemporary climate (Left) and future RCP 2.6 (Central) and RCP 8.5 (Right) climates in 2080. The white line is the permafrost border that divides the realized (below the border) and non-realized (above the border) seed zones.
The seed zone shift may amount within 500 to 1000 km, following shifting vegetation zones in a warming climate [31] that would bring new plant species from Europe to Asia over the Ural Mountain barrier and change the future flora in southern Siberia, as was reconstructed for the mid-Holocene at about 5500 years BP [33,34].

3.4. The 40-Year Common Garden Trial in the Boguchany

Time series data of seed mass from 42 provenances collected and measured for the 1999–2010 period at the Boguchany test site allowed for the bioclimatic modeling of seed mass depending on the weather conditions of each year (departures from the multi-year climatic norm).

We started from modeling the relationship between local provenance (Boguchany) seed mass and provenance seed mass that arrived in 1974, which was originally used for the establishment a common garden trial at the Boguchany settlement (Figure 5). From Figure 5, it followed that trees grown from the lighter seeds of 1974 in the Boguchany set site produced heavier seeds than in their home provenances for 1999–2003 and 2010. On the contrary, trees grown from the heavier seeds from 1974 produced lighter seeds than in their home provenances for 1999–2003 and 2010.

\[ M_i, g = 4.1 + 0.412 M_{1974}; \]

\[ N = 70; r = 0.44; R^2 = 0.196; p < 0.0001; \text{Std. Er. of est.: } 0.88 \]  

(3)

The seed mass of 25–37-year old trees from 42 provenances in the site test in central Siberia was found to vary from seed mass in home provenances due to the difference in environmental conditions. Otherwise, in the absence of the environmental impact, the seed masses at the test site were the same as in the home provenances.

Figure 5. The relationship between provenance seed mass (\(M_i\)) for 1999–2003 and 2010 in the Boguchany common garden trial and provenance seed mass in 1974.

Seed mass at the test site was analyzed depending on a) the latitude of provenance (Figure 6a) and on b) the differences between the July temperature of the i-th year of seed measurements in the Boguchany test site and the multi-year mean (1960–1990) of provenance (Figure 6b) and on the c) differences between the January temperature of the i-th year of seed measurements in Boguchany and the multi-year mean (1960–1990) of provenance. The determination coefficients were weak (\(R^2 = 0.14\) and \(R^2 = 0.21\)) for both the July and January temperature simple regressions; however, the multiple linear regression including both temperatures was good (\(R^2 = 0.30\), Equation (4), Figure 7).

\[ M_i = 7.09 - 0.153 \Delta T_7 + 0.044 \Delta T_1 \]
The evident outcome of this analysis was that seeds from the southerly (warmer) provenances are heavier than the local provenance seeds from Boguchany, and seeds from northerly (cooler) provenances are lighter than local provenance seeds from Boguchany. Kuzmina and Kuzmin came to the same conclusion by analyzing the previously obtained seed mass data of 25-year-old Scots pines from the same common garden experiment [20].

\[ r = 0.56; R_{adj}^2 = 0.30; n = 72; \] (4)

The difference between provenance seed mass and that of the Boguchany test site (\(\Delta M\)) is the indicator of the genetic component of the variation in the seed mass in the same ecological conditions. This difference indicates how favorable the local climate is for the tested seed provenance: the less seed mass difference, the more favorable climate is (Equation (5)):

\[ \Delta M_i = -1.23 + 0.19 T_7, \]

\[ N = 55; r = 0.47; R^2 = 0.22; \text{St. err.} = 0.71; p < 0.00026 \] (5)

The difference between provenance and local seed mass (\(\Delta M_i\)) in a given year at the test site characterized the genetic component of provenance (Equation (6)):

\[ \Delta M_i = -0.79 - 0.09 \Delta LAT \]
The difference of the July temperatures ($\Delta T_7$) in a given year in the test site and the multi-year mean of provenance explain 22% of the seed mass variation by the genetic component (Figure 8a). The difference between the latitudes ($\Delta L_{\text{LAT}}$) of provenance and the test sites explained 30% of the seed mass variation (Figure 8b), likely due to the impact of photoperiodism in addition to heat resources.

\[ N = 59, r = 0.54; R^2 = 0.30; \text{St. Err.} = 0.68; p < 0.00008 \]  

Figure 7. The dependence of a $j$-provenance seed mass on the differences of the July ($\Delta T_7$) and January temperatures ($\Delta T_1$) in the $i$-th year for 1999–2003 and 2010 (a year of seed measurements in the test site) and the multi-year $T_1$ and $T_7$ means of $j$-provenance, respectively.

