

Abies sibirica Male Reproductive Cones Developmental Shift at Introduction

Elena V. Bazhina

V.N. Sukachev Institute of Forest, Siberian Branch of Russian Academy of Sciences, Krasnoyarsk, Russia
Email: genetics@ksc.krasn.ru

Received 19 March 2014; revised 19 April 2014; accepted 25 April 2014

Copyright © 2014 by author and Scientific Research Publishing Inc.
This work is licensed under the Creative Commons Attribution International License (CC BY).

<http://creativecommons.org/licenses/by/4.0/>



Open Access

Abstract

A strong effect of climate on phenological events in conifers has been documented by several studies. To study adaptation of reproductive processes in *Abies sibirica* Ledeb. to changing environment, the phenology of the development of the species male reproductive cones at introduction was studied. Phenological shift in *Abies sibirica* meiosis and pollination was observed. An earlier start of male bud reproductive development is founded in V.N. Sukachev Institute of Forest Arboretum resulted in increasing meiosis and pollen irregularities. Insufficient high quality pollen in the species at its pollination stage may be a major factor responsible for the incapability to produce the viable seeds in quantities sufficient for pollination in seed gardens. Responses of the fir male cone development to the current environmental conditions at the Arboretum may be considered as a model of adaptation of the species to climatic changes.

Keywords

Abies sibirica Ledeb., Forest Arboretum, Male Buds Development, Phenological Shifts

1. Introduction

Several studies have documented the strong effect of climate on phenological events of conifers, such as cone initiation, meiosis, pollination and seed development [1]-[6]. Due to their longevity, multiple reproductive cycles and exposure to large year-to-year environmental heterogeneity within their prolonged lifespan, conifers have improved their phenotypes to tolerate changes in climatic conditions [7] and formed a number of climotypes. Ecological conditions experienced by parents could directly influence the progenies in succeeding generations [8]-[13]. The temperature regime which prevailed during megagametogenesis, zygotic embryogenesis and seed maturation induced shifts in the embryo development program to result in long-term phenotypic changes affecting the growth cycle of the progeny [14]. Provenance trials have shown that southern and western climo-

types of conifers begin to grow at lower air temperature and their seasonal developmental stages are shifted to an earlier period of time and to lower accumulated temperature as compared to northern and eastern climotypes [15]-[18]. Even slight changes of air temperature and relative humidity can have marked effects on climotypes growth, ontogenesis, and reproductive system. High sensitivity to new conditions is characteristic of the juvenile plants and of the beginning of the reproductive period during sporogenesis and gametogenesis adaptation to new temperature and light regimes [19] [20].

Studying the adaptation of reproductive processes in plants to changing environmental conditions is crucially important. It has been shown [21] [22] that insufficient high quality pollen in the species at its pollination time may be a major factor responsible for the incapability to produce the viable seeds in quantities sufficient for pollination in seed gardens. Because male reproductive organs are very sensitive to small variations in climate, especially to temperature, phenological records can be a useful proxy for temperature in historical climatology, especially in the studying climate change and global warming.

The aim of the work is to study phenology of *Abies sibirica* Ledeb. male reproductive cones development at introduction.

2. Material and Methods

The study was conducted in 2002-2004 and in 2011. Two study plots were laid out in fir stands growing in the East Sayan Mountains and one plot in the arboretum of the V.N. Sukachev Institute of Forest. The study sites were found in the extremely continental climate having an average annual temperature of 0.8°C. The weather information provided by Krasnoyarsk Weather Service showed that April and May air temperatures in 2002 and 2003 were within their average multi-year range, whereas the 2004 spring came 7 - 12 days later than usual and in 2011 late frosts occurred [23].

The sampled fir trees grew in the low-mountain zone, more specifically in the Laletina River valley (450 - 520 m a.s.l.), in the middle mountains (the Upper Kaltat, 640 - 720 m a.s.l.) and in V.N. Sukachev Institute of Forest arboretum which located at the wildland/Krasnoyarsk town interface, on a terrace (275 m a.s.l.) on the left bank of Yenisei River. Notwithstanding its proximity to Krasnoyarsk, the arboretum is not affected by industrial pollution, as it is situated outside the prevailing industrial emission transfer [24]. Siberian fir saplings were transferred to the arboretum in 1977 from the forest nursery of Siberian Institute of Fruit Growing (Barnaul, Altai, Altai Region, Russia) found in a moderately continental climate with the average annual temperature being 4.0°C. They were grown from seeds collected from Siberian fir stands naturally occurring in Altai region.

Pollen cones of Siberian fir were collected at the dormancy stage (in October), and at 1 - 3 days intervals during the pollen development period (from mid-April to mid-May), and at the time of pollination (late May). Samples were fixed in alcohol mixed with acetic acid at a ratio of 3:1 for one day after their appropriate trimming or dissection. Then they were dehydrated in a xylol alcogol series [25], embedded in paraffin tissueprep, sectioned at 6 - 12 µm and stained in iron-hemotoxylin. A number of samples were transferred to 70% alcohol, and stained with acetohe-matoxylin. More than thirteen thousands of developing pollen grains were tested using Micromed-2 microscope. On each plot, the pollen cones were collected from 10 - 15 sample trees and the pollen was analyzed for viability (*in vitro* % germination and tube length, in µm) and size (two perpendicular diameters of grain body, and length and height of air sacs, µm). Up to 300 pollen grains were analyzed per sample tree. STATISTICA 7.0 [26] was used to calculate descriptive statistics including the standard deviations and the confidence levels of the differences.

