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Dynamics of Annual Cone Crops of Siberian Fir (*Abies sibirica* Ledeb.) in Conifer Forests of Pre-Ural Region (Russia) Based on 47 Years of Observations

Alexandr Davydychev and Gleb Zaitsev *

Laboratory of Forestry, Ufa Institute of Biology, Ufa Federal Research Centre, Russian Academy of Sciences, Ufa 450054, Russia; shur25@yandex.ru
* Correspondence: forestry@mail.ru

Abstract: Because seed reproduction is the sole means of reproduction available for coniferous tree species, it plays a crucial role in determining the species' ecological adaptability and the competitiveness of species under specific biocoenosis conditions. Therefore, the primary goal of studying the periodicity and cyclical production of cones (seeds) is to forecast the peaks and recessions of natural renewal in various forest ecosystems. The crop dynamics of Siberian fir (*Abies sibirica* Ledeb.) cones in three mature natural conifer forests in the broad-leaf coniferous forest subzone of the pre-Ural region (Russia) was analysed based on long-term observations spanning 47 years. The conifer forests investigated had a considerable deficit of cones (seeds) for natural renewal under the forest canopy. High cone crops occur every 10 years or twice a decade under most favourable conditions. However, cone production has no distinct periodicity, and it is impossible to forecast a high crop of cones based only on long-term data. The levels of fir crop cones were clearly correlated with climate factors. Late winter climate in previous (weak and moderate positive correlation) and current years (weak and moderate negative correlation) affected the fir cone crop. High and even average fir cone crops occur spontaneously with no discernible pattern. In coniferous forests, cone crops are highest on slopes with high insolation levels and on sustainably wet soils.

Keywords: fir cones; level of crops; climate indicators; forest regeneration; forest type; conifer forests

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1. Introduction

Seed production by woody plants is an important mechanism for regulating the recovery and resilience of both natural and damaged forest communities [1]. Because coniferous tree species are older in terms of evolution than deciduous ones, they have little or no vegetative reproduction. As a result, their competitiveness and ecological adaptability within the specific constraints of forest communities are determined by seed reproduction [2].

Tree seed crops are influenced by both environmental (climatic, soil, and biotic conditions) and biological (ecobiological traits of tree species and stand characteristics) variables [3]. Therefore, evaluating the periodicity and cyclicity of cone production is crucial for understanding conifer seed regeneration because it allows for the forecasting of cone crop peaks and declines at the stand level. Tree seed production may differ significantly from season to season [4–6]. At the same time, cone (seed) crops can also range from completely absent cones (100% cone-free) to extreme bumper yields (known as mast years) [7,8]. Although determining the yearly cone production of tree stands by long-term monitoring

is challenging, the results yield accurate data on the seed reproductive potential of forest communities [9–11].

The annual dynamics of woody plant cone crops have long been the focus of research. Previously, several features of the annual crop of cones in the genera *Pinus* [12–15], *Picea* [16–19], and *Larix* [20–22] were investigated. In contrast, very little is known about the dynamics of the annual crop of cones in *Abies* species [23–26]. Siberian fir (*Abies sibirica* Ledeb.) grows in a cold boreal climate on moist soils in mountains or river basins at altitudes ranging from 1900 to 2400 m. This species is typical of the boreal region and is found throughout the Siberian taiga. Native to boreal (taiga) and mountain forests, Siberian fir can grow in pure or mixed stands with other hardwoods and conifers [27,28]. The range is located in northern and central Eurasia, extending from the southern Ural Mountains and northeastern European Russia across Siberia (thus the species name), north of the Chinese and Mongolian border, to the Uda and Amur Rivers, and to the central Heilongjiang Province (China), with an outlier in the Tian Shan (Kyrgyzstan) [29]. They are slender, monecious evergreen trees that may grow up to 35 m high and 100 cm in diameter. They typically have a single stem and a conical crown; however, elderly trees sometimes have numerous crowns. They have been introduced as an amenity tree throughout Central and Eastern Europe (with various forms and cultivars) [30]. Because the wood of Siberian fir is susceptible to fungal decay, the tree seldom survives for more than 200 years [31]. Siberian fir is a commercially significant wood species.

General patterns of the geography, biology, and ecology of cone and seed production for Siberian fir have been established, as summarised in some monographs [32–34]. The mast years of fir occur every 3–4 years, and every 2 years in favourable climatic zones, according to research [35,36]. The earliest generalisations of the dynamics of the annual crop of Siberian fir cones for the region where our research was conducted were based on data spanning 15–25 years of observations [37,38]. Our investigations extend the time of continuous observation by nearly twofold (up to 47 years), allowing us to make more reasonable inferences regarding the annual dynamics of the Siberian fir cone crop. Therefore, the current research focused on analysing data on the crop dynamics of Siberian fir cones that were collected via direct observations in conifer forests of the pre-Ural region (Russia) between 1975 and 2021 (47 years). Specifically, we aim to address the following questions: (1) What are the long-term dynamics of the yearly Siberian fir cone crop? (2) To what extent do the fir cone crop vary among forest types? (3) How do the current and previous year's climatic conditions impact the fir cone crop? This study will contribute to a better understanding of the long-term dynamics of Siberian fir cone crop.

2. Materials and Methods

2.1. Site Descriptions

This study was conducted on three mature natural conifer forests on the Ufa Plateau, which are located inside the Pavlovka Reservoir water protection zone (Ufa River, pre-Ural, Russia). Figure 1 shows the locations of the test sites. Situated in the Ufa River basin, the Ufa Plateau is located in the eastern region of Central Russia, west of the Ural Mountains. At an absolute height of 400–450 m, the Ufa Plateau rises 150–200 m above the surrounding area. The region has a continental climate with an average annual air temperature of 2.0 °C and precipitation ranging from 550 to 600 mm (mean 574 mm). The Ufa Plateau has significantly different climatic conditions than the surrounding regions, with lower average winter and summer temperatures, a shorter frost-free season, and abundant precipitation. The physiographic and climatic features of the Ufa Plateau have been previously described in depth [39].

