

DEVELOPMENT OF GAMETOPHYTES OF THE INTRODUCED *PICEA* SPECIES (PINACEAE) IN THE TAIGA ZONE (KARELIA)

© 2021 г. I. T. Kishchenko^{1,*} and V. V. Trenin¹

¹ Petrozavodsk State University
Lenina Ave., 33, Petrozavodsk, 185910, Russia
*e-mail: ivanki@karelia.ru

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The study was carried out in the middle taiga subzone. The study is aimed at determining the features of the individual stages of sporogenesis, gametogenesis, and embryogenesis in the indigenous and introduced species of *Picea* A. Dietr. in the taiga zone (Karelia). The appearance of microspores' tetrads in *P. abies* is observed 5–9 days earlier than that in the introduced species. The male gametophyte formation of the studied species lasts 3–8 days. Pollen dispersion in *P. abies* and *P. canadensis* begins (end of May) a week earlier than that in *P. pungens*. For the full development of pollen grains in *P. abies* and *P. canadensis*, the sum of positive temperatures of ($>+5^{\circ}\text{C}$) 250°C is required, and in *P. pungens* – 360°C . The study revealed that in mid-May the female gametophyte is still at a free-nuclear stage, and by the beginning of June it already has a cellular structure. Embryogenesis begins at the end of July and ends in the second ten-day period of August. In the introduced species, various deviations are observed in the development of the female generative sphere and during embryogenesis. From 37 to 51% of the seeds of the introduced species lack an embryo. The highest percentage of empty seeds and the latest terms of the main stages of morphogenesis are observed in *P. pungens*.

Keywords: conifers, embryogenesis, gametogenesis, introduction, *Picea*, pollen grain, sporogenesis

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The dendroflora of the northwest of Russia needs to be enriched with new species of woody plants that are resistant to environmental pollution. In this regard, introduction is becoming more and more important. For this purpose special attention should be paid to the genus *Picea*. Many species of this genus, characterised by their high gas resistance and decorativeness, can be used for landscaping, when organizing forest parks and reconstructing forests in green zones, as well as brought under cultivation.

The potential of the introduced species is assessed by a number of signs. The most important of them is the degree to which the rhythm of growth and development of plants corresponds to the ecological factors dynamics of the place of introduction. The study of the introduced plants resistance to new conditions cannot be limited to observations of external morphological changes arising in the process of growth and development. It is necessary to clarify the features and changes occurring within the vegetative and generative buds, as well as in the strobilae (Sedaeva et al., 2008; Vorobyov, Tebenkova, 2013; Zalyvskaya, 2014; Popova et al., 2016). It is the features of all stages of generative organs development and the degree of male and female gametophytes formation that determine the quantity and quality of seed production (Antosiewicz, 1961; Wilson, 1963; Elliot, 1979). A new species can be

introduced only by selecting the individuals most adapted to new conditions, grown from seeds of local introduction (Weekly, 1982; Pausheva, 1988).

The study is aimed at determining the features of the individual stages of sporogenesis, gametogenesis, and embryogenesis in the indigenous and introduced species of *Picea* A. Dietr. in the taiga zone (Karelia).

MATERIALS AND METHODS

The study was carried out at the Botanical Garden of Petrozavodsk State University, located on the northern shore of the Petrozavodsk Bay of Lake Onega (middle subzone of the taiga, $61^{\circ}47'$ N, $34^{\circ}20'$ E) during two growing seasons. The soil type is humus-ferruginous-illuvial podzol (pH 4.7).

The subjects of the study were an indigenous species, *Picea abies* (L.) Karst., and two introduced species, *P. pungens* Engelm. f. *glauca* Regel. and *P. canadensis* (Mill.) Britt. The age and height of *P. abies* – 47 years and 16 m, *P. pungens* – 36 years and 12 m, *P. canadensis* – 32 years and 6 m, respectively. Seed production is observed in all species (Table 1).

Meiosis and pollen development were studied on temporary pressed preparations. Male buds were harvested starting from the first days of May every 3 days and fixed in aceto-alcohol (glacial acetic acid-alcohol,

Table 1. Age and height of trees of the studied *Picea* species

Species	Origin of the planting material	Average age, years	Average height, m	Seed production
<i>Picea pungens</i> f. <i>glauca</i>	St. Petersburg	45 ± 3	16.2 ± 0.7	present
<i>P. canadensis</i>	St. Petersburg	42 ± 4	16.7 ± 0.9	"-
<i>P. abies</i>	Petrozavodsk	56 ± 5	19.1 ± 1.1.	"-

1 : 3) for 4 hours and stored in 70% alcohol in a refrigerator. The anthers were macerated with a dissecting needle in a dye (aceto-carmin) on a glass slide (Pausheva, 1988).