3. Results

3.1. Pollen Bud Development

Siberian fir pollen cones develop during 12 month, from late June till the end of May. Pollen-cone buds usually differentiate from axillary buds that have formed in axils of leaves on the sides and lower surfaces of the shoots (Figure 1). The pollen cones of sampled trees were clustered (up to 35 cones in a cluster). Each pollen cone in a cluster occurred in a at leaf base and was sessile. The pollen buds became conspicuous at the end of June-beginning of July and developed until early October, since when they became totally enclosed in imbricate scales. They were made up by large numbers of spirally arranged bisporangiate microsporophylls. All microsporophylls were initiated during the first month of pollen bud development. Sporogenous tissue in microsporangia was



Figure 1. *Abies sibirica* shoot bearing pollen bud at meiosis (a) and pollen-cone at pollination time (b). P—developing pollen cones, LB—latent bud.

formed during August. In late August, microsporangia in sample fir trees increased to be 212×147 μm in size. They stayed dormant at the premeiotic stage of the pollen mother cells (PMC), with tapetal cells remaining uninucleate (**Figure 2(a)**).

3.2. Time of Meiosis and Pollen Development

Pollen buds in sample trees enlarged in spring and developed during May (**Table 1**). The rate of development of the post-dormancy pollen cones strongly depended on site conditions and air temperature; it increased in warm weather and decreased when it became cooler.

In the East Sayan study populations meiotic division usually starts in the pollen mother cells (PMCs) at accumulated temperatures ranging 40.8°C to 47.8°C during the first ten days (in low mountains) and the 10th through the 20th (middle mountains) of May (**Figure 2(b)**). In 2002, 2003 and 2011 in the low mountains meiosis was observed to begin on the 5th and 7th of May, and lasted one - two days (**Figure 3**). In 2004, meiosis started as late as May 13-15. This delay was presumably due to the cold spring of 2004. Meiotic division lasted for 2 - 3 days (from diakinesis through the tetrad stage). The time of meiosis varied no more than one day among the sample trees. Meiosis occurred at a generally higher rate in microsporangia situated in the lower parts of the strobile as compared to those found in the upper parts. At the end of meiosis, microspore tetrads separated quickly. Early microspores were initially angular and gradually became orbicular. During in about two weeks following meiosis, pollen grains were forming air sacs. Haploid microspore cells then experienced three unequal divisions: the first two divisions resulted in production of two small lens-shaped prothallial cells on the microspore proximal side and a small generative and large tube cells resulted from the third division.

At the Arboretum, the pollen cones collected in April of 2002, 2003 and 2011 contained PMC at early meiosis stages and first meiotic divisions were observed on the 23rd April, at an accumulated temperature of 11.2°C - 23.7°C in while this process only started on the 5th May in the cold spring of 2004, with the accumulated temperature being 57.5°C . Meiotic division lasted for 13 - 17 days; microspore cells experienced divisions and increased in size during ten days.

3.3. Meiosis and Pollen Irregularities

The fir trees moved to the arboretum had species-specific features, such as rapid progression through telophases I and II, and conspicuous prophase II, elongated chromosomes (**Figure 2(c)**), and asynchrony (**Figure 2(d)**) characteristic of where the species occurs naturally. Although meiosis proceeded in a fairly regular way in most cells, irregularities of general and specific types were found nearly throughout meiosis and pollen formation (the irregularities occurred in 11.7%, 13.3%, and 17.9% of the cells in low mountains, middle mountains and in the arboretum (**Figures 2(e)-(f)**). In the Arboretum, irregularities frequency of occurrence increased at all meiotic stages and reached 48.2% at anaphase I [27]. Regular Siberian fir pollen grains have, as a rule, two large symmetrical air sacs. However, our study identified five-cell pollen grains containing a stalk cell adjacent to two prothallial cells, a tube cell, and a body cell. We also found grains that had either no, or one, three, or four air sacs (**Figure 2(g)** and **Figure 2(h)**). Irregular pollen grains were less than 1% of all pollen produced annually by each tree.