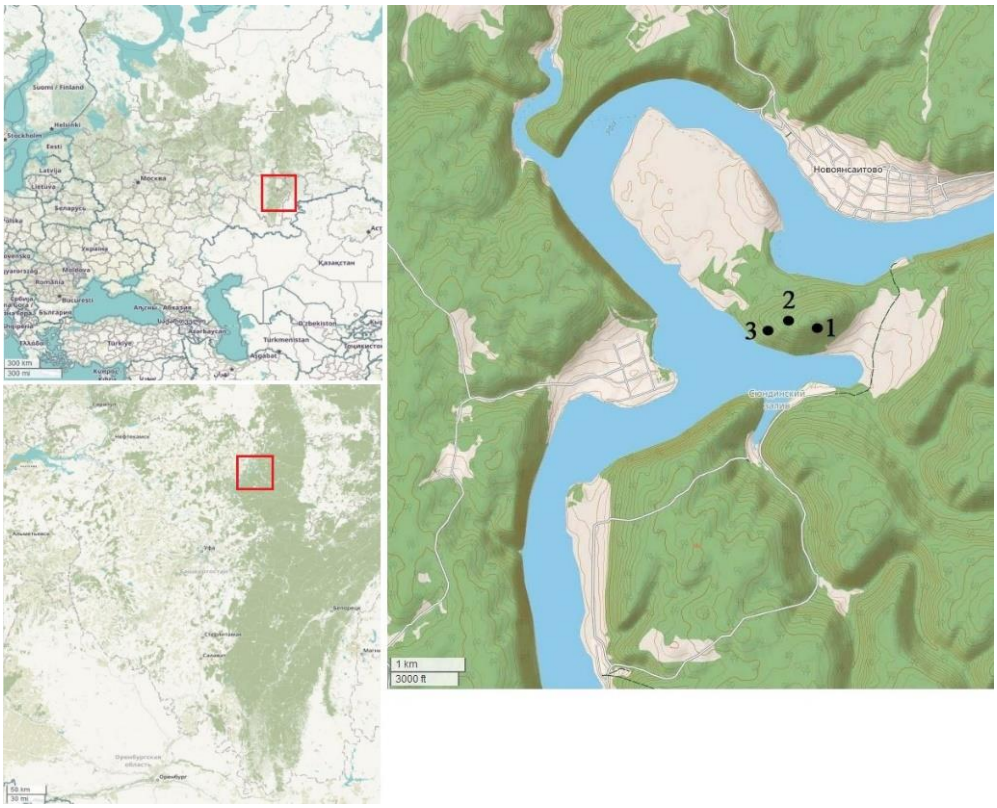


Figure 1. Location of the test sites in the water protection zone of the Pavlovka Reservoir (pre-Ural, Russia): 1—Fir–spruce forests with big ferns and goutweed in the herbaceous layer (FSF (BFG)). 2—Fir–spruce forests with several species of sedge green mosses in the herbaceous layer (FSF (SGM)). 3—Fir forests with goutweed, wood sorrel, and horsetail in the herbaceous layer (FF (HWSG)). The location of the research area is shown by the red frame.

2.2. Stand Characteristics

Annual Siberian fir cone crops were recorded in the three most prevalent types of conifer forests, with fir trees being the dominant species in the stand composition. About half of the area covered by forests in the study region was occupied by these three types of forest growth conditions [40]. Tables 1–3 summarise the key characteristics of the examined coniferous forests.

Table 1. Key features of fir–spruce forests (FSF (BFG)) in the Pavlovka Reservoir water protection zone in the pre-Ural region (Russia).

Stand Formula *	Age, Years	Stocking	Growth Class	Tree Height, m	Tree Diameter, cm	Growing Stock, m^3/ha **
			1972			
1 layer: 3S3F4B sngl. P	70	0.74	I	21.8	26.3	298
2 layers: 8F1S1L + B, E sngl. M, A	50	0.28		11.9	11.2	
			2018			
1 layer: 4S4F2B sngl. P, L	115	0.66	II	26.6	39.9	313
2 layers: 7F2L1M sngl. E	80	0.10		13.8	13.8	

* S—spruce, F—fir, B—birch, P—pine, L—linden, E—elm, M—maple, A—aspen. ** Timber volume estimated for fir.

Table 2. Key features of fir–spruce forests (FSF (SGM)) in the Pavlovka Reservoir water protection zone in the pre-Ural region (Russia).

Stand Formula *	Age, Years	Stocking	Growth Class	Tree Height, m	Tree Diameter, cm	Growing Stock, m^3/ha **
			1984			
1 layer: 6S4F sngl. P, B 2 layers: 9P1S sngl. B, L, W	80 70	0.75 0.07	II	22.5 9.9	24.4 8.5	320
			2018			
1 layer: 5S5F + P, B 2 layers: 7P1S1M1L	110 75	0.40 0.04	II	28.2 12.4	29.9 10.9	290

* S—spruce, F—fir, B—birch, P—pine, L—linden, W—willow, M—maple. ** Timber volume estimated for fir.

Table 3. Key features of fir forests (FF (HWSG)) in the Pavlovka Reservoir water protection zone in the pre-Ural region (Russia).

Stand Formula *	Age, Years	Stocking	Growth Class	Tree Height, m	Tree Diameter, cm	Growing Stock, m^3/ha
			1984			
1 layer: 6P2S2B + P, sngl. A 2 layers: 8P2S + B, sngl. E, L	80 70	0.90 0.15	I	24.8 12.5	21.0 11.4	326
			2018			
1 layer: 5P4S1B sngl. P, A 2 layers: 8P1M1L + E, sngl. S	110 70	0.60 0.03	II	25.2 13.0	23.4 12.2	391

* S—spruce, B—birch, P—pine, A—aspen, E—elm, L—linden, M—maple.

Fir–spruce forests (FSF (BFG)) (Table 1), which are dominated by big ferns (*Dryopteris filix-mas* (L.) Schott, *D. cartusiana* (Vill.), and *Pteridium aquilinum* (L.) Kuhn) and goutweed (*Aegopodium podagraria* L.) in their grass cover, were selected as the first forest type. These forests are found on a broad plateau with grey mountain-forest soils formed on limestone foliated eluvium [38]. Undergrowth (across all tree species) totals 21.7 thousand units/ha, of which 2.7 thousand units/ha are large undergrowth (over 50 cm in height). The number of fir undergrowth units per hectare is 16.8 thousand, with large undergrowths accounting for 2.7 thousand per hectare. Under the forest canopy, *Sorbus aucuparia* L., *Padus avium* L., *Rubus idaeus* L., *Lonicera xylosteum* L., *Corylus avellana* (L.) H.Karst., and *Euonymus verrucosa* Scop. grows in addition to coniferous trees. The grass layer provides 80% coverage. The grass layer contains species of both boreal (*Fragaria vesca* L., *Urtica dioica* L., *Dryopteris filix-mas* (dominant species) and *Pteridium aquilinum* (dominant species)) and nemoral (*Aegopodium podagraria* (dominant species), *Asarum europaeum* L., and *Viola mirabilis* L.) plants. Approximately 20% of the surface is covered with green mosses, which are mostly found on fallen trees in various states of decomposition.

The second type of coniferous forest chosen for examination was fir–spruce forest (FSF (SGM)) (Table 2), where the herbaceous layer was dominated by several species of sedge (*Carex digitata* L., *C. macroura* Meinch., *C. muricata* L., and *C. rhizina* Blytt ex Lindbl.) and green mosses (*Pleurozium schreberii* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) Lindb., *H. polysetum* (Hedw.) Lindb, *Dicranum scoparium* Hedw., *D. polysetum* Sw. (Hedw.) De Not., *Ptilium crista-castrensis* (Hedw.) De Not., and *Rhodobrium roseum* (Hedw.) Limpr.). Growing on sustainably wetted humus-carbonate mountain-forest soil formed on limestone rubble-clay diluvia, these forests are found on slopes with exposures to the south, southeast, and southwest [38]. There are 40.8 thousand undergrowth units/ha total for all tree species, including 2.5 thousand large undergrowth units/ha. Fir undergrowth units per hectare total 21.9 thousand, with large undergrowths accounting for 1.4 thousand per hectare.

Along with coniferous trees, Sorbus aucuparia, Padus avium, and Lonicera xylosteum grow under the forest canopy. The grass layer covers approximately 60% of the surface. In the herbaceous layer, *Rubus saxatilis*, *Oxalis acetosella*, *Orthilia secunda*, *Aegopodium podagraria*, and *Asarum europaeum* grow in addition to *Carex* species. Green mosses cover almost 90% of the ground.

The third type of coniferous forest we selected was fir forest (FF (HWSG)) (Table 3), with goutweed (*Equisetum sylvaticum* L.), wood sorrel (*Oxalis acetosella* L.), and horsetail dominating the herbaceous layer. Grown on the light-grey, bleached mountain-forest soils created by clay deluvia, these forests cover the base of the slopes of all expositions [38]. Across all the tree species, there were 51.0 thousand undergrowth units/ha in total, with 2.2 thousand units/ha of large undergrowth. There are 31.2 thousand fir undergrowth units per hectare, of which 1.6 thousand are large undergrowth units. In addition to coniferous species, *Sorbus aucuparia*, *Padus avium*, and *Rubus idaeus* can grow under the canopy of fir forest. The grass layer provides approximately 80% coverage. In addition to the three predominant herbaceous species, *Urtica dioica* L. and *Asarum europaeum* L. are rather common in the grass layer. Green moss cover is approximately 20% and is mostly found in fallen trees during the last phases of decomposition.

