

30-year cone production dynamics in Siberian stone pine (*Pinus sibirica*) in the southern boreal zone: a causal interpretation

Sergey Goroshkevich, Svetlana Velisevich, Aleksandr Popov, Oleg Khutornoy & Galina Vasilyeva*

Institute of Monitoring of Climatic and Ecological Systems, Siberian Branch of the Russian Academy of Sciences, Tomsk, Russia

*Corresponding author: galina_biology@mail.ru

Background and aims – Siberian stone pine is a keystone species for Siberia, and numerous studies have analyzed Siberian stone pine seeding dynamics in connection with the dynamics of weather conditions. However, all studies were based on observations before 1990. The aim of the study was to expand our knowledge about the balance of weather and climatic factors in the regulation of cone production to enable conclusions about the current reproductive function in Siberian stone pine.

Material and methods – We monitored Siberian stone pine cone production in the southeastern region of the Western Siberian Plain, in association with climatic factors, over a period of 30 years. To analyze the relationship with weather conditions, we used the trait mature cone number per tree and weather data obtained from the weather station in Tomsk.

Key results – During this period, cone production decreased by about one-third, mainly caused by the complete absence of high yields. The main factor negatively affecting cone production was late spring frost: severe frost occurring with a large accumulated sum of effective temperatures resulted in full cone loss, and light frost substantially reduced cone number. A less important but significant climatic factor was September temperature: as the temperature increased, the cone number decreased in the following year. Over the last 30 years, the sum of the effective temperatures at which the last spring frost occurs, as well as the average September temperature, increased considerably, resulting in reduced cone production.

Conclusion – If the current climatic trend is maintained, and especially if it is strengthened, Siberian stone pine cone production in the southern boreal forest zone on the Western Siberian Plane is unlikely to provide for the effective renewal of the species.

Keywords – Climate change; cone production dynamics; Siberian stone pine; spring frost; weather conditions.

INTRODUCTION

Cone production dynamics of forest tree species is of great importance for ecosystems, because seeds are essential for the reproduction of the species and they serve as a food resource (mast) for numerous forest animals. There are masting and non-masting tree species (Silvertown 1980; Norden et al. 2007), and masting can vary in severity and pattern (Kelly 1994).

Seed production is influenced by preceding seed production and weather conditions, and species differ

in the relative role of the factors (Pearse et al. 2016). Numerous studies have investigated the influence of weather conditions on the fruiting (seeding) of forest trees. However, controversial and discrepant results impede generalization (Burns 2012; Crone & Rapp 2014; Roland et al. 2014; Zamorano et al. 2018). Many growth traits are influenced by weather conditions over the course of weeks, months, and even years (Speer 2010). Long-term trends in weather changes are, undoubtedly, also important for fruiting (Carevic et al. 2010; Pérez-Ramos et al. 2014; Roland et al. 2014; Buechling et al. 2016; Nussbaumer et al. 2018).

© 2021 Sergey Goroshkevich, Svetlana Velisevich, Aleksandr Popov, Oleg Khutornoy, Galina Vasilyeva.

This article is published and distributed in Open Access under the terms of the [Creative Commons Attribution License \(CC BY 4.0\)](https://creativecommons.org/licenses/by/4.0/), which permits use, distribution, and reproduction in any medium, provided the original work (author and source) is properly cited.

Plant Ecology and Evolution is published by Meise Botanic Garden and Royal Botanical Society of Belgium
ISSN: 2032-3913 (print) – 2032-3921 (online)

However, short-term weather events are crucial in many cases. For instance, a complete absence of seed production is often associated with the negative impact of a single late frost (Sork et al. 1993; Houle 1999; Juday et al. 2003; Pons & Pausas 2012). Forest tree species differ greatly in patterns of year-to-year seed production dynamics, and not all of these differences can be satisfactorily interpreted (Koenig & Knops 2005; Burns 2012; Pearse et al. 2016). Plant science is currently still at the stage of information accumulation, which precedes the generalization stage. Therefore, the continuation of such studies, especially on for example ecologically important species with vast ranges, is relevant.

Siberian stone pine (*Pinus sibirica* Du Tour) is widespread, mainly in Russia. It is the main tree species that forms the most productive Siberian forest ecosystems. The special importance of Siberian stone pine is determined by its nut production. The large and nutritious pine nuts (on average, 260 mg) are agents for species renewal, food resources for many forest animals, and a valuable food product for humans. Primack (1998: 44) provided the following definition of keystone species: “Within biological communities, certain species may determine the ability of a large number of other species to persist in the community”. Siberian stone pine is undoubtedly a keystone species for Siberia, and numerous studies have analyzed Siberian stone pine seeding dynamics in connection with the dynamics of weather conditions (Nekrasova 1972, 1983; Iroshnikov 1974; Vorobjev 1983; Nesvetajlo 1987; Vorobjev et al. 1989; Tretyakova 1990). There are, however, abundant discrepancies in the articles, although they deal with the same species. Moreover, these studies were based on observations during a period of relatively stable climate, before 1990, and novel data were not published.

In this paper, we present observations from a period of 30 years under the “new climate”. These data were obtained by annual monitoring of the representative tree samples. The aim of the study was to expand our knowledge about the balance of weather and climatic factors in the regulation of cone production to enable conclusions about the current reproductive function in Siberian stone pine in the south of the boreal zone and to predict cone production against the background of a changing climate.

MATERIAL AND METHODS

The study was carried out in the south eastern part of the West Siberian Plain, 20 km southwest of Tomsk (fig. 1). According to the Köppen-Geiger climate classification scheme, it is on the boundary of subarctic or boreal and warm summer continental or hemiboreal climates. According to the Tomsk weather station, the mean annual temperature was +1.16°C and annual precipitation was 577 mm for the last 30 years. It is located in the south of the boreal forest and at the extreme south of the Siberian stone pine range. Therefore, Siberian stone pine only occurs in valleys of small rivers. Our study site is located in the valley of one of these rivers, the Poros, where we studied a Siberian stone pine stand on the first floodplain terrace near the settlement Nizhne-Sechenovo. In such forest, local villagers fell deciduous trees (mainly birch and aspen) and preserved conifers (Siberian stone pine and

fir). This results in an open forest canopy and low crowns for Siberian stone pines. The soil is deep, loamy, fertile, and well moistened.

The Siberian stone pine stand had a minor admixture of *Abies sibirica* Ledeb. The medium dense undergrowth consists mainly of *Sorbus sibirica* Hedl., *Rosa cinamomea* L., *Rubus idaeus* L., *Spiraea chamaedrifolia* L., *Rhamnus frangula* L., and *Padus racemosa* Gilib. The soil cover is dominated by *Carex macroura* Miensh., *Majanthemum bifolium* (L.) F.W.Schmidt, and *Oxalis acetosella* L. Moss cover occurs in separate small spots near trunks and stumps. On average, the trees were 180–220 years old, with a height of 23 m and a stem diameter at breast height of 64 cm. Canopy density was approximately 50%.

Thirty trees, with a mean height of ± 2.5 m and a mean stem diameter of ± 5 cm, were evaluated. In the study, trees were selected randomly. All trees were located on a flat area of about one hectare in the same soil and hydrological conditions.

The number of the mature cones was determined annually from 1990 to 2019, immediately after cone ripening, from August 10 to 15. Mature cones of the Siberian stone pine are easily separated from the branches. Cones were shaken from tree branches with traditionally used tools (wooden cosh and wooden rod) and the number of cones on the ground was then determined. To analyze the relationship between reproductive output and weather conditions, we used the trait mature cone number per tree.