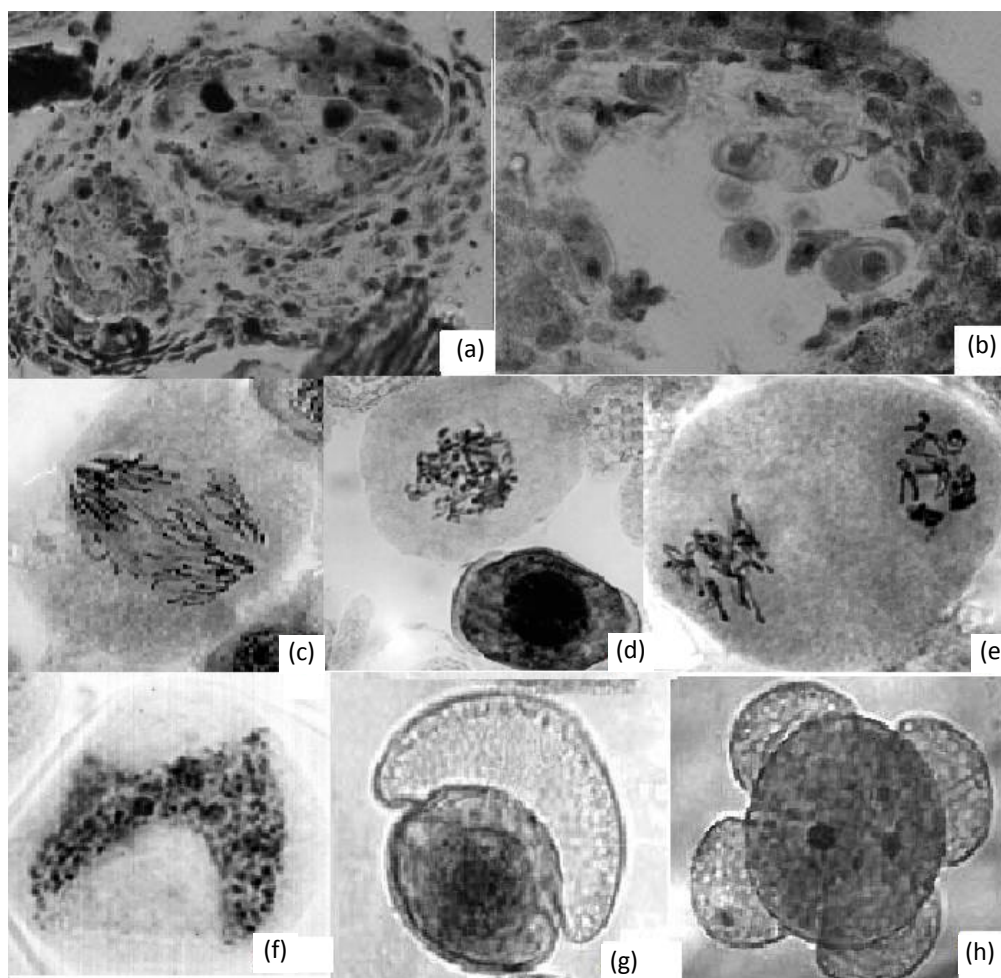
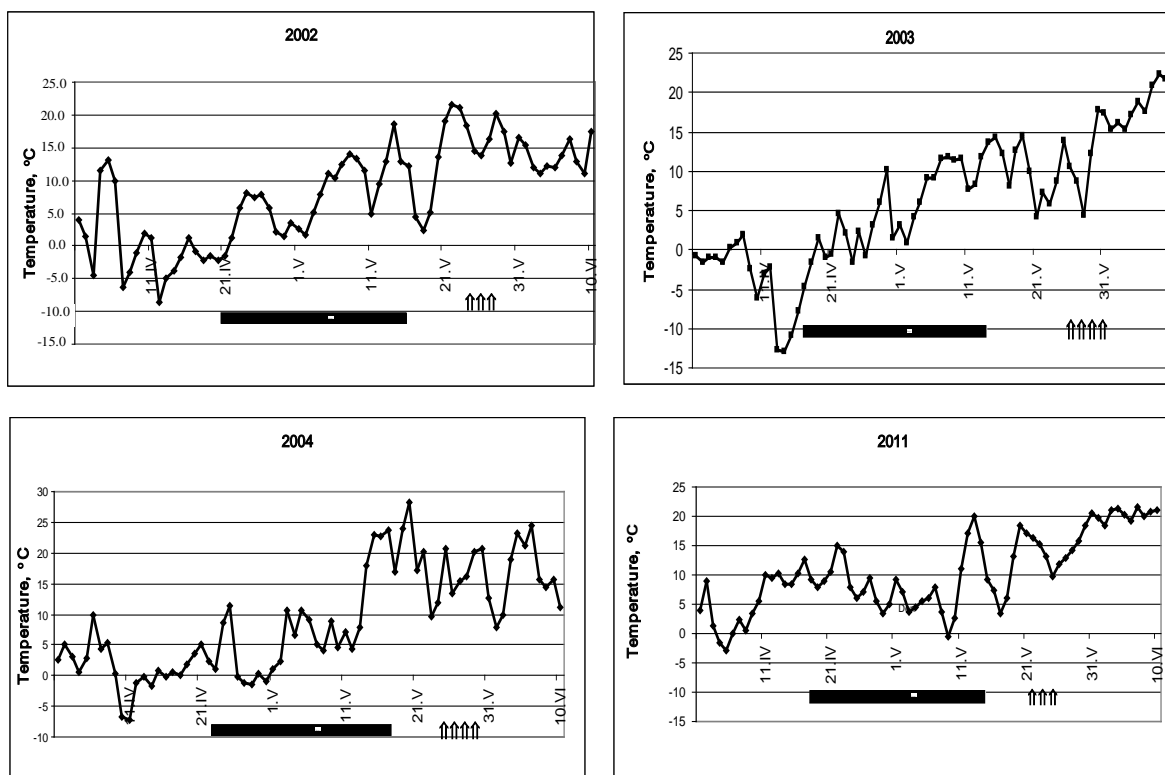