2.3. Forest Inventory Procedure

To investigate the crop dynamics of fir cones in each type of coniferous forest, a test site measuring 50 × 50 m (0.25 hectares) was chosen. In the fir–spruce forest (FSF (BFG)), the first test site was established in 1972. Two additional test sites were established in the fir–spruce (FSF (SGM)) and fir forests (FF (HWSG)) in 1984. The forest inventories of the test sites were conducted at the start of the experiment (in 1972 and 1984) and in 2018. The forest inventory was conducted using standard procedure principles [41]. Every tree (at the first and second levels of the stand) at each test site was thoroughly inventoried. For every tree with a diameter greater than 6 cm, the diameter was measured at breast height (DBH). Tree height was measured using an altimeter with 0.1 m precision (in 2018, the Haglof Electronic Clinometer (Haglof Sweden AB, Langsele, Sweden, https://haglofsweden.com/project/ec-ii-d/ (accessed on 10 July 2024)) was used). For each stand layer, the age of the main tree species was determined. Using an increment borer (Haglof Sweden AB, Langsele, Sweden, https://haglofsweden.com/project/increment-borers/ (accessed on 10 July 2024)), cores were collected from 10 first-layer trees and 10 second-layer trees to assess their age. The number of yearly rings was then calculated. Stocking was established using the widely accepted metric of the total basal area of all trees [42,43]. The Orlov table [44] was used to establish the growth class (also known as the bonitet), which is based on the average age and height of trees as well as the stand origin (vegetative or seminal). Based on the timber volume, the stand formula, which characterises the forest species composition of trees, was calculated [44].

2.4. Cone Crop Determination

For this study, each tree (from the first layer of the stand) at each test site was numbered using a water-resistant paint. During the 47-year monitoring period, the original tree numbering was maintained. Every ten years, the original number of trees was repainted to prevent the numerals from wearing off the trunks. During the experiment, additional trees were not added when the initial trees began to die. This eliminated the potential influence of age-related variations in the cone crop of trees, as older trees tend to produce more cones than younger ones [45].

One of the most common approaches to measuring conifer cone production is the visual count method, which involves counting cones in a coniferous crown using binoc-

ulars [14,46–51]. Every year, the crop of cones for each numbered tree was calculated using the systematic guidelines set by Kapper [52] and Korchagin [53] based on the visual evaluation scale of cone crops (Table 4).

Table 4. Cone crop scale for a mature coniferous tree.

Level of Cone Crops		Cone Locations on Tree Crowns
Points	**Grade**	
0	lack	There were no cones on the tree crowns.
1	very low	Single cones on separate branches in the upper and middle parts of the crown. Predominantly on the southern side, mainly in the topmost crown sector.
2	low	A few branches, mostly in the top sectors of the crown, particularly on the southern side, have a small number of cones. In the middle crown sector, cones are rare.
3	average	Average number of cones that occur uniformly or in groups on numerous branches in the crown's upper and middle sections, particularly on the southern side.
4	high	Most branches in the top and middle parts of the crown have many cones. Cones are concentrated in groups on branches in the upper-crown sector, where there are particularly many.
5	very high	Every branch in the middle and higher parts of the crown has an abundance of cones.

Siberian fir cones form within two years [34], and mature cones (cones from the second year of development) were investigated in this study. Cones in the crowns of the fir trees growing at each site were counted and recorded by the observer using central-focus prism binoculars (15–50×). Throughout the observation period, the yearly crop of cones was determined at precisely the same time in the third week of August. Nikolay Martyanov, a laboratory scientist who died abruptly in 2002, initiated the observations, which were completed by Alexandr Davydychev. This strategy minimised the visual counting mistakes caused by diverse observers because the procedure relies on visual evaluation of the number of cones. Thus, the following scheme was followed for the observations and estimation of the crop of fir cones: from 1975 to 2001, the first observer (N. Martyanov) made 26 years of observations; in 2001, two observers (N. Martyanov and A. Davydychev) jointly determined the crop (training of estimation methods); and from 2002 to 2021, a second observer (A. Davydychev) made 20 years of observations.

After determining the level of cone crop for each tree, the total annual Siberian fir cone crop for the entire stand was calculated. Several parameters have been established to enable the most precise and reliable assessment of the multi-year dynamics of cone crops across a whole stand.

The first parameter, the average crop point (level of cone crops), was determined using Equation (1), which is the arithmetic mean of the points of cone crops for all trees at the test site:

$$LCC = \frac{1}{n}\sum_{i=1}^{n} x_i \quad (1)$$

where LCC is the average level of cone crops for the entire stand, xi is the level of crop points of the i-tree (calculated using Table 4), and n is the number of trees at the test site.

The second parameter is the proportion (%) of trees (C) in the whole stand with a level of crop point equal to "one" or greater (as defined using in Table 4) and is determined using Equation (2):

$$C = \frac{\sum_{i=1}^{n}(x_1 + x_2 + x_3 + x_4 + x_5)}{N} \times 100\% \quad (2)$$

where C is the percentage of trees with a crop point of at least "one", x_1 represents the number of trees with a level of crop point equal to "one" (defined in Table 4), $x_2 \ldots x_5$ are

the number of trees with a level of crop point equal to "two", "three", "four", and "five", respectively, and N is the number of trees at the test site.

Equation (3) was used to derive the third parameter, which was the percentage of trees (Ca) with an average level of cone crops (equal to "three points" in Table 4):

$$C_a = \frac{\sum_{i=1}^{n} x_3}{N} \times 100\% \quad (3)$$

where Ca is the percentage of trees with an average level of cone crops, x3 is the number of trees with a level of crop point equal to "three" (calculated using Table 4), and N is the number of trees on the test site.

Using Equation (4), the percentage of trees (Ch) with high and very high levels of cone crops (corresponding to "four" and "five" in Table 4) was the fourth parameter to be estimated:

$$C_h = \frac{\sum_{i=1}^{n} (x_4 + x_5)}{N} \times 100\% \quad (4)$$

where Ch is the percentage of trees with high and very high cone crop levels, x4 . . . x5 are the numbers of trees with crop points equal to "four" and "five", respectively, and N is the number of trees at the test site.

Cone crop categorisation for the entire stand is necessary when there are notable variations in the production of cones between years. We divided the total cone crop for the entire stand by the following gradients using four criteria (Equations (1)–(4)) to estimate the cone crop:

High crop of fir cones: had an average crop above 1.9; cones were present on more than 85% of the trees, and more than 10% of the trees had a high or very high cone crop.

Average crop of fir cones: average crop ranged from 1.2 to 1.8; between 70% and 85% of the trees had cones, with over 10% of the trees having an average, high, or very high crop of fir cones.

Low crop of fir cones: average crop of less than 1.1; cones were found on 10%–70% of the trees, whereas trees with high, average, and very high crops were either non-existent or only present in single individuals.

No fir cone crop: the average crop was 0–0.1, with no cones or solitary cones on individual trees.