Weather data were obtained from the weather station in Tomsk, which belongs to the Russian Federal Service for Hydrometeorology and Environmental Monitoring (Roshydromet) and is located 20 km north of the studied site. The relationships between cone number and the following meteorological parameters were analyzed:

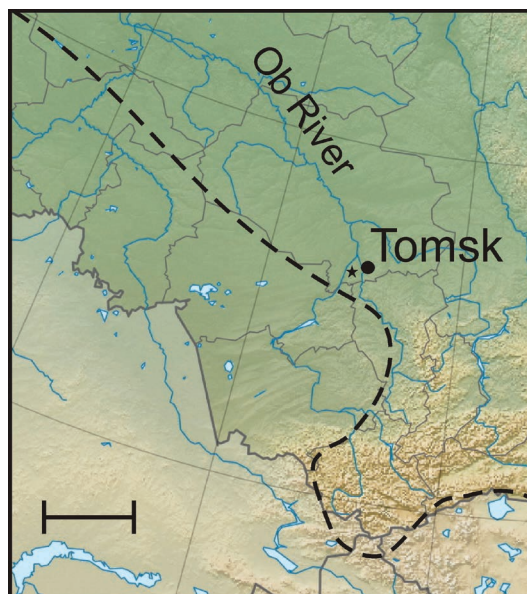


Figure 1 – The location of the study area is marked by an asterisk. The dashed line indicates the southern boundary of the geographic distribution of *Pinus sibirica*. The bar represents 400 km.

- mean monthly precipitation sum (from April to September);
- precipitation sum during the vegetation period (April to September), year (vegetation period and previous 6 months), 1.5 years (vegetation period and previous 12 months), and 2 years (vegetation period and previous 18 months);
- sum of annual effective temperatures, represented by the sum of the positive differences between diurnal mean temperatures and 5°C (SET) for the year;
- mean monthly temperature sum (from April to September);
- mean temperature over 10 days (from April to September);
- SET before spring frost from -4.6 to -6.0°C, from -3.1 to -4.5°C, from -1.6 to -3.0°C, and from -0.1 to -1.5°C. Therefore, frost was considered in view of the accumulated SET.

In total, 39 meteorological parameters were analyzed in the seed cone initiation year ($t-2$), the pollination year ($t-1$), and the maturation year (t). To analyze the relationship between weather condition and mature cone number, Spearman’s correlation coefficient was used. In total, 117 (39×3) correlation coefficients were computed, and those which reached statistical significance ($p < 0.05$) are presented with an asterisk in the Results section.

Generally, complete variational series including data for all years are used to analyze the effects of weather conditions on cone or seed production. However, if some factor has already shown an impact, for example, fully impeded the initiation of reproductive structures, this can greatly distort the results. In case it can be proved that a certain factor completely destroyed the cones at a relatively early stage of their development, it is reasonable to exclude this generation of cones from the variational series used for the analysis of factors acting at later developmental stages. We applied the

following principle, after establishing the cause of full (or almost full) loss of cones, the given generation of cones was excluded from further analysis.

RESULTS

Cone number per tree ranged from 0 to 740 in different years (fig. 2). Mean cone number per tree was 314, with a standard deviation of 230 and a coefficient of variation of 73%. When dividing this range into several parts, then distribution will be highly unusual (fig. 3). The graph shows three pronounced unequal peaks in the area of low, medium, and high cone production. Thus, cone number distribution was platykurtic, positively skewed, but without any tendency to bimodality.

Low cone production (< 200 cones per tree) was often observed with equal frequency, while high cone production (> 600 cones per tree) was rare and occurred only before 2007; after this, cone production was never higher than 500 cones per tree. Therefore, during the 30-year observation period, the tendency to reduced cone number per tree first appeared and then increased; mean cone number per tree was 358, 343, and 243 in the first, second, and third decade, respectively. Basic climatic characteristics did not show a similarly pronounced trend: the average annual temperature was 1.06, 1.27, 1.16°C; the annual precipitation was 555, 602, and 575 mm in the first, second, and third decade, respectively.

There was no correlation between cone number in the year t and in the year $t-2$ ($r = -0.07$). Also, cone number in year $t-1$ and total cone number in the two previous years ($t-2$ and $t-1$) were not related with cone number in year t , $r = -0.26$ and $r = -0.30$, respectively; correlation coefficients did not reach statistical significance.

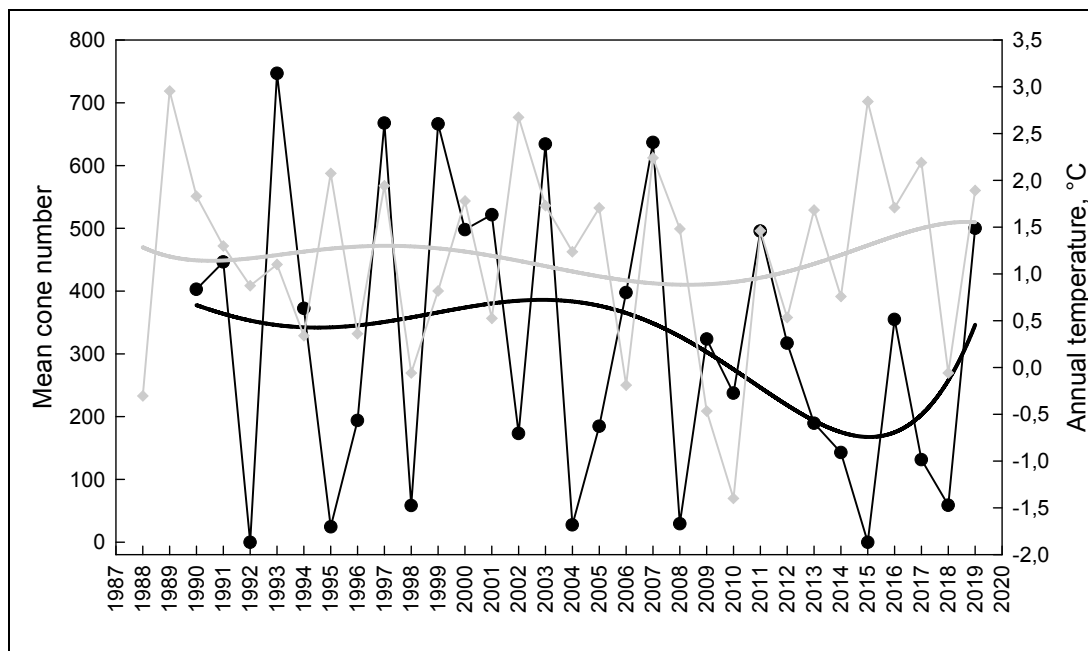


Figure 2 – Cone production and annual temperatures dynamics: mean cone number per tree (black line with data points) and 5-year moving average with polynomial approximation (black bold smooth line); annual temperatures, °C (grey line with data points) and 5-year moving average with polynomial approximation (grey bold smooth line).

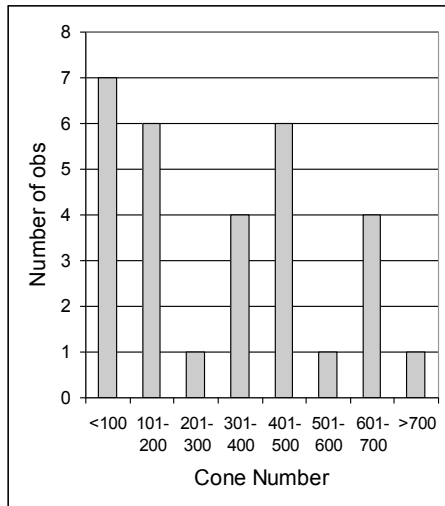


Figure 3 – Frequency of cone number observed during the 30-year period.