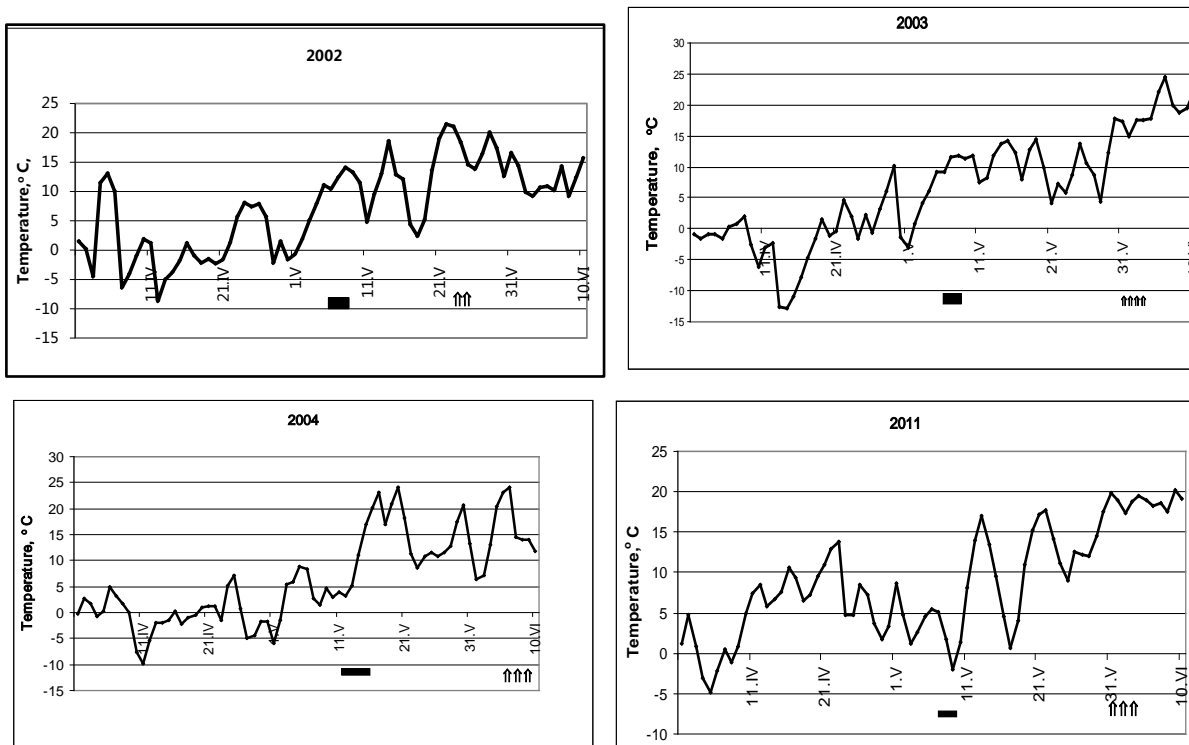
Figure 2. Pollen development and some peculiarities and irregularities: microsporangia containing PMC: (a) dormant, October, 1; (b) April, 24; (c) elongated chromosomes (anaphase I); (d) pollen mother cell and immature pollen grain in the same microsporangia; (e) chaotic chromosome arrangement (metaphase II); (f) union of nuclei in dyad; irregular pollen grain: (g) with one saccy, (h) two microspores with common membrane.

Table 1. Durations of *Abies sibirica* microsporogenesis and pollen development at Arboretum.

Date	Stage of development
23rd April, 2002-2003, 2011; 5th May, 2004	Pollen mother cell (PMC)
23rd, 24th April-6th May 2002-2003, 2011; 24th April-13th May, 2004	Meiosis of PMC
26th April-8th May, 2002; 27th April-13th May, 2003, 2011; 5th-11th May, 2004	Formation of tetrads
6th-11th May, 2002, 2004; 25th April-8th May, 2003, 2011;	Free microspores without air sacs
6th-11th May, 2002; 28th April-13th May, 2003, 2011 5th-11th May, 2004	Free microspores with air sacs
7th-14th May, 2002, 2003, 2011; 17th May, 2004	Uninucleate microspore with large vacuole
12th May, 2002-2003, 2011; 23rd May, 2004	Matured pollen grains



(a)



(b)

Figure 3. Dates of *Abies sibirica* meiosis and pollination (bars on the x-axis) in relation to mean daily temperatures in 2002-2004, 2011 at Arboretum (a) and in natural populations (b): ■—meiosis, ↑↑↑—pollination, x-axis—date.

3.4. Pollen Size

The pollen grain size varied considerably among sample trees (**Table 2**). Mature pollen grain variability in diameter was 5% - 12% among the years of observation, 12% - 21% among individual trees, with the respective ranges being 4.0% - 9.0% and 2.6% - 9.3% for air sac size. It should be noted that the mature pollen grains from the arboretum were the same size as in low-mountain Siberian fir populations and 17.1% - 46.6% larger than in middle-mountain populations found at elevation 640 - 720 m a.s.l.