2.5. Source of Meteorological Data

The weather land surface station at Duvan (Bashkortostan, Russia) provided the following meteorological data: average annual air temperature, average monthly air temperature, average annual precipitation, and monthly precipitation during the observation period (Table S1). In the Global Historical Climate Network daily (GHCNd) integrated database (https://www.ncei.noaa.gov/products/land-based-station/global-historical-climatology-network-daily (accessed on 20 June 2024)), the land surface station identifier was RSM00028537. The land surface station coordinates (latitude/longitude) were 55.70° N, 57.91° E. This weather land surface station, which recorded meteorological indicators over the whole observation period, was closest to the research area. The station was located 67 km east of the research sites site and had the same latitude as the study area. An open database (http://aisori-m.meteo.ru/waisori/ (accessed on 20 June 2024)) with specialised data arrays for climate study [54] was the source of meteorological data from this weather station. This open database was created by the All-Russian Research Institute for Hydrometeorological Information—World Data Centre (The Federal Service for Hydrometeorology and Environmental Monitoring of the Russian Federation (Rosgidromet)), and data relevance was maintained in compliance with current legislation [55].

2.6. Data Analysis

The statistical analysis [56] and data processing were conducted using Statistica 8.0, JASP 0.18.3, and MS Excel. To determine statistically significant variations in cone crop levels among various coniferous forests, we ran a one-way ANOVA (Duncan's multiple comparisons test) on the selected indicators, with a probability level less than 0.05. Pearson's correlation coefficient (r) was utilised to evaluate the degree of dependence between cone crop levels and meteorological data. The statistical analyses were conducted with a 95% significance level ($\alpha = 0.05$).

3. Results

Fir trees had a high mortality rate in the examined coniferous forests (Table 5). At the end of the research period, only 28%–29% of the fir trees remained in the FSF (BFG) and FF (HWSG). FSF (SGM) had a greater survival rate, with 52% of the fir trees still standing at the end of the research.

Table 5. Number of living fir trees (in the first stand layer) at the test sites during the study period.

Forest Type	Year of Forest Inventory					
	1975	1984	1994	2004	2014	2021
FSF (BFG)	44	41	40	29	15	13
FF (HWSG)	-	106	86	76	54	30
FSF (SGM)	-	70	65	61	53	37

Fir cone crops are variable, unstable, and inconsistent from year to year. Fir cone crops vary from non-existent to highly level. In the FSF (BFG), the largest level of the fir cone crop was recorded in 1976. The average cone crop point in this year was 3.2 ± 0.23. A high and very high crop of cones was observed on more than 48% of the fir trees. Over 9% of the trees had an average level of fir cone crops. Furthermore, this year, only 2% of the fir trees lacked cones. The highest cone crop level in the FF (HWSG) was observed in 2005. In that year, the cone crop average point was 2.5 ± 0.18. More than 26% of the fir trees had high or very high crop of cones. Average levels of fir cone crops were present on more than 30% of the trees. Only 10% of the fir trees in that year had no cones. The cone crop in the FSF (SGM) peaked in 1994. The cone crop average point was 3.5 ± 0.13. A high or very high crop of cones was recorded on more than half of the fir trees. Approximately 30% of the trees had an average level of fir cone crops. There were no trees without cones this year because every other tree had cones.

In the examined coniferous forests, high crops of fir cones are rare (Tables 6 and 7). For example, only 5 out of 47 years (approximately once every ten years) saw high crops of cones in the FSF (BFG). In the FF (HWSG), a comparable trend was noted. Here, only 5 of the 38 years had high cone crops, or approximately once every 10 years. Compared to other types of forests, the FSF (SGM) had more fir cone crops more frequently. Further, 9 years out of 38 years were distinguished by high cone crops, i.e., high cone crops were distinguished approximately twice every 10 years. Coniferous forest studies show statistically significant differences in cone crops; these differences are more common in years with high cone crops than in years with average cone crops. No statistically significant differences were detected between the examined coniferous forests in the years with low levels of cone crops.

Table 6. Trends of the fir cone crops in three coniferous forests in the water protection zone of the Pavlovka Reservoir in the pre-Ural region (Russia).

Year	Average Level of Cone Crops (in Points)			ANOVA: Single Factor	
	Forest Type				
	FSF (BFG)	FF (HWSG)	FSF (SGM)	*F*	*p* Value
1975	0.5 ± 0.13	-	-	-	-
1976	3.2 ± 0.23	-	-	-	-
1977	1.5 ± 0.15	-	-	-	-
1978	1.3 ± 0.13	-	-	-	-
1979	0.1 ± 0.04	-	-	-	-
1980	1.3 ± 0.16	-	-	-	-
1981	0.6 ± 0.11	-	-	-	-
1982	1.7 ± 0.14	-	-	-	-
1983	0.1 ± 0.06	-	-	-	-
1984	1.2 ± 0.16	0.6 ± 0.08	1.0 ± 0.11	**7.5999**	**0.0006**
1985	1.1 ± 0.15	1.3 ± 0.09	1.9 ± 0.12	**10.1751**	**0.0001**
1986	0.4 ± 0.08	0.7 ± 0.07	0.5 ± 0.07	2.4389	0.0897
1987	0.2 ± 0.06	0.2 ± 0.04	0.4 ± 0.07	**3.1952**	**0.0429**
1988	0.1 ± 0.04	0.1 ± 0.03	0.2 ± 0.05	2.8029	0.0629
1989	0	0	0	-	-
1990	0	0	0	-	-
1991	0	0.1 ± 0.02	0.2 ± 0.07	-	-
1992	2.1 ± 0.20	2.0 ± 0.12	2.7 ± 0.14	**8.5438**	**0.0003**
1993	0.2 ± 0.08	0.1 ± 0.03	0.1 ± 0.04	2.5537	0.0802
1994	2.4 ± 0.28	2.6 ± 0.15	3.5 ± 0.13	**10.7168**	$\mathbf{3.91 \times 10^{-5}}$
1995	0	0	0.1 ± 0.03	-	-
1996	1.5 ± 0.18	1.7 ± 0.11	2.7 ± 0.14	**23.5420**	$\mathbf{7.60 \times 10^{-10}}$
1997	0	0	0.2 ± 0.05	-	-
1998	0.1 ± 0.04	0.1 ± 0.03	0.2 ± 0.06	2.3983	0.0937
1999	0.3 ± 0.09	0.4 ± 0.08	0.4 ± 0.08	0.7279	0.4843
2000	0	0	0.3 ± 0.08	-	-
2001	1.9 ± 0.29	2.1 ± 0.16	3.1 ± 0.19	**10.1216**	**0.0001**
2002	0	0	0.3 ± 0.07	-	-
2003	1.1 ± 0.16	1.5 ± 0.14	2.0 ± 0.13	**7.0843**	**0.0011**
2004	0.1 ± 0.06	0	0.1 ± 0.05	-	-
2005	1.5 ± 0.21	2.5 ± 0.18	3.0 ± 0.17	**11.5155**	$\mathbf{2.15 \times 10^{-5}}$
2006	0	0	0	-	-
2007	0.7 ± 0.18	0.9 ± 0.10	0.9 ± 0.11	0.7797	0.4604
2008	0.1 ± 0.12	0.2 ± 0.05	1.2 ± 0.15	**29.5870**	$\mathbf{1.47 \times 10^{-11}}$
2009	0.6 ± 0.22	0.9 ± 0.10	0.9 ± 0.10	1.1438	0.3215
2010	1.2 ± 0.24	1.7 ± 0.15	2.2 ± 0.15	**6.9192**	**0.0014**
2011	0.8 ± 0.17	1.8 ± 0.13	2.1 ± 0.14	**13.6787**	$\mathbf{3.67 \times 10^{-6}}$
2012	0.1 ± 0.05	0.1 ± 0.03	0.1 ± 0.04	-	-
2013	1.9 ± 0.30	1.9 ± 0.13	2.3 ± 0.14	2.6238	0.0765
2014	0.1 ± 0.13	0.1 ± 0.04	0.1 ± 0.06	0.3613	0.6975
2015	0.5 ± 0.24	0.5 ± 0.11	0.9 ± 0.13	**3.7062**	**0.0275**
2016	0.6 ± 0.21	1.7 ± 0.18	2.2 ± 0.19	**9.3487**	**0.0002**
2017	0.3 ± 0.16	0.3 ± 0.06	0.3 ± 0.08	0.1648	0.8482
2018	0.5 ± 0.17	1.2 ± 0.17	1.2 ± 0.14	**3.6753**	**0.0287**
2019	0.8 ± 0.19	1.2 ± 0.16	1.3 ± 0.14	1.0274	0.3620
2020	0.2 ± 0.12	0	0	-	-
2021	0.9 ± 0.29	2.0 ± 0.19	2.4 ± 0.15	**8.8916**	**0.0003**