There were no correlations between cone number in year t and any climatic parameters in years $t-2$ and t . Also, no correlations were observed between any precipitation sum, SET, mean monthly temperature sum (from April to September), mean temperature over 10 days (from April to September) in year $t-1$ and cone number in year t .

The main factor determining cone production dynamics was the late spring frost in year $t-1$. Depending on frost temperature and accumulated SET, the frost either fully annihilated the cones or did not affect their development at all, with one exception, described below.

Severe frost (temperatures from -4.6 to -6.0°C) occurred once (in 1994), when a large sum of effective temperatures (81°C) had already been accumulated (fig. 4A). This determined an extremely low (24 cones per tree) cone production in 1995. In all other years, the last severe frost occurred at the accumulation of the sum of effective temperatures less than 50°C , with no effect on cone production in the following year. As the extremely low

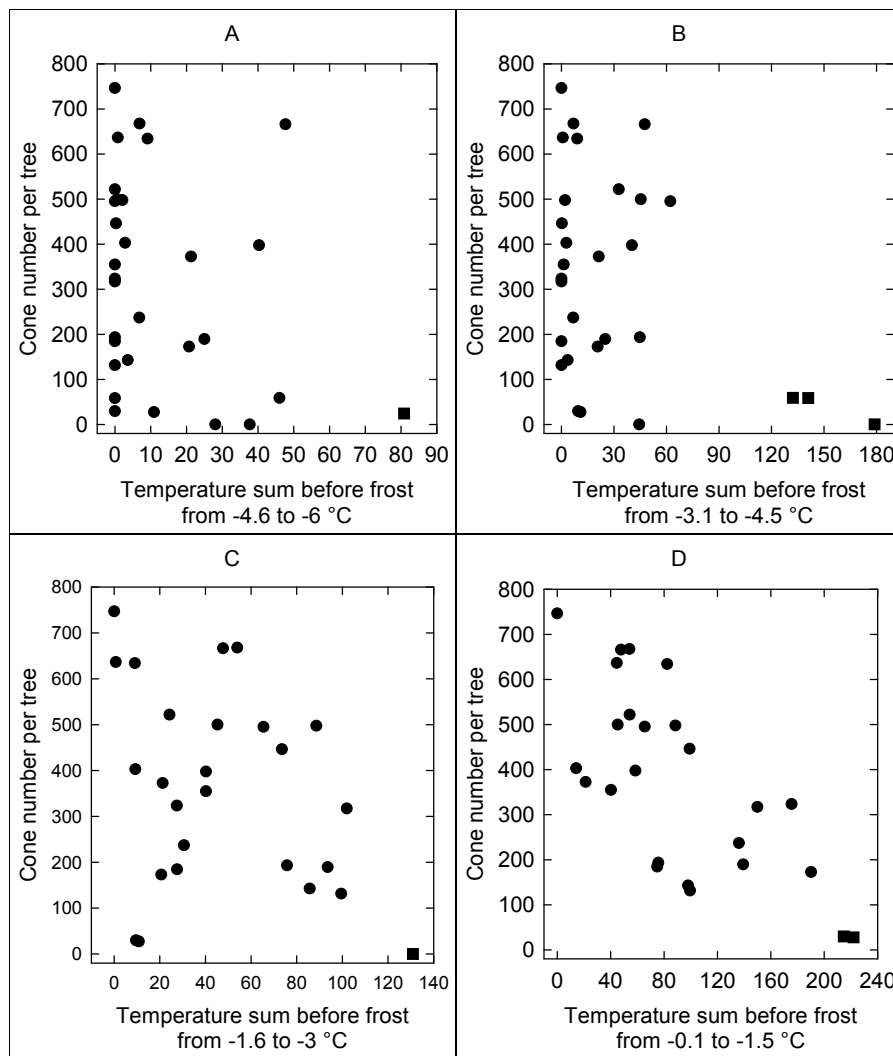


Figure 4 – Relationship between cone number and sum of average daily temperatures above 5°C before the last spring frost from -4.6 to -6.0°C (A), from -3.1 to -4.5°C (B), from -1.6 to -3.0°C (C), and from -0.1 to -1.5°C (D) in the year of pollination. Square markers indicate years with low or no cone production, explained by the given weather factor.

cone production in 1995 was explained by the given factor, analysis of the other factors was carried out in a residual sample consisting of 29 years.

Slightly lower severe frosts (temperature from -3.1 to -4.5°C) occurred three times (in 1991, 1997, and 2017), when the SET was 179, 141, and 132°C , respectively (fig. 4B). This resulted in zero (in 1992) or very low cone production (58 and 59 cones per tree) in 1998 and 2018, respectively. In all other years, the last severe frost occurred with the accumulation of SET less than 63°C , with no impacts on cone production in the following year. As the low cone production in 1992, 1998, and 2018 was explained by this frost, analysis of the other factors was carried out in a residual sample consisting of 26 years.

Only once in 26 years (in 2014), the temperature dropped to 1.6 – 3.0°C below zero, when the SET was 131°C (fig. 4C). This resulted in a lack of cones in 2015. In all other years, the last severe frost occurred with an SET accumulation below 100°C , without an impact on cone production in the following year. Thus, the frost in 2014 explained the lack of cones in 2015, and analysis of the other factors was carried out in a residual sample consisting of 25 years.

Light frost (temperatures from -0.1 to -1.5°C) occurred twice (in 2003 and 2007) over 25 years, at relatively high SET values of 222 and 215°C , respectively (fig. 4D). This resulted in low cone production in 2004 and 2008, with 28 and 30 cones per tree, respectively. In contrast to more severe frost (1.6 – 6.0°C below zero), light frost (up to -1.5°C) had a different impact. With increasing SET values before the frost was accumulated, the cone number decreased ($r = -0.71^*$).

After removing 2004 and 2008 from the analysis, the correlation was still significant ($r = -0.62^*$) in the residual sample of 23 years. When frost occurred after the SET had reached 100°C , cone number was always below the mean value. This factor explained the low cone production (< 250 cones per tree) in 3 out of 7 years, namely in 2001, 2011, and 2012. In contrast, maximal cone number during the 30-year period (747 cones per tree) was observed in 1993, most likely because there was no spring frost after the first day with a mean temperature above $+5^{\circ}\text{C}$ in year $t-1$.

The last significant factor was mean temperature of September in year $t-1$. As the temperature increased, the cone number in the following year decreased ($r = -0.44^*$, fig. 5). A warm September (mean temperature higher than 11°C) resulted in a low cone production (up to 200 cones per tree) in the following years (2012 and 2016). In contrast, a cool September (mean temperature less than 7°C) resulted in a high cone production (> 650 cones per tree) in 2003, 2007, and 2009.

As shown above, the pronounced reduction of cone number in the second half of the observation period can be explained by the absence of years with high cone production rather than an increased frequency of years with low cone production. Weather factors leading to a low cone production, namely severe frost with a high accumulated SET, did not show any tendency during the 30-year period. However, both factors that ensure some seeding but substantially decrease cone number showed a certain tendency (fig. 6). Light frost (from -0.1 to -1.5°C) when the SET was higher than 130°C

occurred three times during the first 15 years and eight times during the second 15 years. For the first 18 years, before 2006, when the last high cone production was observed, the mean September temperature was above 10°C only four times, while for the last 12 years, this occurred five times. This is a small difference, but they can contribute to the cone number reduction. Thus, decreasing cone production resulted from changes in the frequency of both these climatic factors.