3.5. Time of Pollination

We presume there was a relationship between the climatic conditions and the pollen dispersal period. The air temperature-caused differences in rate of development of the post-dormancy pollen cones resulted in differences in pollination time (**Figure 3**). In the naturally growing populations pollination was occurred between May 23 and June 5 at accumulated temperature 243°C - 267°C; earlier in warm weather and later when it became cooler. In the trees sampled in arboretum, the pollen was dispersed between 21st and 31st of May in different years of observation, with the accumulated temperature ranging 155.6°C to 292.2°C. In the natural populations, wind pollination lasted for 3 - 5 days, as opposed to 3 day at the arboretum. Pollen viability at the arboretum was low: in 2002 and 2003, pollen germination varied among sample trees from none to 89.2% and none to 20%, respectively [28]. In 2004 and 2011, pollen germination was 34.4% - 96.0% almost three times more that in the former two years.

4. Discussion

Plant responses to the environment are controlled by naturally evolving mechanisms of adaptation responsible for plant environmental tolerance, including tolerance of environmental constraints, and resistance external influences [29] [30]. *A. sibirica* belongs to a group of species within the genus *Abies* in which buds start to enlarge earlier in spring than in nearly all other conifers [31]. In this group, microsporogenesis and pollen development start in early spring, immediately after winter dormancy, when the probability of damaged by low air temperature is very high. Extreme temperatures occurring during pollen development and flowering, with former being the stage at which meiosis is most temperature-sensitive, have a negative impact on meiotic cell division patterns, including a slowdown of meiosis. The slowdown is manifested the structural and physiological disturbances, which strongly affect gamete formation and embryo development [22] [32]-[36]. It was established that firs are affected by spring frosts when buds are in the burst phase [37]. The risk of the low temperature-induced development slowdown is reduced only provided that period of dormancy is sufficiently long [38]. For western fir climotypes transferred from where the climate is less severe, development of male buds clearly tended to begin earlier (and at lower air temperatures) and to occur at a lower rate compared to native trees. A phenotypic shift was presumably a cause of the decrease in the moved plant homeostasis and developmental disturbances. It is likely that dormancy terminated too early and late frosts resulted in increasing number of irregular cells occurring during meiosis, like in 2004. Moreover, PMC damage caused by low air temperatures at the premeiotic phase took a long time to manifest [39].

The lower amount of pollen in the air and the lower pollen viability found in the arboretum compared to the mountain study plots could be factor limiting *A. sibirica* trees pollination in the arboretum. Sampled trees growing in the arboretum were characterized by high pollen sterility [28]. Climatic differences between high-eleva-

Table 2. *Abies sibirica* pollen size at low mountains and Arboretum, mcm.

Year	Stage of development			
	Diameter 1	Diameter 2	Length	Height
2002	79 ± 1.9 (12.2)	84 ± 1.8 (10.7)	46 ± 1.2 (13.1)	67 ± 1.9 (13.9)
2003	76 ± 2.0 (5.2)	74 ± 3.7 (10.0)	44 ± 1.1(4.8)	61 ± 2.0 (6.5)
2004	80 ± 2.0 (8.7)	85 ± 1.8 (7.5)	46 ± 1.2 (7.6)	67 ± 1.8 (7.9)
2011	80 ± 1.8 (7.9)	83 ± 1.6 (7.2)	46 ± 1.1 (9.7)	67 ± 1.8 (8.9)

tion location of natural Siberian fir stands and low-elevation locations of the arboretum might be a major factor accounting for low Siberian fir seed viability in the arboretum. While pollination periods recorded for *Abies sp.* take long, from 18 days in *A. homolepis* [40] to as long as one month in *A. pinsapo* [41] in *A. sibirica* it usually lasts only 3 - 5 days. The earlier start of male cone reproductive development observed for sampled trees from arboretum might prevent cross-pollination with individuals of natural population. In the arboretum, the probability of sample fir trees self-pollination was high, because natural populations are situated more than 10 km away from arboretum and fir pollen is usually dispersed to fairly short distances. Fir pollen is relatively heavy, for which reason pollination distances greater than 60 m may be another factor limiting viable seed production [42]. In some conifers, self-pollination is an important cause of empty seed formation [43] [44]. It is generally accepted that isolated tree populations may have low genetic diversity which may be responsible for the lower species performance of such populations [45] [46].

Woody plants have developed adaptation mechanisms to modify their phenotype to tolerate changes in climatic conditions. It have been recognized that the phenology vary within species at different elevations and latitudes [47]-[51]. To remain alive in changing climate, plant species have to be flexible in their responses by changing their phenology or physiology, adapting to new climate condition via selection, migration to suitable climates, otherwise they will become extinct. Recent studies have shown that different environmental factors may induce epigenetic changes in the mother trees, which changes are through the seeds to offspring and, can alter offspring gene activity by modifying its phenotype [7] [11] [52] [55]. This phenomenon may be due to genetic features of the trees, since pollen development is genetically controlled and since epigenetic mechanisms are also genetically determined [56]-[58].

Result of phenological shift research studies at introduction can be a useful proxy for studying climate change and global warming. Responses of ontogenetic development of the male reproductive buds of the Siberian fir sampled in the arboretum to environmental conditions may be considered as a model of species adaptation to climate change.

Acknowledgements

Author thanks Dr. Olga Kvitko for conducting of some cytological investigations as well as Prof. Elena N. Muratova for supporting the researches.

The work was supported by Russian Foundation of Basic Research and Krasnoyarsk Foundation, projects 11-04-00281 and r_sibir_a 13-04-98045.