The statistically significant differences between test sites at the 95% significance level (F_{crit} = 3.0943, α = 0.05) are shown in bold.

Table 7. The contribution of fir trees to the production of cone crops in various coniferous forests in the water protection zone of the Pavlovka Reservoir in the pre-Ural region (Russia).

Year	Percentage of Trees with Cones, %								
	FSF (BFG)			FF (HWSG)			FSF (SGM)		
	C	Ca	Ch	C	Ca	Ch	C	Ca	Ch
1975	38.6	2.3	2.3	-	-	-	-	-	-
1976	97.7	9.1	47.7	-	-	-	-	-	-
1977	90.9	13.6	2.3	-	-	-	-	-	-
1978	86.4	4.5	2.3	-	-	-	-	-	-
1979	6.8	0.0	0.0	-	-	-	-	-	-
1980	77.3	6.8	4.5	-	-	-	-	-	
1981	52.4	0.0	0.0	-	-	-	-	-	-
1982	88.1	16.7	0.0	-	-	-	-	-	-
1983	7.1	0.0	0.0	-	-	-	-	-	-
1984	73.2	9.8	2.4	47.2	1.9	0.9	74.3	4.3	2.9
1985	73.2	9.8	2.4	80.2	13.2	0.9	91.4	22.9	4.3
1986	36.6	0.0	0.0	50.9	2.8	0.0	50.0	0.0	0.0
1987	17.1	0.0	0.0	17.9	0.0	0.0	30.0	0.0	0.0
1988	7.3	0.0	0.0	9.4	0.0	0.0	20.0	0.0	0.0
1989	2.5	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0
1990	2.5	0.0	0.0	0.9	0.0	0.0	1.4	0.0	0.0
1991	2.5	0.0	0.0	4.8	0.0	0.0	15.7	1.4	0.0
1992	87.5	25.0	10.0	85.6	22.1	10.6	94.3	34.3	25.7
1993	17.5	0.0	0.0	6.8	0.0	0.0	7.1	0.0	0.0
1994	75.0	22.5	32.5	90.7	25.6	25.6	100.0	32.3	50.8
1995	0.0	0.0	0.0	3.5	0.0	0.0	7.7	0.0	0.0
1996	77.5	5.0	7.5	90.6	15.3	3.5	100.0	26.2	24.6
1997	0.0	0.0	0.0	1.2	0.0	0.0	16.9	0.0	0.0
1998	7.5	0.0	0.0	6.1	0.0	0.0	13.8	0.0	0.0
1999	25.0	0.0	0.0	34.6	2.5	0.0	28.1	0.0	0.0
2000	0.0	0.0	0.0	3.7	0.0	0.0	28.6	1.6	0.0
2001	71.4	8.6	25.7	86.1	20.3	16.5	95.2	14.3	19.0
2002	3.3	0.0	0.0	2.6	0.0	0.0	23.0	1.6	0.0
2003	73.3	6.7	0.0	80.5	20.8	6.5	95.1	23.0	6.6
2004	10.3	0.0	0.0	3.9	0.0	0.0	13.1	0.0	0.0
2005	82.1	7.1	7.1	91.5	31.0	26.8	96.7	29.5	36.1
2006	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0
2007	50.0	0.0	3.8	69.6	4.3	0.0	66.1	5.1	0.0
2008	3.8	3.8	0.0	20.6	0.0	0.0	69.5	6.8	5.1
2009	36.0	0.0	4.0	68.2	3.0	1.5	66.7	3.5	0.0
2010	64.0	4.0	8.0	83.1	13.8	9.2	91.2	33.3	10.5
2011	54.2	4.2	0.0	90.8	26.2	4.6	87.7	28.1	7.0
2012	5.3	0.0	0.0	4.7	0.0	0.0	8.8	0.0	0.0
2013	83.3	22.2	11.1	96.4	26.8	3.6	96.3	27.8	13.0
2014	6.7	0.0	0.0	3.7	0.0	0.0	7.5	1.9	0.0
2015	26.7	6.7	0.0	30.8	3.8	0.0	57.7	5.8	0.0
2016	40.0	0.0	0.0	80.0	24.0	6.0	95.8	18.8	18.8
2017	26.7	0.0	0.0	25.0	0.0	0.0	22.9	0.0	0.0
2018	40.0	0.0	0.0	67.4	6.5	6.5	73.3	8.9	0.0
2019	69.2	0.0	0.0	66.7	9.5	0.0	82.9	4.9	2.4
2020	23.1	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0
2021	53.8	7.7	0.0	89.7	23.1	10.3	100.0	18.9	16.2

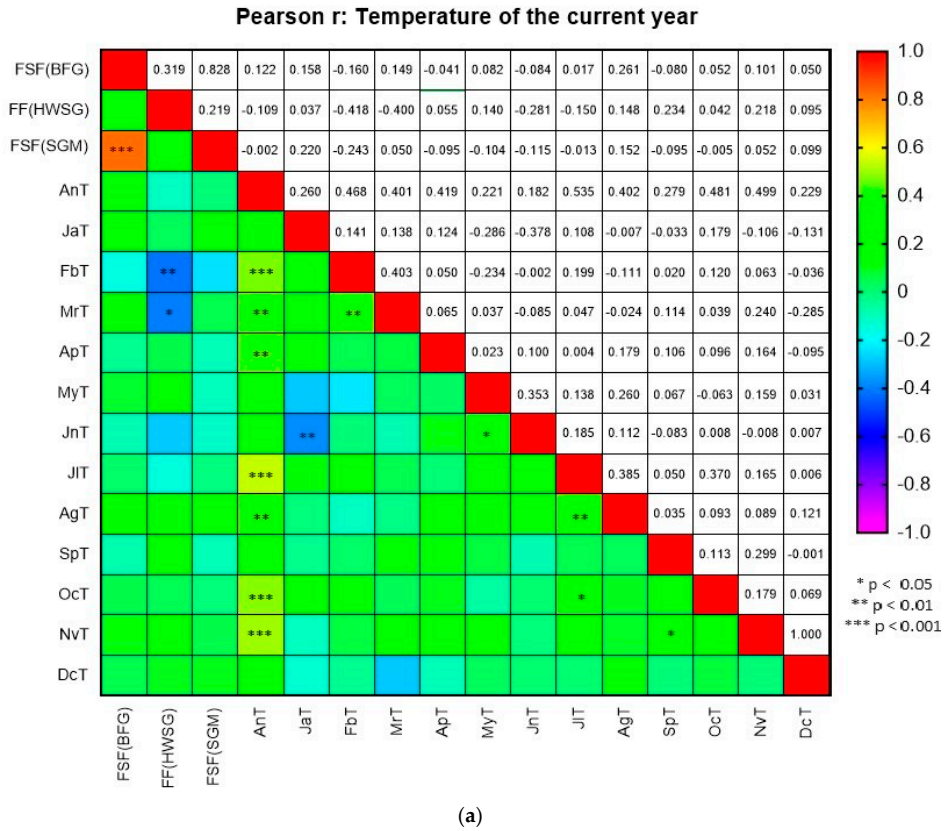
C is the percentage of trees with a crop point of at least "one", Ca is the percentage of trees with an average level of cone crops (crop point equal to "three" points), and Ch is the percentage of trees with high and very high cone crop levels (crop points equal to "four" and "five").