Figure 8. The dependence of the seed mass provenance differences and local seed mass ($\Delta M_i$) in measurement years 1999–2003 and 2010 in the Boguchany test site (the genetic component) on the July temperature difference in the measurement year at Boguchany and the multi-year mean of provenance (a) and the difference of Boguchany latitudes and provenance (b).

4. Discussion

A bioclimatic seed mass model of P. sylvestris was built depending on heat, cold and moisture conditions within its range across Russia. As the most common plastic tree species, P. sylvestris stretches through all vegetation zones except for treeless tundra at the very north and the semidesert at the very south and the forests laid by permafrost in the heart of inner Eurasia. P. sylvestris genetic and morphology variability has been studied in detail by Russian and European foresters from the 19th century [1–4]. Due to its plasticity, Scots pine is the most used tree species across Russia for restoring and regenerating lands...
of failed forests after natural and man-made disturbances, primarily caused by forest fire and clearcutting. Seed mass is the most important grade indicator of the State Standardization System (GOST in Russian) in Russian forestry. Scots pine seed mass varies 2–3 times along its range: from 3 g (1000 seeds) in the north to 10–11 g in the pure pine forests in Kazakhstan at the very southern edge of the range.

The Scots pine range spreads extensively over Eurasia, more extensively than all other species of the genus Pinus, and even of the whole Pinaceae family. The Scots pine range covers 14 thousand km from Spain in the west to interior Yakutia in the east and 2.7 thousand km from northern Scandinavia to the Sierra Nevada Mountains in Spain [35]. In the former Soviet Union, its range covered the distance between 40 to 70° N and from 20 to 138° E [1]. Thus, as the P. sylvestris range is mostly located in the former Soviet Union, it was better studied in the Russian literature as a major forest-forming conifer of the Russian boreal forest. Studies of the seed mass variation in other regions beyond the former Soviet Union showed that the seed mass only exceeded the seed mass range across the former Soviet Union in the southernmost sites. In Turkey, at the elevation 1160 m, seed mass varied in 8.6–13.2 g intervals among the clones and in 7.1–15.9 g intervals within the clones [16]. The seed mass economic seed stands and seed orchards in Poland ranged from 5.2 to 9.1 g [36]. In 1970, Antosiewicz [36] found the mean seed mass of 1000 seeds to be 6.2 g within the range from 4.5 to 8.5 g. Przybylski [37] revealed that the mean seed mass in six Scots pine populations in Poland ranged from 5.49 to 6.60 g, with the averaged value being 6.01 g. The seed mass of southern populations of Scots pine in Spanish mountains was much higher than that of northern populations in Finland [17]. The seed mass of Scots pine provenances from a wide geographic area (19 from Finland, 4 from former Soviet Union (Arkhangelsk, Latvia, Novosibirsk, Yakutsk), 6 from Central or Western Europe (Poland, Scotland, France, Belgium, Hungary, Bulgaria) and 1 from Turkey), varied from 3.1 g to 9.2 g, with average 5.2 g [38]. The seed mass for 16 years (1973–1988) in Swedish Scots pine seed orchards varied from 5.31 g to 6.93 g in the north, from 5.43 g to 7.15 g in the middle, and from 5.86 g to 7.31 g in the south [39]. Thus, the seed mass was heavier in the south than in the north. In northern Mongolia [18], seed mass varied between 4.58 to 6.97 g, which was within the range of our seed mass data in Russia.