References

- [1] Kohmann, K. and Johnsen, O. (1994) The Timing of Bud Set in Seedlings of *Picea abies* from Seed Crops of a Cool versus a Warm Spring and Summer. *Silvae Genetica*, **43**, 329-333.
- [2] Levanič, T., Gricar, J., Gagen, M., Jalkanen, R., Loader, N.J., McCarroll, D., Oven, P. and Robertson, I. (2009) The Climate Sensitivity of Norway Spruce [*Picea abies* (L.) Karst.] in the Southeastern European Alps. *Trees*, **23**, 169-180. <http://dx.doi.org/10.1007/s00468-008-0265-0>
- [3] Messaud, Y., Bergeron, Y. and Asselin, H. (2007) Reproductive Potential of Balsam Fir (*Abies balsamea*), White Spruce (*Picea glauca*), and Black Spruce (*P. mariana*) at the Ecotone between Mixedwood and Coniferous Forests in the Boreal Zone of Western Quebec. *American Journal of Botany*, **94**, 746-754. <http://dx.doi.org/10.3732/ajb.94.5.746>
- [4] Owens, J.N. and Blake, M.D. (1985) Forest Tree Seed Production. A Review of the Literature and Recommendations for Future Research. Information Report PI-X-53. Canadian Forest Service, Petawawa, National Forestry Institute, Ontario.
- [5] Sirois, L. (2000) Spatiotemporal Variation in Black Spruce Cone and Seed Crops along a Boreal Forest-Tree Line Transect. *Canadian Journal of Forest Research*, **30**, 900-909. <http://dx.doi.org/10.1139/x00-015>
- [6] Zhang, W.H., Xu, X.B. and Zhou, J.Y. (2006) Study on Reproduction Ecology of Endangered Species *Abies chensiensis*. *Acta Ecologica Sinica*, **26**, 2417-2424. [http://dx.doi.org/10.1016/S1872-2032\(06\)60036-X](http://dx.doi.org/10.1016/S1872-2032(06)60036-X)
- [7] Herman, J.J. and Sultan, S.E. (2011). Adaptive Transgenerational Plasticity in Plants: Case Studies, Mechanisms, and Implications for Natural Populations. *Frontiers in Plant Science*, **2**, 1-10. <http://dx.doi.org/10.3389/fpls.2011.00102>
- [8] Andersson, B. (1994) After-Effects of Maternal Environment on Autumn Frost Hardiness in *Pinus sylvestris* Seedlings in Relation to Cultivation Techniques. *Tree Physiology*, **14**, 313-322. <http://dx.doi.org/10.1093/treephys/14.3.313>
- [9] Greenwood, M.S. and Hutchison, K.W. (1996) Genetic Aftereffects of Increased Temperature in *Larix*. In: Hom, J.,