In two of the three forest types examined, the number of years with an average cone crop was approximately twice the number of years with a high crop. The average crop of cones in the FSF (BFG) was recorded for 9 of 47 years, or approximately twice every 10 years. In the FF (HWSG), the average crop was reported for 9 of the 38 years, or twice in 10 years. The number of years in the FSF (SGM) with an average cone crop throughout the studied period is half the number of years with high crops. Here, the average cone crop was recorded for 5 of the 38 years, or once every 10 years. The remaining years were characterised by low or non-existent fir cone crops. Cone crops were completely absent in the following sequences: FF (HWSG), 15 years out of 38 (39%); FSF (BFG), 16 years out

of 47 (34%); and FSF (SGM), 9 years out of 38 (23%). In all other years, low levels of cone crops were recorded in the studied coniferous forests.

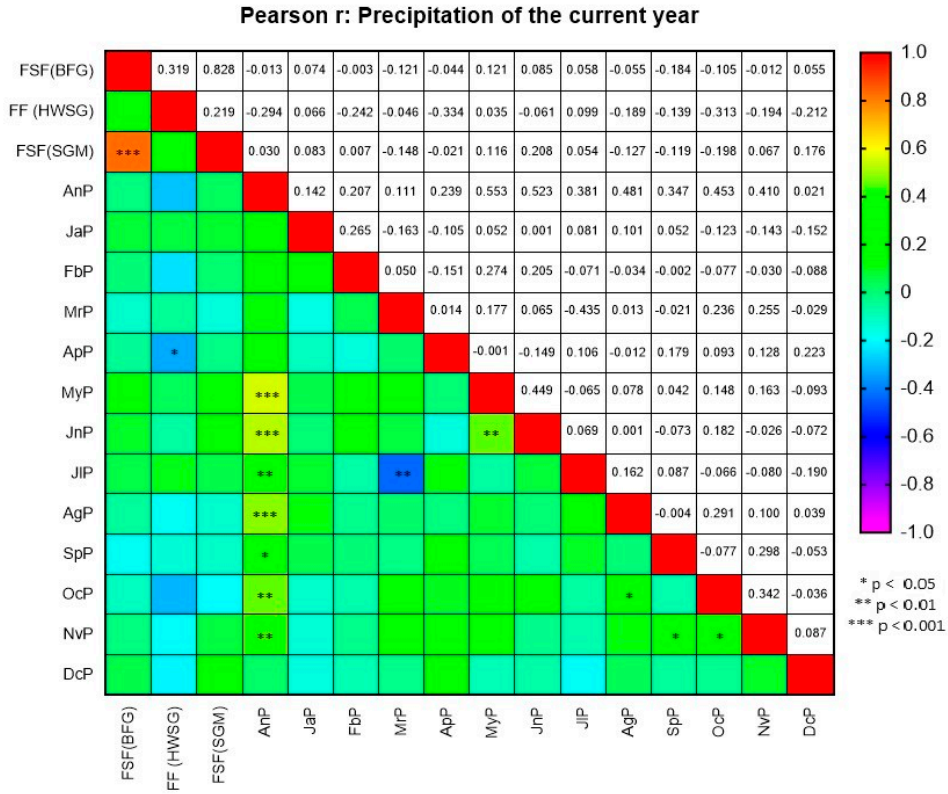
There were no evident trends in the meteorological factors influencing the fir cone crops. In the FF (HWSG), the level of fir cone crops had a moderate negative correlation with the temperature in February ($r = -0.418$, $p < 0.01$) and March ($r = -0.400$, $p < 0.05$) of the current year (Figure 2a) and a weak negative correlation ($r = -0.334$, $p < 0.05$) with precipitation in April of the current year (Figure 2b). In the FSF (SGM), the temperature in February of the previous year (Figure 3a) and the fir cone crop had a weak positive correlation ($r = 0.332$, $p < 0.05$), whereas the precipitation in January of the previous year (Figure 3b) and the crop had a moderate positive correlation ($r = 0.458$, $p < 0.01$). In the FSF (BFG), the temperature in February of the previous year (Figure 3a) and the fir cone crop had a weak positive correlation ($r = 0.334$, $p < 0.05$).

Cone production was unaffected by precipitation during the growing season, even in years with abnormally low precipitation (dry years). Throughout the growing season (May to August), the average precipitation based on records spanning 47 years was 251 mm (Table S1). In all the years of observation, 2010 was the driest year. During the growing season this year, there was only 92 mm of precipitation, or 37% of the average amount. In this year, average and high levels of cone crops were recorded (Table 6). Following the driest year in 2011, average and high levels of cone crops were recorded, indicating that the crop was at the same level. In the growing season, 2012 was the second year with the least amount of precipitation. Only 109 mm of precipitation was recorded during the growing season this year, which is 42% of the norm. Low levels of cone crops were recorded during the observation period, in contrast to 2010. However, average and high levels of cone crops were observed during the next year. In contrast, the cones were totally absent in 1989 and 1990, or two consecutive years. In 1989 and 1990, 249 and 294 mm of precipitation, respectively, occurred throughout the growing season (with an average level of 251 mm).



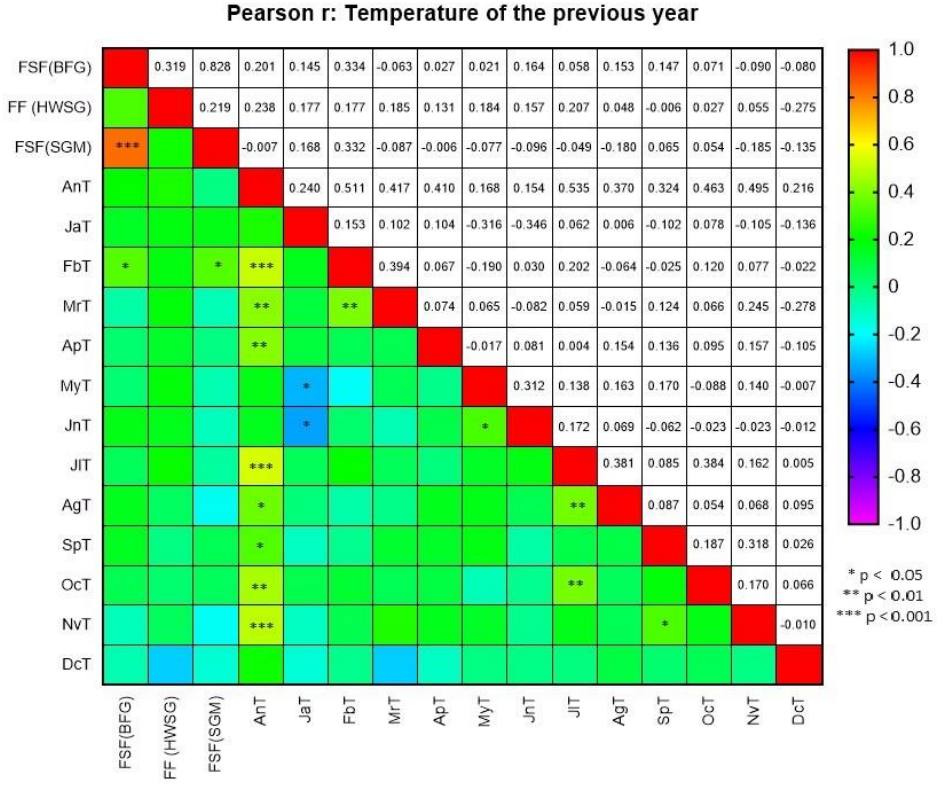
(**a**)