DISCUSSION

Instability of seed production in long-term year-to-year dynamics is a general characteristic of many perennial plant species and does not prevent successful reproduction (Herrera et al. 1998; Schaubert et al. 2002). Regular fruiting can be deleterious for the reproduction of plants whose seeds are used by animals as food (Crawley & Long 1995; Krebs et al. 2009, 2010).

On the contrary, irregularity of fruiting by year allows these species to live and to successfully reproduce. Hence, this characteristic is an adaptive trait and is maintained by natural selection (Silvertown 1980; Visser et al. 2001). As a rule, populations of the seed predators are substantially reduced in lean years because of a lack of food reserves (Kataev 2012; Krebs et al. 2014; Bogdziewicz et al. 2015), which results in abundant seedlings in the mast year following the lean year (Visser et al. 2001; Crone & Rapp 2014). Siberian stone pine seeds are the basis of several food chains in Siberian forest ecosystems. Therefore, this is no surprise that seed production of this species is characterized by irregularity and high variability in year-to-year dynamics. A previous study has shown this for relatively short period of 18 years (Goroshkevich 2017), and here, we show this for a 30-year period.

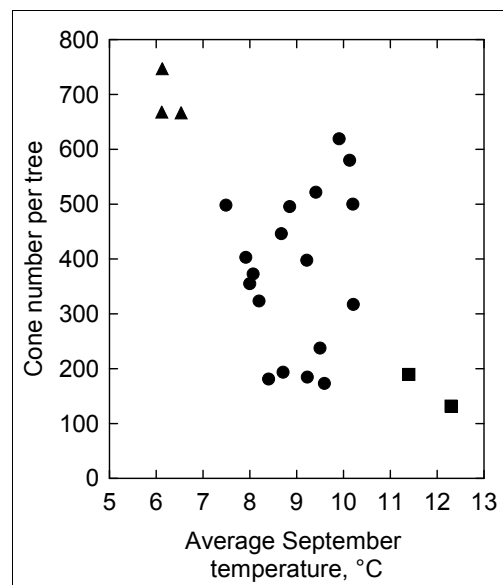


Figure 5 – Relationship between cone number and average September temperature in the year of pollination. Square markers indicate years with low or no cone production, and triangular markers indicate years with high cone production, explained by the given weather factor.

Masting and non-masting species are no discrete categories. Kelly (1994) recognized three types of masting patterns: (1) strict masting, with bimodal mast production of either zero or large quantities of seeds, in spite of continuous environmental variations; (2) normal masting, under which either bimodal mast year distributions are statistically significant or there is evidence for diversion of plant resources from vegetative growth to reproduction; and (3) putative masting, indicated by a high annual variation in reproduction but without bimodal mast year distribution

or evidence of resource switching. In fact, the third pattern is intermediate between masting and non-masting. A year-to-year seeding dynamics was revealed in Siberian stone pine, i.e. cone production distribution was platykurtic, slight positive skewed, but without any tendency to bimodality. The seed cone development cycle of Siberian stone pine extends over more than two years or three vegetation seasons, with cone initiation year, pollination year, and maturation year. For this reason, we focus on the results within the 3-year cycle.

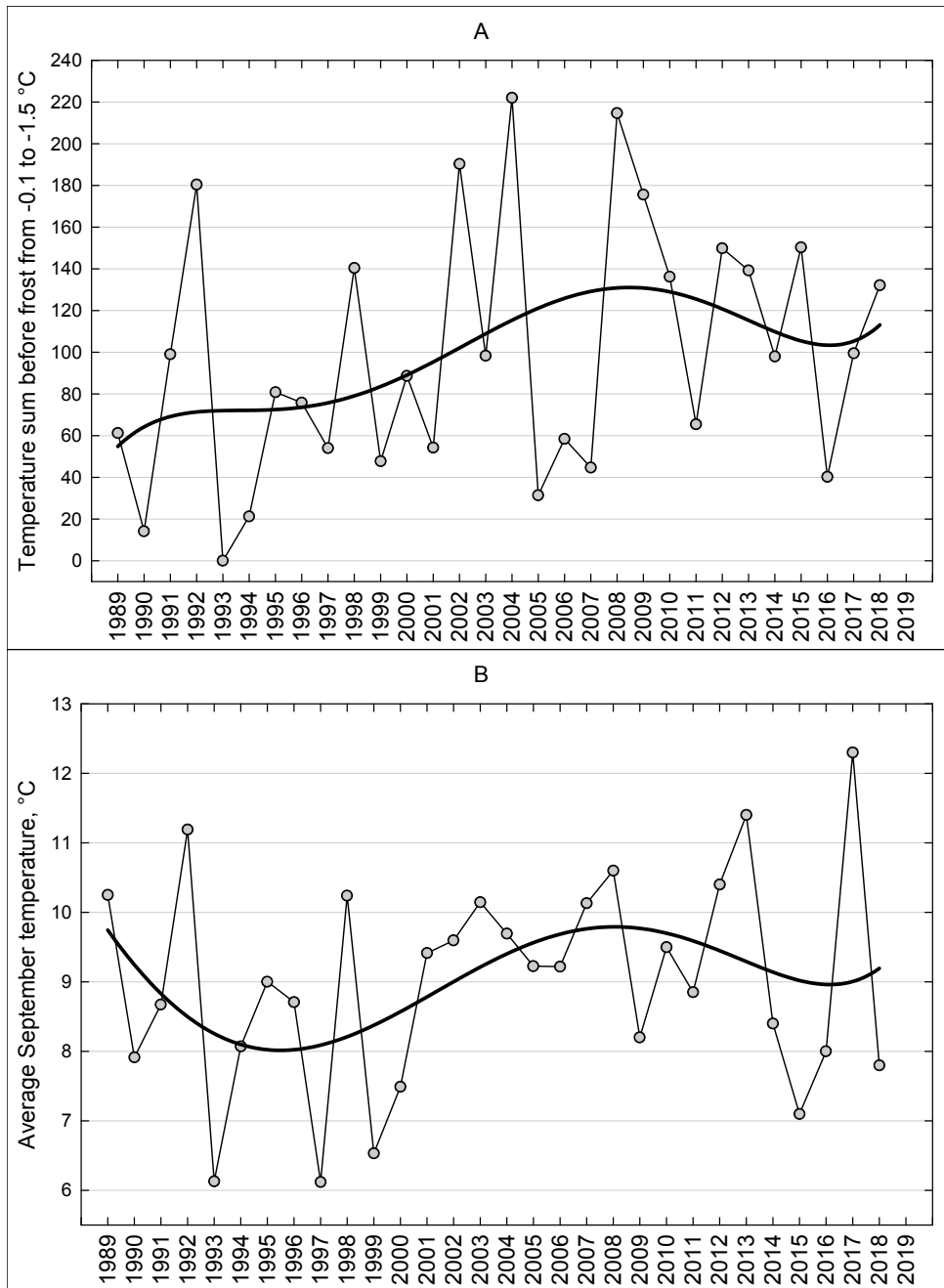


Figure 6 – Sum of average daily temperatures above 5°C before the last spring frost from -0.1 to -1.5°C (A) and average September temperatures (B) in the pollination year during the 30-year period. Actual data (line with data points) and 5-year moving average with polynomial approximation (bold smooth line).