In order to study the development of the female generative sphere, one shoot with generative buds was cut from 10 trees of each species, and then strobilae were cut from the southwestern side of the crown every 3 days. Then they were fixed in a mixture of alcohol and glycerol (ratio 3 : 1). The date of the onset of a particular stage of morphogenesis was taken as the time when it was noted in at least 30% of the buds of a particular species. The sample size for each stage of morphogenesis was 10 buds, followed by strobilae for each species. The development of the female gametophyte and the embryo was studied on permanent preparations. Preparations for anatomical studies of the buds were prepared according to the standard technique (Weekly, 1982; Pausheva, 1988). In this case, we used double fixation in glutaraldehyde and osmium, dehydration by alcohol and acetone, and encapsulation in epoxy resin. Sections with a thickness of about 1 µm were prepared with the use of an ultramicrotome and stained in a 1% aqueous solution of methylin blue.

Air temperature data were obtained from the Sulazhgora meteorological station (Petrozavodsk Hydrometeorological Observatory) located 3 km from the Botanical Garden. The sum of effective temperatures was calculated as the sum of average daily temperatures of more than 5°C from the moment of their appearance in spring until the beginning of a process in the generative development of a pollen grain.

RESULTS AND DISCUSSION

Development of the male gametophyte

The study of the introduction of plants should primarily be aimed at identifying the features of the generative sphere development, including the development of the male gametophyte. The first sampling of male buds, carried out on May 6, 2012, showed that the microsporocytes in the microsporangia were isolated, i.e., meiosis had already begun in them (Table 2). Moreover, in *P. abies* (an indigenous species), this process was at a more advanced stage. Further observations revealed that the general pattern of meiosis in all studied *Picea* species is basically the same.

The calendar dates of individual stages of microsporogenesis and microgametogenesis in the studied species in 2012 are shown in Table 2. It was found

that in microsporocytes of a separate sporangium, meiosis begins almost synchronously, but in its course, deviations in the rate of passage of individual phases are observed in different cells. Therefore, the percentage of cells in one or another phase was given in the table to characterise these deviations.

The time period from the beginning of the active phases of meiosis (diakinesis and further to the stage of microspore tetrads) in *P. pungens* is 6 days, and in *P. abies* – 4 days. At the stage of microspore tetrads in all studied species, synchronization of cell development occurs, i.e. 'lagging' microsporocytes 'catch up' in development with the others at this stage.

The study showed that the studied *Picea* species differ quite noticeably in the timing of the meiosis in microsporocytes. In 2012, the stage of microspore tetrads in *P. abies* was recorded on May, 8, in *P. canadensis* – on May, 13, in *P. pungens* – on May, 19. Thus, the indigenous species considerably advanced (by 5–11 days) the introduced species by the time of meiosis onset in microsporocytes.

As a result of microsporogenesis, microspores are formed. Their nuclei are divided twice according to the type of mitosis, which leads to male gametophytes formation. There are four cell divisions from the microsporocyte stage to the mature pollen stage. Mature pollen consists of the remains of two protallial, siphonogenic, spermogenic, and sterile cells. In all studied species, the development of the male gametophyte (up to the stage of mature pollen) lasted about 10 days. In 2012, pollen dispersion in *P. abies* and *P. canadensis* began on May, 29, and in *P. pungens* – only on June 5. The pollen dispersion lasted 2–3 days.

The repeated observations of the course of meiosis and the development of pollen, carried out in 2013, showed that on April 29, microsporocytes in the microsporangia of *P. abies*, *P. canadensis*, and *P. pungens* were still in the prophase of meiosis I. But already on May 5, meiosis in *P. abies* and *P. canadensis* ended, and tetrads of microspores were formed in the microsporangia. Meanwhile, the completion of meiosis in *P. pungens* was recorded much later – only on May, 11. Thus, microsporogenesis in 2013 in the studied species ended 3–8 days earlier than that in 2012. In 2013, mature pollen in the anthers of *P. abies* and *P. canadensis* was recorded already on May, 17, but pollen dispersion itself, due to the cooling, began only on May, 25. In *P. pungens*, this phenomenon began on June 3. Thus, for two years of observation, the pollen