Seed mass depends on tree age; however, the dependence is ambiguous. There is no consensus on this issue in the literature. Pravdin [1] reviewed studies that related seed mass to tree age. In [1], Kurdiani (1932) and Kapper (1954) made conclusions on a stable seed mass decline from 8.0 g to 5.5 g with ages from 50 to 160 years old. Others found the seed mass decrease from 20 to 60 years old followed by an increase. Mamaev et al. [2] mentioned that many researchers noted the seed mass decrease with aging at mature to overmature age. Additionally, Mamaev et al. [2] concluded that coniferous tree species maintained their ability to produce high-quality seeds for an indefinitely long time. Debain et al. [40] found no effect of age on seed dimensions and mass while comparing two Scots pine stands in southern France that were of the ages of 22–27- and 30–40-years-old, although both seed dimension and mass varied between and within trees. Significant correlations ($R^2 = 0.96$) were found between the age of the parents stands (124 to 180 years old) and the average seed weight, which decreased by approximately 15% as the Scots pine trees grew older [41].

In [3], Azniev (1956), Pikhelgas (1971), and Shulga (1972) came to the conclusion that there was no seed mass dependence on tree age and found no difference between seed quality of trees at various ages.

In our study, we have not aimed to find a relationship between seed mass and tree age because our data was limited by the age range of 25–36 years, which was not sufficient to draw robust conclusions. However, assuming that seeds planted in 1974 in our common garden experiment were collected from trees of 100 years of age and older that had been cut during clearcutting, our data demonstrated some seed mass decreases at mature age (Figure 5) compared to seed mass at 25–36 yr$^{-1}$ of age in our experiment.
A qualitative relationship between seed mass and latitude across Russia was established in the 1960s [1]. Cherepnin [3] established a quantitative relationship between seed mass and heat resources (temperature sums for the period with temperatures >10 °C) for large ecoregions. This study established robust regressions that related *P. sylvestris* seed mass with average climatic conditions: heat resources (mean July and January temperatures, growing degree days, 5 °C), and climate severity (negative degree days, 0 °C). Noting that moisture conditions (annual precipitation, annual moisture index) did not contribute to Scots pine seed mass much, it was still significant (Equation (1)). This fact confirms that Scots pine is tolerant to low moisture and poor soils. To adapt to those conditions, it developed a long taproot that was able to reach the water table [42].

Thus, heat resources explained about 70% of the seed mass variation over Russia. In this study, Scots pine seed mass over Russia was mapped in contemporary and future climates using our bioclimatic seed mass model. At the end of the century, seed mass may increase from 1 g (a moderate scenario RCP 2.6) to 4 g (an extreme scenario RCP 8.5). Seed mass isolines would shift 500 km north and northeast and would follow the southern permafrost border that controls the northern edge of the Scots pine range. The northerly shift would be slow because the summer thawing of the active layer at the depth of 1.5–2 m is necessary for Scots pine to thrive [32] and would be inertial in substrates (soils) due to a larger substrate heat capacity than that of the ambient air. Thus, the permafrost border would follow near-surface air warming with some lag [43].

Another regression that related to the provenance seed mass and the climates of 1974 (the year of seed collecting) was constructed to determine how much the climate of 1974 rather than the average multi-year climate was important for seed mass in each provenance. The correlation between seed mass and the provenance climates of 1974 was low but significant (r = 0.30; p < 0.000). Adding provenance latitudes to this regression significantly improved the correlation (r = 0.78; p < 0.000) because the latitude is not only a proxy of heat, but photoperiodism (daylight and dark periods), a phenomenon of equal importance that Russian forestry classics [1,44] emphasized in seed transfer practices improved the correlation as well.

The third section of this study was to infer the ecological and genetic components of the seed variability of 25–37-year-old trees that produce seeds at the test site. In doing so, this study considered the seed mass of the Boguchany provenance as a normal reaction for the environment; the positive or negative seed mass differences of 42 provenances from the norm were considered as a genetic response to an environmental change. These differences were ordinated around 0 for the Boguchany norm, which was in the center. The main message delivered was that four quadrants of heat/cold differences between provenances and the test site demonstrated that the seed mass of colder provenances were lighter than that of the local provenance Boguchany but were heavier than that at the original provenance; the seed mass of warmer provenances was heavier than that of the local provenance Boguchany but were lighter than that at the original provenance.