Figure 2. *Cont.*



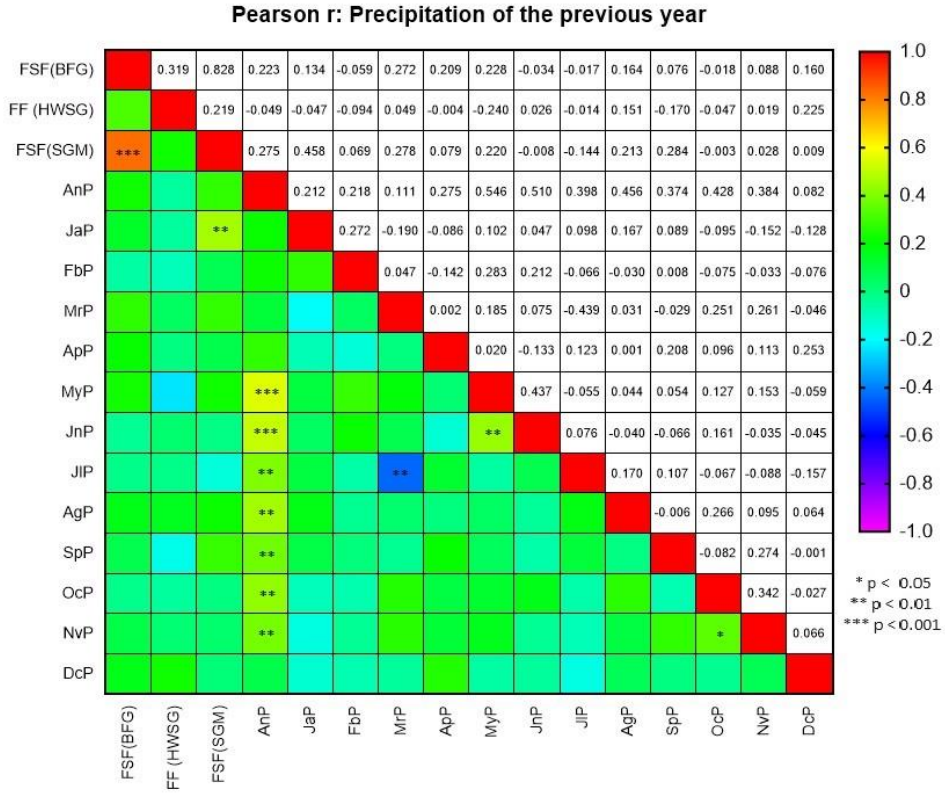
(**b**)

Figure 2. Modelling variable correlation analysis: (**a**) heatmap for correlation analysis of temperature of the current year and level of fir cone crops; (**b**) heatmap for correlation analysis of precipitation of the current year and level of fir cone crops.



(**a**)

Figure 3. *Cont.*



(**b**)

Figure 3. Modelling variable correlation analysis: (**a**) heatmap for correlation analysis of temperature of the previous year and level of fir cone crops; (**b**) heatmap for correlation analysis of precipitation of the previous year and level of fir cone crops.

4. Discussion

The water protection zone of the Pavlovka Reservoir (pre-Ural, Russia) contains mature forests with complex compositions. Almost all species of woody plants found in the South Urals and surrounding territories can be found in this small area, which is bounded by a riverside that is 500–2000 m wide [38]. As a dominant tree species and co-dominant species with other conifers (mainly Siberian spruce), Siberian fir grows in almost all types of forests. The study site is an ideal test region for tracking the crop dynamics of Siberian fir cones because it lacks sources of industrial pollution, recreational load, wildfires, and insect outbreaks throughout the examined period. The evaluation of the three coniferous forest types under study revealed that these forests are growing and developing steadily based on changes in key tree stand characteristics. However, it is worth noting the high mortality rate of mature fir trees. By the end of the 47-year observation period, only 28%–29% of the initial number of fir trees survived at the two test sites. This observation can be explained by the fact that 70%–90% of fir undergrowths form xylorhizomes, and that undergrowths may exhibit long-term depressed states throughout the early phases of ontogeny [39]. As a result, the age at which depressed undergrowth has reached the first layer of stand during growth may vary significantly from that of the fir individuals that did not form a xylorhizome by 40 to 50 years. Because this fir growth feature occurs during the early ontogeny stages, the sample size required for long-term studies must be carefully considered. To ensure that there will be enough living trees remaining at the end of the experiment, at least 50 fir trees should be used to track the long-term dynamics of the cone crop.

The overall number of years with average and high levels of fir cone crops throughout the 47-year observation period ranged from 30% to 40% in all observed stands in the coniferous forests of the water protection zone of the Pavlovka Reservoir (pre-Ural region)

(Figure 4). Simultaneously, the percentage of years with low or non-existent fir cone crops varied from 60% to 70%. Notably, high levels of fir cone crops, which can occur once or twice every 10 years depending on the type of forest, rarely occur. This information partially contradicts the findings of some scholars who, based on far less factual data, concluded that high-level fir cone crops recur every four, three, or even two years (on the southern edge of the range) [35]. Research on Siberian fir cone crops in the Urals revealed a three- to four-year cycle of high cone production [57]. For seven years of study, there were two years of high crops (about every three years) in the fir forests in the southeast part of the West Siberian Plain [35]. During a 10-year study, two high crops of fir cones southw(about every five years) were observed in the Salair Ridge fir forests [36]. Annual fir cone crops were found in the southwestern Altai during a 10-year investigation [58], although the level of crops differed significantly from year to year. In the Pyrenees, silver fir (*Abies alba* Mill.) cone crops varied greatly from year to year, but no distinct cone crop cycle was identified [59]. There was a significant difference between the production of cones and seeds in three-year trials of the silver fir cone crop in the Carpathian foothills [60]. A 36-year count of Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) and grand fir (*Abies grandis* (Douglas ex D. Don) Lindley) cone crops in the Cowichan Lake area (Vancouver Island, British Columbia) revealed a cyclical pattern of good cone crops occurring every four years [61]. Thus, it should be noted that the periodicity of high cone crops changes significantly not only within different environmental conditions of Siberian fir growth but also in other species of the genus *Abies*.