Cone initiation year

The initial cone number is usually considered as the most important factor of matured cone number. The fundamental basis for mast seeding is a plant's available number of limiting resources, and if sufficient, the plant will allocate some portions of its resources to reproductive structure initiation, with different concepts of resource dynamics such as resource matching, resource depletion, or resource switching (Crone & Rapp 2014; Pearse et al. 2016). However, Silvertown (1980) showed that most tree species (43 out of 67 studied species) are non-masting species, i.e. seeding (fruiting) occurs almost every year without any resource matching, depletion, or switching. Undoubtedly, annual initiation of reproductive structures precedes annual seeding. It is still unclear why masting species do not have the same annual initiation of reproductive structures. One explanation might be that the depletion of resources in the mast years is much more pronounced than that with regular fruiting in non-masting species.

A previous study of Siberian stone pine showed that in masting species, at least in putative masting ones, annual and abundant initiation of reproductive structures is possible (Goroshkevich 2008). In the stand studied here, the number of initiated seed cones per shoot varied from 1.88 to 2.86, and the coefficient of variation was 11%. These results were obtained by the retrospective study of cone initiation and maturation dynamics, using scars on the branch bark (Vorobjev et al. 1994; Redmond et al. 2016). Low variability in cone initiation was recorded in other locations of Siberian stone pine, including the most northern part of the boreal zone (Mishukov 1972).

There is substantial information about the effects of various factors in the reproductive structure initiation year on seed production in different tree species. First, the weather conditions and number of maturing reproductive structures in the initiation year and/or in the previous year play an important role (Krebs et al. 2009; Roland et al. 2014; Bisi et al. 2016; Buechling et al. 2016). However, this was not observed in our study. Mature cone number did not depend on the cone number in the previous two years; it neither depended on the weather conditions in year $t-2$ year. In Siberian stone pine trees in this location, mature cone number did not depend on the initiated cone number that always ready to provide a high yield. Quite possibly, this is not related to favourable climatic and soil conditions, but might be a part of the reproductive strategy of the species.

Cone pollination year

In boreal five-needle pines, pollen cones are usually differentiated in the initiation year and spend the winter in the archesporium stage, while seed cones spend the winter as undifferentiated primordia (Owens et al. 2008). In this respect, Siberian stone pine is a typical five-needle pine (Nekrasova 1983).

Spring development of both pollen and seed cones was traditionally considered as the most crucial and vulnerable stage of the reproductive cycle (Owens & Blake 1985). The importance of this period is determined by processes preceding flowering and the flowering itself, and

vulnerability is governed by coinciding with the season when frosts are possible. Based on a previous study, spring frost can damage pollen and seed cones (Houle 1999; Juday et al. 2003). However, the severity of the damages can be different, ranging from reduced pollen quality to the full loss of reproductive structures (Stephenson 1981). Late frosts that occur during the second division of meiosis, prior to flowering and the flowering itself, are especially dangerous (Philipson 1997; Owens 2006, 2008).

Spring phenology in Siberian stone pine is shifted 10–40 days later compared to other Pinaceae species (Nekrasova 1983). However, spring frosts can affect the reproductive structures in the species. For instance, numerous cases of partly or completely dead pollen and seed cones caused by frost in both budding and flowering periods have been noted in the mountains of South Siberia (Iroshnikov 1974; Vorobjev 1983). In this region, frost during the second division of meiosis dramatically decreased pollen quantity and quality and, hence, final seed yield (Tretyakova 1990). On the plain in the southern part of the forest zone, spring frost is not dangerous for microstrobili and cone development in the pollination year (Nekrasova 1972). Our results revealed that the most crucial environmental factor affecting the reproductive structure in the pollination year is early frost, prior to the second (and sometimes the first) division of meiosis. There are, however, no publications on the effect of early frost on developing cones in any pine species.

Evolution results in the conformity between annual tree cycles and climatic cycles, and physiological processes interact with environmental signals to optimize the beginning of bud development, taking into account the possibility of late spring frost (Inouye 2000; Delpierre et al. 2016). Growth processes are instigated by early long thaw in some years. Cells and tissues lose their resistance to low temperatures and can easily be damaged when frost resumes. Bud scales defend the bud content only during light, short frosts (up to -3°C) while more severe and longer frosts can destroy the reproductive structure. In Siberian stone pine cone production, climatic adaptation occurs, but there is no reason to assume that this pattern is universal.

Irregular cone production is a crucial adaptive trait. Plant species differ in the time of the onset of this irregularity, at the initiation stage or later during the development process (Pallardy 2007; Pearse et al. 2016). The latter is characteristic to Siberian stone pine; abundant cone initiation occurs yearly (Goroshkevich 2008) and is an effective strategy because a low number of resources is spent on cone primordium initiation. Irregular cone production is provided by the loss of initiated cones in 3 out of 4 years. It is reasonable to assume that the earlier such loss occurs, the more resources can be saved. The optimal time for this loss is early spring in the pollination year, when the probability of fatal frost is high. The mechanism of irregular cone production consists of the correlation between SET accumulation in spring and the seasonal cycle of reproductive structure development, which is fixed in the population's gene pool. Due to this correlation, initiated cones avoid the fatal spring frost only once every few years. Frost damage is tissue-specific (Inouye 2000), and the reproductive organs generally more sensitive to frost than the vegetative ones (Sakai & Malla 1981). The death of

young vegetative shoots caused by low temperatures can be fatal for the plant, and such shoots are therefore not damaged by spring frost. If regular fruiting was necessary for the species, natural selection would result in fruiting irrespective of the influence of frost.

The statement that only late spring frost is dangerous for the development of cones (e.g. Owens 2006, 2008) is based on the premise that the sensitivity of reproductive tissues to frost increases as they develop. This was also observed in the current study. Seed cones were lost when temperature decreased up to -4.5°C at an SET of about 75°C . Light frost (up to -1.5°C) resulted in the full loss of cones when the SET was above 200°C and in a partly loss when the SET was $140\text{--}180^{\circ}\text{C}$.

Weather conditions in autumn have, so far, not been considered as limiting the cone development in *Pinus* species. In our study, autumn weather conditions, namely in September, significantly affected the final seed yield; with increasing temperatures, cone loss also increased. However, the underlying mechanism is still unclear.

To understand this issue, we provide an analogy with vegetative shoot growth. In many tree species of the temperate zone, abnormal late season shoots (lammas, proleptic or sylleptic) originated from buds that were supposed to start growing only after a period of winter dormancy (Pallardy 2007). These shoots are often damaged by autumn and winter frosts because of incomplete lignification. Abnormal late-season shoots are formed at the end of the vegetation season when favourable weather conditions occur again (Kaya et al. 1994). Abnormal shoot formation varies year-to-year and correlates with the weather conditions in late summer and early autumn (Hallgren & Helms 1988).

It is commonly believed that the cessation of primary shoot growth and bud-set is controlled by the photoperiod, acting on phytochromes in most of the temperate tree species (Tanino et al. 2010; Way 2011). However, experiments showed that temperature also takes part in this process in many temperate and boreal tree species (Salminen & Jalkanen 2007; Rohde et al. 2011).

Abnormal late-season cone growth in the pollination year, i.e. reproductive lammas growth, has been described in Siberian stone pine as a rare aberration (Iroshnikov 1974; Tretiyakova & Lukina 2016). The ovules in the abnormal cones are fully collapsed, and the sound seeds are not formed. It is reasonable to suppose that abnormal activity, not visible by naked eye, in the conelet is instigated by warm September weather, and subsequent frost damage of the conelets is therefore more common.