Using seed mass data dated by the year 1974 of seed collection, a reverse ordination of the seed mass difference in original provenances and those in the Boguchany test site was examined. A greater seed mass in the test site compared to a local provenance was demonstrated by northerly provenances, and vice versa—a smaller seed mass in the trial site compared to a local provenance was demonstrated by southerly provenances. Hence, the outcome of these findings is that we recommend seeds from southerly provenances to improve seed mass and quality over reforestation/afforestation lands. However, this study has not considered the impacts of fungi and pathogens on seed mass and quality (survival) from various provenances in our common garden trial in the Boguchany site.

In our Russian seed mass models (Equations (1) and (2)), seed mass varied between 3.5–10 g in the current climate. We used our model to predict seed mass in the extremely warm RCP 8.5 climate (Table 2). We extended the predictive power of our seed mass model based on the assumption that models with high explanatory power are inherently of high predictive power [45]. Research in southerly landscapes beyond our study area confirmed
our model predictions that the seed mass should be heavier in warmer conditions, e.g., in Turkey, which is south of Russia, the overall mean of 1000 seed masses was 10.9 g, with a range of 8.6 to 13.2 g in a 13 year-old *P. sylvestris* L. clonal seed orchard that included 30 clones [16].

Additionally, this study needs to take into account the understanding of seed transfer and seed zones/climate types in forestry practices under climate warming. Rehfeldt et al. [28–30] established the number, size, and distribution of *P. sylvestris* seed zones/climate types across Russia using transfer functions for growing degree days, negative degree days, and annual moisture index developed from common garden data across Russia. The GDD5 seed zone breadth was found to be 480 °C or 3.5 °C of the July temperatures, which corresponds to ~ 5 degrees of latitude [3]. Forestry practitioners recommended transferring seed from the origin to planting sites within this distance of 5 degrees of latitude [23,44].

At present, the least productive seed zones with seed mass being less than 2 g and 2–4 g dominate the forest-tundra and northern taiga in cold climates. More productive seed zones with seed mass of 4–6 up to 6 g dominate the middle, southern, and subtaiga in moderately warm climates. In a warming climate under the RCP 2.6 scenario, more productive seed zones with a seed mass from 2–4 to 6–8 g would dominate the southern landscapes. The most productive seed zones, with seed mass 8–10 g, could be found in small areas of the temperate forest-steppe in East Europe. In the extremely warm climate under the RCP 8.5 scenario, seed zones with a seed mass 8–12 g were predicted to dominate larger temperate forest-steppe lands in Eastern Europe; however, the water availability would be a limiting factor at the southern border of the Scots pine range.

5. Conclusions

For the whole range of *P. sylvestris* L. that is distributed over the former Soviet Union, its bioclimatic model of seed mass explains 70% of the variation by site climatic variables. A one degree increase of the July temperature caused a 0.5 g increase of 1000 seeds, and a one degree increase of the January temperature caused a 0.1 g increase of 1000 seeds. The bioclimatic model was applied to the future moderate (RCP 2.6) and extreme (RCP 8.5) climate change scenarios. Climate warming would result in seed mass increase in each site by 1 to 4 g on average in both scenarios accordingly by the end of the century. Scots pine seed mass measurements in a common garden experiment in south central Siberia showed that trees of northerly origins produced lighter seeds than local trees but heavier ones than at the original site. Trees of southerly origins produce heavier seeds than local trees but lighter seeds than those at the original site. This study’s findings would serve as blueprints for predicting new landscapes with climatic optima for *P. sylvestris* to produce better quality seeds to adjust to a warming climate.

**Supplementary Materials:** The following are available online at https://www.mdpi.com/article/10.3390/f12081097/s1, Table S1: Comparison of the temperature sums TSt < 0 and TS t > 10 calculated from a sine function and linear regressions between temperature sums and January and July mean temperature.

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