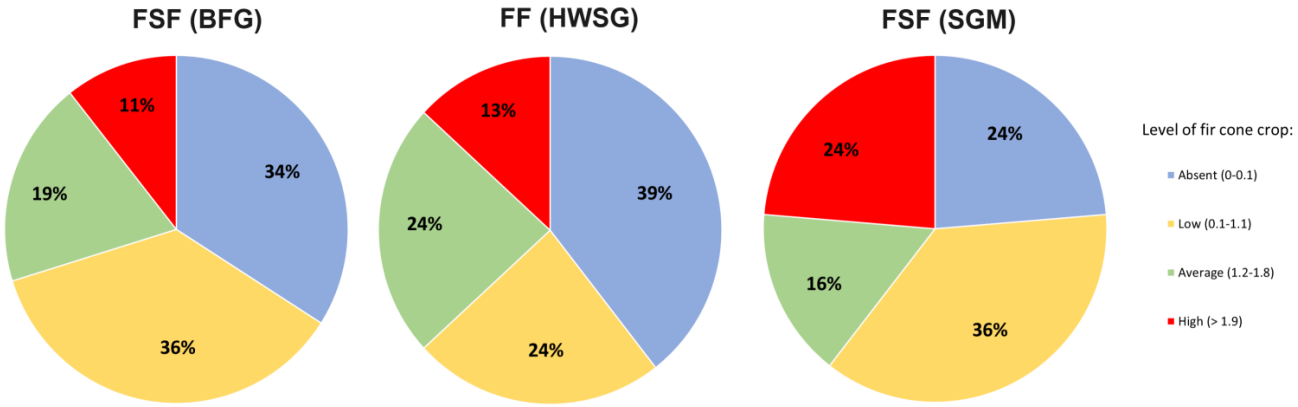


Figure 4. Proportion of years with varying Siberian fir cone crops throughout a 47-year observation period in various coniferous forests in the water protection zone of the Pavlovka Reservoir in the pre-Ural region (Russia).

Up to 80% of the seeds a stand produces in a particular period come from years with high cone production [62]. Fir seeds are poorly stored in the soil (almost no seed bank is formed) and germination rates are low (up to 65%) [34,36]. Based on the collected data, it is possible to conclude that there is a general paucity of seeds available for successful natural regeneration of fir under a forest canopy.

Annual variations in cone crops have been documented for many conifer species [63,64]. The causes of these changes include fluctuations in climate, the availability of resources, variations in pollination, the effects of animals and pests, and other variables [7,65,66]. The production of cones from Siberian fir was influenced by climatic conditions in both positive and negative correlations. Cones, including Siberian spruce, are produced by many conifers over a two-year cycle [67,68]. In the first year, cone buds are formed, and in the following year, cones grow and mature. Therefore, climatic conditions in the current (year of observation) and preceding years affect the creation of the fir cone crop. Low temperatures

in February affect cone buds (damage from frost), which explains the positive correlation between the level of cone crops and the temperature in February of the preceding year (the first year of the cone production cycle). Previously, similar effects were observed in other conifers [69,70]. A process akin to the formation of frost cracks on tree stems can explain the negative correlation between the level of cone crops and the temperature in February and March of the current year. Typically, frost cracks appear in late winter and early spring [71,72]. The bark warms on bright days in late winter and early spring, causing the cells in the bark and the wood just beneath it to enlarge. The temperature decreases rapidly when the sun settles, which causes the bark to cool and contract. The bark becomes damaged as the wood beneath it cools more slowly. The cones undergo an analogous damaging process. To minimise self-pollination, conifer seed cones usually form in the upper third of the tree, whereas pollen buds form in the lower third [73,74]. Because the upper parts of trees receive more heat on bright days, the crop of fir cones decreases because seed cones sustain damage first.

Isolating the influence of a single environmental factor on the fir cone crops is challenging because of the complex interactions among environmental factors, which either boost or diminish each other's degree of effect [75]. Thus, the following series of favourabilities for the production of fir cones may be constructed by analysing data on the level of fir cone crops in various types of coniferous forests. Fir cone crops are highest in coniferous forests (FSF (SGM)) growing on south-facing slopes with sustainably wetted humus-carbonate mountain-forest soil. The second-highest level of fir cone crops is found in coniferous forests (FF (HWSG)), which grow at the base of slopes with grey bleached mountain-forest soils. The fir cone crop level of coniferous forests (FSF (BFG)), which grow on a broad plateau with grey mountain-forest soils, was the lowest in this series.

Most frequently, research on cone crop frequency (seed production) is conducted to create forecasting techniques for cone crops, which in turn helps determine the likelihood that forest communities will regenerate [17,33]. However, research conducted over short observation periods often forms the basis for these estimations of cone crops [17,76]. Any trends that previous researchers, e.g., [32,36], may have noticed, for instance, the frequency of high cone crops after a specific number of years, are not evident as a consequence of this study. For instance, in various coniferous forests, average fir cone crop levels may alternate with low crop levels for 12 years (1977–1988), after which there may be a three-year period during which there are no cones at all (1989–1991). In addition, during the period of 1992 to 2006, high fir cone crop levels were followed after five years by low crops for four years and then high crops after one year again during the next five years. In other words, it is very difficult to predict fir cone crop dynamics because the dynamics of the crop are unexpected.

Low cone crops are frequently repeated in the patterns of Siberian fir cone crop dynamics that have been recorded, which helps to expand our understanding of the ecological and biological traits of this tree species. These data are valuable for forest management because they remind foresters that they cannot rely exclusively on natural Siberian fir regeneration. There are also some issues with the artificial regeneration of this tree species. Rare years with high levels of cone crops, low-quality seeds, and challenging seed collecting make it challenging to cultivate planting material and promote artificial reforestation. Therefore, it is recommended to employ cutting techniques that conserve as many natural undergrowths as possible while managing forests that are mostly composed of Siberian fir trees. Practical foresters may have a false image of fir biology and ecology if we ignore the frequent presence of low-level fir cone crops. This may result in the deployment of inappropriate forest management techniques. From the perspective of forest management, this may lead to a disastrous reduction in valuable fir forests and their replacement by low-value birch and aspen forests.

5. Conclusions

In the absence of harmful influences (industrial pollution sources, recreational loads, wildfires, and insect outbreaks), the coniferous forests in the study area grow and develop steadily. The dynamics of changes in the key tree stand characteristics support these findings.

Because of the low level of cone crops in all three types of coniferous forests, it is feasible to forecast a lack of seeds that will be necessary for the effective natural regeneration of fir under the forest canopy. Moreover, the long-term crop dynamics of fir cones are unpredictable. In various types of coniferous forests, statistically significant variations in the level of fir cone crops mostly occurred in years with medium- and high-cone crops. The coniferous forests growing on south-facing slopes with sustainably wetted humus-carbonate mountain-forest soil had the highest crop of cones during the same period.

The impact of meteorological factors on the fir cone crop did not appear to follow any clear trends. The fir cone crop and weather indications for the previous year and the current year for late winter and early spring (February and March) were positively and negatively correlated.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f16020234/s1, Table S1: Meteorological data from 47 years of observation at a weather land surface station in Duvan (Bashkortostan, Russia). A: average annual air temperature and average monthly air temperature; B: average annual precipitation and monthly precipitation.

Author Contributions: Conceptualization, A.D. and G.Z.; methodology, A.D. and G.Z.; software, A.D.; validation, A.D. and G.Z.; formal analysis, A.D. and G.Z.; investigation, A.D. and G.Z.; resources, G.Z.; data curation, A.D.; writing—original draft preparation, A.D. and G.Z.; writing—review and editing, A.D. and G.Z.; visualisation, G.Z.; supervision, G.Z.; project administration, G.Z.; funding acquisition, G.Z. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The original contributions presented in the study are included in the article/Supplementary Materials, and further inquiries can be directed to the corresponding author/s.

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

FSF (BFG)	Fir–spruce forests with big ferns and goutweed in the herbaceous layer.
FSF (SGM)	Fir–spruce forests with several species of sedge and green mosses in the herbaceous layer.
FF (HWSG)	Fir forests with goutweed, wood sorrel, and horsetail in the herbaceous layer.

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