Cone maturation year

In Siberian stone pine, overwintered seed cones are aborted much less frequently than conelets, and yield forecast based on conelet number before winter is therefore reliable (Nekrasova 1972). Nevertheless, cone and fruit loss caused by various climatic factors in the maturation year are observed in different forest tree species (Kelly & Sork 2002; Pearse et al. 2016; Nussbaumer et al. 2018). In our study, however, cone loss in the maturation year did not occur because of the spring frost, which resulted in conelet loss.

Frost damage is common and generally specific to certain developmental stages (Inouye 2000). Cone resistance to frost is quite efficient, mainly because large amounts of nutrients have already been used up, and the seeds will mature within a few months. It is reasonable that crucial processes in cones occur beyond the frost-hazardous period, and natural selection maintains this adaptive trait.

ECOLOGICAL INTERPRETATION

The economy of scale hypothesis is the main hypothesis for the evolution of mast seeding (Silvertown 1980; Kelly 1994; Burns 2012). Predator satiation is the main economy of scale: the proportion of seeds consumed by seed predators is inversely correlated with the number of seeds produced (see review by Kelly & Sork 2002). Most conifers are wind-dispersed and therefore benefit from low seed predator numbers in years with a high seed production. For this reason, there are strict or normal masting species (sensu Kelly 1994) when mast years occur after several non-mast years. If seed production is regulated by the weather, then it should be large-scale (macroclimatic) factors, such as temperature and precipitation that have the highest impact.

Animal dispersal in conifer species does not benefit from strict masting, because for successful reproduction, a minimal population of seed predators and a sufficient number of scatter-hoarding animals are needed in years with a high seed production. Seed predators are generally sedentary (rodents and others), while disseminators are generally nomadic (birds). Temporal variations in seed production, with a pronounced dynamics of sedentary seed predator numbers and a pronounced spatial variation of seed production, resulting in smooth dynamics of nomadic disseminator numbers, are vital for animal-dispersed conifer species. Temporal and spatial variations are regulated by inconstant weather factors, namely spring frost. The only stone five-needle pine disseminators are nutcracker species of the genus *Nucifraga* sp. (Lanner 1982; Barringer et al. 2012). In this regard, it is not surprising that spring frost in the year of flowering is the main regulator of cone production dynamics in Siberian stone pine.

Climatic changes and cone production

Many researchers fear that climatic change can impact seed production in boreal and temperate forest tree species (Lindner et al. 2010; Roland et al. 2014; Bisi et al. 2016). Indeed, the reproductive effort mainly decreased (Pearse et al. 2017). However, some studies have shown its increase (Richardson et al. 2005; Buechling et al. 2016). Inter-annual variation in seed production increased in most cases over time (Pearse et al. 2017), and there are data showing its decrease (Bogdziewicz et al. 2020). There are, therefore, different forecasts with contrasting results (LaDeau & Clark 2001; Hoch et al. 2013). This inconsistency is mainly a result of the differences in tree species and environmental conditions.

Researchers sometimes associate the observed changes in seed production year-to-year dynamics with the climate elements that are available for climate change scenarios (Zwiers et al. 2013), including the North Atlantic Oscillation

(Fernández-Martínez et al. 2017). More often annual or seasonal temperatures and precipitation, which can be predicted with a certain degree of reliability in future climate change scenarios, are used (Maslin & Austin 2012).

Such events, including spring frosts, are, however, rarely discussed; an exception is the occurrence of enormous economic damage, which has been reported by Vitasse & Rebetez (2018). In Switzerland and Germany, April 2017 was very warm, and plants started growing early. However, dry and cold Arctic air entered the region from April 20 to 24. Several morning frosts damaged wild and cultivated plants, particularly in orchards and vineyards. The economic costs amounted to about 3.3 billion euros. This was an extraordinary event, and the frequency of frosts dangerous to plants has not changed significantly over the last 150 years.

The same event (the so-called “false spring”), with damages up to 1.6 billion dollars, occurred in April 2007 in the eastern USA (Marino et al. 2011). Retrospective analysis of the weather conditions over the last 100 years in this case also does not show any pronounced general tendency to increase the SET at which frosts dangerous to plants occurred. However, some local tendency in some regions was revealed. Global warming is not only characterized by higher temperatures, but also by an increased temperature variability and a higher fluctuation range (Rigby & Porporato 2008).

Our results show that year-to-year dynamics of cone production can be explained only by short-time weather events in some cases. It is reasonable to assume that, against the background of a changing climate, a change in cone production will occur. The frequency of severe spring frost has not increased over the 30 years evaluated here. Hence, the frequency of near-zero cone production in Siberian stone pine also did not increase. However, the frequencies of both high temperature sum before frost from -0.1 to -1.5°C and warm Septembers, which impede the occurrence of mast years, significantly increased, resulting in an overall decline of cone production.

CONCLUSION

In Siberian stone pine in the southern part of the Western Siberian boreal zone, year-to-year dynamics of cone production are determined by short-time weather events in the pollination year. We identified three crucial periods in reproductive structure development:

- the first half of spring (when a large SET is accumulated, severe frost results in full loss of seed cones);
- the second half of spring (light May frost leads to partial seed cone loss);
- the first half of autumn (warm September days result in partial seed cone loss).

During the first period, it is determined whether or not cones will be produced in the following year, while during the second and third periods, the cone amount in the following year is determined. The sum of the effective temperatures at which the last spring frost occurs, as well the average September temperature, have increased substantially over the past 30 years, resulting in a significant reduction in

cone production. In general, abundant seedlings of Siberian stone pine are produced after real mast years. If the current climate is maintained, especially if the mentioned trends are strengthened, Siberian stone pine cone production in the southern boreal forest zone on the Western Siberian Plain is unlikely to provide for the effective renewal of the species.