Table 2. Microsporogenesis and pollen development of the studied *Picea* species in 2012

Date	Sum of effective temperatures, °C	Species		
		<i>Picea pungens</i>	<i>P. canadensis</i>	<i>P. abies</i>
6. V	47	prophase I	prophase I	metaphase I – 4%, dyads – 70%, metaphase II – 11%, anaphase II – 3.5%, microspore tetrads – 1.5%
8. V	61	prophase I	prophase I – 44%, metaphase I – 42%, anaphase – 6%, dyads – 8%	microspore tetrads, singly meta- and telophase II
10. V	78	prophase I	prophase I – 5%, metaphase I – 5.5%, anaphase I – 6.5%, dyads – 73%	microspore tetrads
13. V	90	prophase I	microspore tetrads	microspore tetrads
19. V	142	microspore tetrads	moment of disintegration of microspore tetrads	free microspores
24. V	179	microspores	microspores	1 st division passed
27. V	219	free microspores	3-celled pollen	3–4-celled pollen
29. V	251	free microspores	beginning of pollen dispersion	beginning of pollen dispersion
2. VI	317	4-celled pollen		
5. VI	364	beginning of pollen dispersion		

dispersion of the studied species took place almost at the same time, differing by no more than 1–4 days.

While investigating the process of microsporogenesis in *Picea obovata*, Yu.F. Rozhdestvensky (1981) also observed a high sensitivity of microsporocytes during prophase I to the effects of unfavorable weather factors, in particular, to fluctuations in air temperature. The author noted that a decrease in temperature caused an increase in the number of abnormal deviations in the developing gametophyte.

No investigations on the development of pollen grains in *P. pungens* was found. For *P. canadensis*, one can compare the results of our studies with others (Owens, Molder, 1979). According to this author, under the conditions of British Columbia (Canada), prophase in the mother cells of pollen of this species in 1975 began on April 14, and the appearance of mature pollen was recorded on May 26. In 1976, these stages were recorded on April 12 and May 21, respectively, i.e. almost at the same time. Interestingly, in the same area, but 500 m higher, in 1975, the prophase of meiosis and mature pollen in *P. canadensis* were observed much later – on May 26 and June 9, respectively. Unfortunately, this comparison gives little to explain such significant differences and understand the adaptation mechanism, since the authors did not provide data on the air temperature regime.

Thus, the studies showed that the duration and timing of meiosis phases are determined both by the

biological characteristics of the species and by the specific conditions of the growing season. Most researchers consider the air temperature regime to be the decisive factor for microsporogenesis (Mergen et al., 1965; Luomatoki, 1977; Rozhdestvensky, 1981; Cram, 1984; Williams, 2009; Vorobiev, Tebenkova, 2013). Moreover, each phenological phase occurs at a certain sum of positive temperatures (Sarvas, 1970; Cram, 1984). This sum of temperatures always represents almost the same percentage of the annual sum of temperatures. This fact was determined by Professor Lensser, the director of the Pulkovo Observatory, back in 1867 (Sarvas, 1970).

According to our data, under the conditions of Karelia, the sum of effective temperatures for the full development of pollen by the time of pollen dispersion in *P. abies* and *P. canadensis* reaches 250°C, which is 14% of the sum of effective temperatures for the growing season, whereas in *P. pungens* – 360°C and 20%, respectively. It is known that introduced species, which start growth processes relatively early and finish them early, are most adapted to new conditions (Vstovskaya, 1983; Plotnikova, 1988; Shkutko, 1991; Popova et al., 2016). Whereas, the least adapted species are those with late start and end of vegetation. Consequently, in our study of the introduced species *P. canadensis* is characterised by a greater degree of adaptation than *P. pungens*. Having studied these introduced species in the Nizhnii Novgorod region,

Table 3. Stages of development of the female gametophyte and embryogenesis of the studied *Picea* species

Species	Year of observation	Stages					
		free nuclear structure	cellular structure	archegonia ripe	early embryogenesis	late embryogenesis	seeds with degenerated archegonia, %
<i>Picea pungens</i> f. <i>glauca</i>	2012	16. V	1. VI	26. VI	28. VII	11. VIII	34
	2013	17. V	5. VI	7. VII	9. VIII	20. VIII	51
<i>P. canadensis</i>	2012	16. V	1. VI	21. VI	22. VII	7. VIII	27
	2013	17. V	5. VI	5. VII	30. VII	15. VIII	35
<i>P. abies</i>	2012	16. V	1. VI	15. VI	15. VII	1. VIII	3
	2013	17. V	5. VI	2. VII	28. VII	9. VIII	6

R.A. Vorobiev and D.N. Tebenkova (2013) came to a similar conclusion.