- Birdsey, R. and O'Brian, K., Eds., *Proceedings of the 1995 Meeting of the Northern Global Change Program*, USDA Forest Service Report, Radnor, 56-62.
- [10] Johnsen, O., Skroppa, T., Haug, G., Apeland, I. and Ostreng, G. (1995) Sexual Reproduction in a Greenhouse and Reduced Autumn Frost Hardiness of *Picea abies* Progenies. *Tree Physiology*, **15**, 551-555. <http://dx.doi.org/10.1093/treephys/15.7-8.551>
- [11] Johnsen, O., Skroppa, T., Junttila, O. and Dæhlen, O.G. (1996) Influence of the Female Flowering Environment on Autumn Frost-Hardiness of *Picea abies* Progenies. *Theoretical and Applied Genetics*, **92**, 797-802. <http://dx.doi.org/10.1007/BF00221890>
- [12] Owens, J.N., Johnsen, Ø., Dæhlen, O.G. and Skroppa, T. (2001) Potential Effects of Temperature on Early Reproductive Development and Progeny Performance in *Picea abies* (L.) Karst. *Scandinavian Journal of Forest Research*, **16**, 221-237. <http://dx.doi.org/10.1080/02827580117248>
- [13] Stoehr, M.U., L'Hirondelle, S.J., Binder, W.D. and Webber, J.E. (1998) Parental Environment Aftereffects on Germination, Growth, and Adaptive Traits in Selected Spruce Families. *Canadian Journal of Forest Research*, **28**, 418-426. <http://dx.doi.org/10.1139/x98-012>
- [14] Skroppa, T., Kohmann, K., Johnsen, O., Steffendrem, A. and Edvardsen, O.M. (2007) Field Performance and Early Test Results of Offspring from Two Norway Spruce Seed Orchards Containing Clones Transferred to Warmerclimates. *Canadian Journal of Forest Research*, **37**, 515-522. <http://dx.doi.org/10.1139/X06-253>
- [15] Beuker, E. (1994) Adaptation to Climatic Changes of the Timing of Bud Burst in Population of *Pinus sylvestris* L. and *Picea abies* (L.) Karst. *Tree Physiology*, **14**, 961-970. <http://dx.doi.org/10.1093/treephys/14.7-8-9.961> PMID:14967662
- [16] Beuker, E., Valtonen, E. and Repo, T. (1998) Seasonal Variation in the Frost Hardiness of Scots Pine and Norway Spruce in Old Provenance Experiments in Finland. *Forest Ecology and Management*, **107**, 87-98. [http://dx.doi.org/10.1016/S0378-1127\(97\)00344-7](http://dx.doi.org/10.1016/S0378-1127(97)00344-7)
- [17] Olsen, J. (2010) Light and Temperature Sensing and Signaling in Induction of Bud Dormancy in Woody Plants. *Plant Molecular Biology*, **73**, 37-47. <http://dx.doi.org/10.1007/s11103-010-9620-9>
- [18] Pravdin, L.F. (1964) Immediate Tasks of Scientific Researches and Practice on Forest Genetics and Breeding in Siberia. Breeding of Woody Species in East Siberia. Nauka, Moscow.
- [19] Gavrilov, I.A. and Butorina, A.K. (2005) Cytogenetics of the Canadian Hemlock upon Introduction in the Voronezh District. *Russian Forestry Science (Lesovedenie)*, **3**, 60-65.
- [20] Shkutko, N.V. (1973) Development of Generative Buds in Coniferous Plants Introduced in the Byelorussia. Materials of I Vsesoyuz. simp. "Polovaya reproduktsiya khvoynyk" [Materials of the 1st All-Union Symposium "Sexual Reproduction of Coniferous Plants"], Novosibirsk, 2, 132-134.
- [21] Arista, M. and Talavera, S. (1994) Pollen Dispersal Capacity and Pollen Viability of *Abies pinsapo* Boiss. *Silvae Genetica*, **43**, 155-158.
- [22] Hak, O. and Russell, J.H. (2004) Environmental Effects on Yellow-Cedar Pollen Quality. Forest Genetic Council, Extension Note, 05, 9.
- [23] Server "Pogoda of Russia". <http://meteo.infospace.ru>
- [24] Varpholomeev, I.V. and Maltsev, Y.M. (Eds.) (2006) Gosudarstvennii doklad O sostoyanii i ohrane okruzhajuschei sredii v Krasnoyarskom kraje v 2006 [State Report about Environmental Status and Protection in Krasnoyarsk Region in 2006]. Priroda, Krasnoyarsk.
- [25] Pausheva, Z.P. (1988) Praktikum po cytologii rastenii. Agropromizdat, Moscow.
- [26] StatSoft, Inc. STATISTICA (2001) Data Analysis Software System, Version 6. <http://www.statsoft.com>
- [27] Bazhina, E.V., Kvitko, O.V. and Muratova, E.N. (2011) Specific Features of Meiosis in the Siberian Fir (*Abies sibirica* Ledeb.) at the the V.N. Sukachev Institute, Russia. *Biodiversity and Conservation*, **20**, 415-428. <http://dx.doi.org/10.1007/s10531-010-9958-y>
- [28] Bazhina, E. (2012) Siberian Fir (*Abies sibirica* Ledeb.) Pollen Viability at the V.N. Sukachev Institute of Forest Arboretum. *EuroGard VI: 6th European Botanic Gardens in a Changing World*, Chios Island, 28 May-3 June 2012, Abstracts, 86.
- [29] Golubovskaya, I.N. (1985) An Experimental Study of Gene Control of Meiosis in the Maize. In: *Teoreticheskie osnovy s elektzii [Theoretical Found of Selection]*, Nauka, Novosibirsk, 119-135.
- [30] Politi, P.I., Georghiou, K. and Arianoutsou, M. (2011) Reproductive Biology of *Abies cephalonica* Loudon in Mount Aenos National Park, Cephalonia, Greece. *Trees*, **25**, 655-668. <http://dx.doi.org/10.1007/s00468-011-0542-1>
- [31] Debazac, E.F. (1965) Observations sur le derbourrement et la croissance en longueur de quelques espe`ces de sapin. *Revue forestière française*, **2**, 120-130.
- [32] Andersson, E. (1980) Temperature-Conditioned Irregularities in Pollen Mother Cells of *Picea abies* (L.) Karst. *He-*