REFERENCES

- Barringer L.E., Tomback D.F., Wunder M.B. & McKinney S.T. 2012. Whitebark pine stand condition, tree abundance, and cone production as predictors of visitation by Clark's nutcracker. *PLoS ONE* 7(5): e37663. <https://doi.org/10.1371/journal.pone.0037663>
- Bisi F., Von Hardenberg J., Bertolino S., et al. 2016. Current and future conifer seed production in the Alps: testing weather factors as cues behind masting. *European Journal of Forest Research* 135: 743–754. <https://doi.org/10.1007/s10342-016-0969-4>
- Bogdziewicz M., Zwolak R. & Crone E.E. 2015. How do vertebrates respond to mast seeding? *Oikos* 125(3): 300–307. <https://doi.org/10.1111/oik.03012>
- Bogdziewicz M., Kelli D., Thomas P.A., Lageard J.G.A. & Hackett-Pain A. 2020. Climate warming disrupts mast seeding and its fitness benefits in European beech. *Nature Plants* 6(2): 88–94. <https://doi.org/10.1038/s41477-020-0592-8>
- Buechling A., Martin P.H., Canham C.D., Shepperd W.D. & Battaglia M.A. 2016. Climate drivers of seed production in *Picea engelmannii* and response to warming temperatures in the southern Rocky Mountains. *Journal of Ecology* 104(4): 1051–1062. <https://doi.org/10.1111/1365-2745.12572>
- Burns K.C. 2012. Masting in a temperate tree: evidence for environmental prediction. *Austral Ecology* 37(2): 175–182. <https://doi.org/10.1111/j.1442-9993.2011.02260.x>
- Carevic F.S., Fernández M., Alejano R., Vázquez-Piqué J., Tapias R. & Corral E. 2010. Plant water relations and edaphoclimatic conditions affecting acorn production in a holm oak (*Quercus ilex* L. ssp. *ballota*) open woodland. *Agroforestry Systems* 78: 299–308. <https://doi.org/10.1007/s10457-009-9245-7>
- Crawley M.J. & Long C.R. 1995. Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. *Journal of Ecology* 83(4): 683–696.
- Crone E.E. & Rapp J.M. 2014. Resource depletion, pollen coupling, and the ecology of mast seeding. *Annals of the New York Academy of Sciences* 1322: 21–34. <https://doi.org/10.1111/nyas.12465>
- Delpierre N., Vitasse Y., Chuine I., et al. 2016. Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models. *Annals of Forest Science* 73: 5–25. <https://doi.org/10.1007/s13595-015-0477-6>
- Fernández-Martínez M., Vicca S., Janssens I.A., Espelta J.M. & Peñuelas J. 2017. The North Atlantic Oscillation synchronises fruit production in European forests. *Ecography* 40(7): 864–874. <https://doi.org/10.1111/ecog.02296>
- Goroshkevich S.N. 2008. Dynamics of growth and seed production in the Siberian stone pine: the level and pattern of variation in characters. *Russian Journal of Ecology* 39(2): 170–177. <https://doi.org/10.1134/S1067413608020033>
- Goroshkevich S.N. 2017. Dynamics of Siberian stone pine (*Pinus sibirica* Du Tour) growth and seed production: cyclicality or acyclic oscillation? *Tomsk State University Journal of Biology*

- 38: 104–120. [In Russian, English summary].
<https://doi.org/10.17223/19988591/38/6>
- Hallgren S.W. & Helms J.A. 1988. Control of height growth components in seedlings of California red and white fir by seed source and water stress. *Canadian Journal of Forest Research* 18(5): 521–529. <https://doi.org/10.1139/x88-076>
- Herrera C.M., Jordano P., Guitián J. & Traveset A. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *The American Naturalist* 152(4): 576–594. <https://doi.org/10.1086/286191>
- Hoch G., Siegwolf R.T., Keel S.G., Körner C. & Han Q. 2013. Fruit production in three masting tree species does not rely on stored carbon reserves. *Oecologia* 171(3): 653–662. <https://doi.org/10.1007/s00442-012-2579-2>
- Houle G. 1999. Mast seeding in *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* in an old growth, cold temperate forest of north-eastern North America. *Journal of Ecology* 87: 413–422. <https://doi.org/10.1046/j.1365-2745.1999.00352.x>
- Inouye D.W. 2000. The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters* 3(5): 457–463. <https://doi.org/10.1046/j.1461-0248.2000.00165.x>
- Iroshnikov A.I. 1974. Polymorphism of Siberian stone pine populations. In: Minina E.G. & Iroshnikov A.I. (eds) Variability of woody plants in Siberia: 77–103. Institute of Forestry and Timber SB USSR Academy of Sciences, Krasnoyarsk. [In Russian].
- Juday G.P., Barber V., Rupp S., Zasada J.C. & Wilmking M. 2003. A 200-year perspective of climate variability and the response of white spruce in interior Alaska. In: Greenland D., Goodin D.G. & Smith R.C. (eds) Climate variability and ecosystem response at long-term ecological research sites: 226–250. Oxford University Press, Oxford.
- Kataev G.D. 2012. Population monitoring of small mammals in the Kola peninsula over 75 years. *Russian Journal of Ecology* 43(5): 406–408. <https://doi.org/10.1134/S1067413612050086>
- Kaya Z., Adams W.T. & Campbell R.K. 1994. Adaptive significance of the intermittent pattern of shoot growth in Douglas-fir seedlings from southwest Oregon. *Tree Physiology* 14(11): 1277–1289. <https://doi.org/10.1093/treephys/14.11.1277>
- Kelly D. 1994. The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution* 9: 465–470. [https://doi.org/10.1016/0169-5347\(94\)90310-7](https://doi.org/10.1016/0169-5347(94)90310-7)
- Kelly D. & Sork V.L. 2002. Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics* 33: 427–447. <https://doi.org/10.1146/annurev.ecolsys.33.020602.095433>
- Koenig W.D. & Knops J. 2005. The mystery of masting in trees: some trees reproduce synchronously over large areas, with widespread ecological effects, but how and why? *American Scientist* 93(4): 340–347. <https://www.jstor.org/stable/27858609>
- Krebs C.J., Boonstra R., Cowcill K. & Kenney A.J. 2009. Climatic determinants of berry crops in the boreal forest of the southwestern Yukon. *Botany* 87(4): 401–408. <https://doi.org/10.1139/B09-013>
- Krebs C.J., Cowcill K., Boonstra R. & Kenney A.J. 2010. Do changes in berry crops drive population fluctuations of rodents in the southwestern Yukon? *Journal of Mammalogy* 91(2): 500–509. <https://doi.org/10.1644/09-MAMM-A-005.1>
- Krebs C.J., Boonstra R., Boutin S., et al. 2014. Trophic dynamics of the boreal forests of the Kluane region. *Arctic* 67(1): 71–81. <https://doi.org/10.14430/arctic4350>
- LaDeau S.L. & Clark J.S. 2001. Rising CO₂ levels and the fecundity of forest trees. *Science* 292 (5514): 95–98. <https://doi.org/10.1126/science.1057547>
- Lanner R.M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. *Canadian Journal of Forest Research* 12(2): 391–402.
- Lindner M., Maroschek M., Netherer S., et al. 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management* 259(4): 698–709. <https://doi.org/10.1016/j.foreco.2009.09.023>
- Marino G.P., Kaiser D.P., Gu L. & Ricciuto D.M. 2011. Reconstruction of false spring occurrences over the southeastern United States, 1901–2007: an increasing risk of spring freeze damage? *Environmental Research Letters* 6(2): 024015. <https://doi.org/10.1088/1748-9326/6/2/024015>
- Maslin M. & Austin P. 2012. Climate models at their limit? *Nature* 486: 183–184. <https://doi.org/10.1038/486183a>
- Mishukov N.P. 1972. Cone production of Siberian stone pine in the northern taiga. *Proceedings of the SB RAS. Series of Biological Sciences* 15(3): 53–59. [In Russian].
- Nekrasova T.P. 1972. Biological basis of the seed production in Siberian stone pine. Nauka, Novosibirsk. [In Russian].
- Nekrasova T.P. 1983. Pollen and pollen order of conifers in Siberia. Nauka, Novosibirsk. [In Russian].
- Nesvetajlo V.D. 1987. Long-term dynamics of reproductive activity and radial growth of Siberian stone pine in the stand from the southern taiga. *Russian Journal of Ecology* 6: 19–25. [In Russian].
- Norden N., Chave J., Belbenoit P., et al. 2007. Mast fruiting is a frequent strategy in woody species of eastern South America. *PLoS ONE* 2(10): e1079. <https://doi.org/10.1371/journal.pone.0001079>
- Nussbaumer A., Waldner P., Apuhtin V., et al. 2018. Impact of weather cues and resource dynamics on mast occurrence in the main forest tree species in Europe. *Forest Ecology and Management* 429: 336–350. <https://doi.org/10.1016/j.foreco.2018.07.011>
- Owens J.N. 2006. The reproductive biology of lodgepole pine. Forest Genetics Council of British Columbia, Extension Note 07.
- Owens J.N. 2008. The reproductive biology of Western Larch. Forest Genetics Council of British Columbia, Extension Note 08.
- Owens J.N. & Blake M.D. 1985. Forest tree seed production: a review of literature and recommendations for future research. Canadian Forestry Service Information Report PI-X-53: 161.
- Owens J.N., Kittirat T. & Mahalovich M.F. 2008. Whitebark pine (*Pinus albicaulis* Engelm.) seed production in natural stands. *Forest Ecology and Management* 255(3–4): 803–809. <https://doi.org/10.1016/j.foreco.2007.09.067>
- Pallardy S.G. 2007. Physiology of woody plants. Third edition. Academic Press, San Diego.
- Pearse I.S., Koenig W.D. & Kelly D. 2016. Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist* 212(3): 546–562. <https://doi.org/10.1111/nph.14114>
- Pearse I.S., LaMontagne J.M. & Koenig W.D. 2017. Inter-annual variation in seed production has increased over time (1900–2014). *Proceedings of the Royal Society B* 284(1868): 20171666. <https://doi.org/10.1098/rspb.2017.1666>
- Pérez-Ramos I.M., Aponte C., García L.V., Padilla-Díaz C.M. & Marañón T. 2014. Why is seed production so variable among