- reditas*, **92**, 27-35. <http://dx.doi.org/10.1111/j.1601-5223.1980.tb01675.x>
- [33] Chira, E. (1964) Vplyv teploty na pribeh meiozy pelovych materskych buniek *Taxus bassata* L. [The Temperature Influence on *Taxus bassata* L. Meiosis]. *Biologia, Bratislava*, **11**, 235-243.
- [34] Christiansen, H. (1960) On the Effect of Low Temperature on Meiosis and Pollen Fertility in *Larix decidua* Mill. *Silvae Genetica*, **9**, 72-78.
- [35] Eriksson, G. (1968) Temperature Response of Pollen Mother Cells in *Larix* and Its Importance for Pollen Formation. *Studia Forestalia Suecica*, **63**, 1-131.
- [36] Jonsson, A. (1974) A Study on the Temperature Response of Pollen Mother Cells in Norway Spruce. *Studia Forestalia Suecica*, **116**, 1-32.
- [37] Aussenac, G. (1980) Comportement hydrique de rameaux excises de quelques espèces de sapins et de pins noirs en phase de dessiccation. *Annals of Forest Science*, **37**, 201-215. <http://dx.doi.org/10.1051/forest:19800303>
- [38] Luomajoki, A. (1977) Effects of Temperature on Spermatophyte Male Meiosis. *Hereditas*, **85**, 33-48. <http://dx.doi.org/10.1111/j.1601-5223.1977.tb00947.x>
- [39] Luomajoki, A. (1986) Timing of Microsporogenesis in Trees with Reference to Climatic Adaptation. *Acta Forestalia Fennica*, **196**, 1-33.
- [40] Itoo, M. (1975) Flowering and Pollen-Dispersal in a Seed Orchard of *Abies homolepis*. *Journal of Japan Forestry Society*, **57**, 121-124.
- [41] Arista, M. and Talavera, S. (1994) Phenology and Anatomy of the Reproductive Phase of *Abies pinsapo* Boiss. (Pinaceae). *Botanical Journal of the Linnean Society*, **116**, 223-234. <http://dx.doi.org/10.1111/j.1095-8339.1994.tb00431.x>
- [42] Edwards, D.G.W. (2003) Breaking Dormancy in Tree Seeds with Special Reference to firs (*Abies* Species)—The 1.49 Solution. *Proceedings of the ISTA Forest Tree and Shrub Seed Committee Workshop Prague—Příhonice, Czech Republic, October 20-22, 2003: Hosted by Forestry and Game Management Research Institute Jiloviště-Strnady, Czech Republic, Prague, 20-22 October 2003, CR and Forestry Commission Research Agency, UK*, 18-23.
- [43] Owens, J.N., Colangeli, A.M. and Morris, S.J. (1991) Factors Affecting Seed Set in Douglas-Fir (*Pseudotsuga menziesii*). *Canadian Journal of Botany*, **69**, 229-238. <http://dx.doi.org/10.1139/b91-033>
- [44] Sorensen, F.C., Franklin, J.F. and Wollard, R. (1976) Self-Pollination Effects on Seed and Seedling Traits in Noble Fir. *Forest Science*, **22**, 155-159.
- [45] Gitzendanner, M.A. and Soltis, P.S. (2000) Patterns of Genetic Variation in Rare and Widespread Plant Congeners. *American Journal of Botany*, **87**, 783-792. <http://dx.doi.org/10.2307/2656886>
- [46] Godt, M.J.W. and Hamrick J.L. (2001) Genetic Diversity in Rare Southeastern Plants. *Natural Areas Journal*, **21**, 61-70.
- [47] Chung, M.S. (1981) Flowering Characteristics of *Pinus sylvestris* L. with Special Emphasis on the Reproductive Adaptation to Local Temperature Factor. *Acta Forestalia Fennica*, **169**, 69 p.
- [48] Mikola, J. (1982) Bud-Set Phenology as an Indicator of Climatic Adaptation of Scots Pine in Finland. *Sylvae Fennica*, **16**, 178-184.
- [49] Olsen, J. (2010) Light and Temperature Sensing and Signaling in Induction of Bud Dormancy in Woody Plants. *Plant Molecular Biology*, **73**, 37-47. <http://dx.doi.org/10.1007/s11103-010-9620-9>
- [50] Owens, J.N. and Molder, M. (1985) The Reproductive Cycles of True Firs. Information Services Branch Ministry of Forest, Victoria.
- [51] Wright, J.W. and Bull, W.I. (1963) Geographic Variation in Scotch Pine. *Silvae Genetica*, **12**, 1-25.
- [52] Boyko, A. and Kovalchuk, I. (2011) Genome Instability and Epigenetic Modification—Heritable Responses to Environmental Stress? *Current Opinion in Plant Biology*, **14**, 260-266. <http://dx.doi.org/10.1016/j.pbi.2011.03.003>
- [53] Johnsen, Ø., Fossdal, C.G., Nagy, N., Møllmann, J., Dæhlen, O.G. and Skrøppa, T. (2005) Climatic Adaptation in *Picea abies* Progenies Is Affected by the Temperature during Zygotic Embryogenesis and Seed Maturation. *Plant, Cell and Environment*, **28**, 1090-1102. <http://dx.doi.org/10.1111/j.1365-3040.2005.01356.x>
- [54] Skrøppa, T., Nikkanen T., Ruotsalainen, S. and Johnsen, O. (1994) Effect of Sexual Reproduction at Different Latitudes on Performance of the Progeny of *Picea abies*. *Silvae Genetica*, **43**, 297-303.
- [55] Zas, R., Cendán, C. and Sampedro, L. (2013) Mediation of Seed Provisioning in the Transmission of Environmental Maternal Effects in Maritime Pine (*Pinus pinaster* Aiton). *Heredity*, **111**, 248-255. <http://dx.doi.org/10.1038/hdy.2013.44>
- [56] Bogdanov, Y.F. (2003) Variability and Evolution of Meiosis. *Genetika*, **39**, 453-457.
- [57] Khvostova, V.V. and Yachevskaya, G.L. (1975) Chromosome Rearrangements in Meiosis. In: Khvostova, V.V. and Bogdanov, Y.F., Eds., *Tsitologiya i genetika meioza* [Cytology and Genetics of Meiosis], Nauka, Moscow, 232-262.

- [58] Yakovlev, I., Fossdal, C.G., Skrøppa, T., Olsen, J.E., Jahren, A.H. and Johnsen, Ø. (2012) An Adaptive Epigenetic Memory in Conifers with Important Implications for Seed Production. *Seed Science Research*, **22**, 63-76.
<http://dx.doi.org/10.1017/S0960258511000535>