- individuals? A ten-year study with oaks reveals the importance of soil environment. *PLoS ONE* 9(12): e115371. <https://doi.org/10.1371/journal.pone.0115371>
- Philipson J.J. 1997. Predicting cone crop potential in conifers by assessment of developing cone buds and cones. *Forestry* 70(1): 87–96. <https://doi.org/10.1093/forestry/70.1.87>
- Pons J. & Pausas J.G. 2012. The coexistence of acorns with different maturation patterns explains acorn production variability in cork oak. *Oecologia* 169(3): 723–731. <https://doi.org/10.1007/s00442-011-2244-1>
- Primack R.B. 1998. Essentials of conversation biology. Second edition. Sinauer Associates, Sunderland, Massachusetts.
- Redmond M.D., Weisberg P.J., Cobb N.S., Gehring C.A., Whipple A.V. & Whitham T.G. 2016. A robust method to determine historical annual cone production among slow-growing conifers. *Forest Ecology and Management* 368: 1–6. <https://doi.org/10.1016/j.foreco.2016.02.028>
- Richardson S.J., Allen R.B., Whitehead D., Carswell F.E., Ruscoe W.A. & Platt K.H. 2005. Climate and net carbon availability determine temporal patterns of seed production by *Nothofagus*. *Ecology* 86(4): 972–981. <https://doi.org/10.1890/04-0863>
- Rigby J.R. & Porporato A. 2008. Spring frost risk in a changing climate. *Geophysical Research Letters* 35: L12703. <https://doi.org/10.1029/2008GL033955>
- Rohde A., Bastien C. & Boerjan W. 2011. Temperature signals contribute to the timing of photoperiodic growth cessation and bud set in poplar. *Tree Physiology* 31(5): 472–482. <https://doi.org/10.1093/treephys/tpq038>
- Roland C.A., Schmidt J.H. & Johnstone J.F. 2014. Climate sensitivity of reproduction in a mast-seeding boreal conifer across its distributional range from lowland to treeline forests. *Oecologia* 174(3): 665–677. <https://doi.org/10.1007/s00442-013-2821-6>
- Sakai A. & Malla S.B. 1981. Winter hardiness of tree species at high altitudes in the East Himalaya, Nepal. *Ecology* 62(5): 1288–1298. <https://doi.org/10.2307/1937293>
- Salminen H. & Jalkanen R. 2007. Intra-annual height increment of *Pinus sylvestris* at high latitudes in Finland. *Tree Physiology* 27(9): 1347–1353. <https://doi.org/10.1093/treephys/27.9.1347>
- Schauber E.M., Kelly D., Turchin P., et al. 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology* 83(5): 1214–1225. <https://doi.org/10.2307/3071937>
- Silvertown J.W. 1980. The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society* 14(2): 235–250. <https://doi.org/10.1111/j.1095-8312.1980.tb00107.x>
- Sork V.L., Bramble J. & Sexton O. 1993. Ecology of mast-fruiting in three species of north American deciduous oaks. *Ecology* 74(2): 528–541. <https://doi.org/10.2307/1939313>
- Speer J.H. 2010. Fundamentals of tree-ring research. University of Arizona Press, Tucson.
- Stephenson A.G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12: 253–279. <https://doi.org/10.1146/annurev.es.12.110181.001345>
- Tanino K.K., Kalcsits L., Silim S., Kendall E. & Gray G.R. 2010. Temperature-driven plasticity in growth cessation and dormancy development in deciduous woody plants: a working hypothesis suggesting how molecular and cellular function is affected by temperature during dormancy induction. *Plant Molecular Biology* 73(1–2): 49–65. <https://doi.org/10.1007/s11103-010-9610-y>
- Tretiyakova I.N. 1990. Embryology of conifers: physiological aspects. Nauka, Novosibirsk. [in Russian].
- Tretiyakova I.N. & Lukina N.V. 2016. Acceleration of embryonic development of *Pinus sibirica* trees with a one-year reproductive cycle. *Ontogenez* 47(1): 49–56. [In Russian]. <https://doi.org/10.7868/S0475145016010067>
- Visser M.D., Jongejans E., van Breugel M., et al. 2001. Strict mast fruiting for a tropical dipterocarp tree: a demographic cost-benefit analysis of delayed reproduction and seed predation. *Journal of Ecology* 99(4): 1033–1044. <https://doi.org/10.1111/j.1365-2745.2011.01825.x>
- Vitasse Y. & Rebetez M. 2018. Unprecedented risk of spring frost damage in Switzerland and Germany in 2017. *Climatic Change* 149: 233–246. <https://doi.org/10.1007/s10584-018-2234-y>
- Vorobjev V.N. 1983. Biological basis of complex exploitation of Siberian stone pine forests. Nauka, Novosibirsk. [in Russian].
- Vorobjev V.N., Vorobjev N.A. & Goroshkevich S.N. 1989. Growth and sex of Siberian stone pine. Nauka, Novosibirsk. [in Russian].
- Vorobjev V.N., Goroshkevich S.N. & Savchuk D.A. 1994. New trend in dendrochronology: method of retrospective study of seminiference dynamics in *Pinaceae*. In: Proceedings – International workshop on subalpine stone pines and their environment: the status of our knowledge; 1992 September 5–11; St.Moritz, Switzerland: 201–204. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden.
- Way D.A. 2011. Tree phenology responses to warming: spring forward, fall back? *Tree Physiology* 31(5): 469–471. <https://doi.org/10.1093/treephys/tpq044>
- Zamorano J.G., Hokkanen T. & Lehtikoinen A. 2018. Climate-driven synchrony in seed production of masting deciduous and conifer tree species. *Journal of Plant Ecology* 11(2): 180–188. <https://doi.org/10.1093/jpe/rtw117>
- Zwiers F.W., Alexander L.V., Hegerl G.C., et al. 2013. Climate extremes: challenges in estimating and understanding recent changes in the frequency and intensity of extreme climate and weather events. In: Asrar G.R. & Hurrell J.W. (eds) Climate science for serving society: 339–389. Springer, Dordrecht. https://doi.org/10.1007/978-94-007-6692-1_13

Communicating editor: Olivier Chabrerie.

Submission date: 20 Aug. 2020

Acceptance date: 7 May 2021

Publication date: 23 Nov. 2021