Development of the female gametophyte and embryogenesis

In the development of the female gametophyte of conifers, there are two well distinguished stages: free-nuclear and cellular. The first fixations in 2012 and 2013, carried out on May 16–17, respectively, showed that the female gametophyte in all three studied species of the genus *Picea* is at the free-nuclear stage (Table 3). In the middle of the ovule nucellus, there is a cavity lined with a layer of secretory tissue cells, the so-called nucellar tapetum.

On the preparations recorded on June 1 (2012) and June 5 (2013), one can see that the initiation of archegonia has already occurred, and the gametophyte has a cellular structure. At this time, the central cell of the archegonia is surrounded by a single-row layer of sheath cells. The archegonia maturation in the studied species continued until early July in 2013, whereas, in 2012, this process ended in June. Several archegonia are usually formed in one female gametophyte. Introduced species often have signs of archegonian degeneration (Kishchenko et al., 1994). According to scientific literature data, the cause of archegonia degeneration in ovules of conifers is most often under-pollination or pollination with sterile pollen (Mergen et al., 1965; Khromova, 1985; Surso, 2017). Another form of degeneration of the female gametophyte in the introduced species is observed at a later stage, namely, at the stage of early embryogenesis. In this case, the egg cell and the sheath cells are no longer distinguishable, only the cell membranes are partially preserved. No traces of proembryo or embryo were found. The embryonic cavity in the developing seed is empty. Endosperm is present, but its cells are lighter than those of normal seeds. A similar pattern was observed in *Larix sibirica* (Trenin, 1986) and *P. sibirica* (Tretyakova, 1990).

The initial development stages of the coniferous plants embryo occur in the archegonia. On the preparations of the *P. abies* and *P. canadensis* seeds recorded at the end of July, 2013, the embryo was at the final stage of early embryogenesis. In *P. pungens*, a similar stage occurred only on August 9 (Table 2). A similar dependence but 1–2 weeks earlier was found in 2012. The embryo at this stage already has an elongated-cylindrical shape characteristic of conifers. The primordia of the cotyledons and the plume, or the embryonic apex of the shoot, can be seen at the distal end of the embryo. There is no sharp boundary between the distal and proximal poles of the embryo. Its cells are poorly differentiated and characterized by a meristematic organization. The growth of the embryo ends quickly and already in the second ten-day period of August in the seeds of the studied species of the genus *Picea*, it reaches normal size and consists of leaf-like formations, or cotyledons, and the stem part, or hypocotyl, located below the cotyledons. In addition to the rudimentary apex of the shoot, in the embryo, one can find a root rudiment, consisting of a meristem and a massive root cap. After this stage, visible structural changes in the embryo no longer occur (Kishchenko et al., 1994). The stage of late embryogenesis was previously recorded in *P. abies* August 1–9, and most recently in *P. pungens* f. *glauca* (August 11–20).

The embryo in the seeds of the genus *Picea*, like other conifers, is surrounded by endosperm and protected by the seed coat. The endosperm in coniferous seeds is transformed from the cells of the female gametophyte. The transformation of female gametophyte cells into storage tissue cells occurs during fertilization and in the phase of proembryogenesis. Two zones are distinguished by the type of storage substances in the endosperm. The cells of the inner zone, adjoining the developing embryo, contain mainly starch. The inner zone of the endosperm is completely resorbed during embryogenesis. In a mature seed, the embryo is surrounded by an endosperm containing lipids and pro-

teins. These storage substances are utilised during seed germination.

It is worth noting that from 37 to 51% of the introduced seeds lack an embryo, but they sometimes contain endosperm (Table 2). The same phenomenon in *Pinus sibirica* under conditions of introduction was observed by I.N. Tretyakova et al. (2004) and V.S. Svintsova and I.N. Tretyakova (2014). Such deviations in indigenous species are much less common (Bazhina et al., 2018). The true nature of the anomaly remains unclear. There is a hypothesis about the existence of a so-called hidden genetic load (Koski, 1973). According to the author, most of this load remains unexpressed in the course of cross-pollination. However, even with a slight self-pollination, the effect of recessive genes quickly becomes visible. Most of the species of conifers are known to be devoid of mechanisms preventing self-fertilization after self-pollination. The relatively small number of individuals of the studied species and the distance between them prevent cross-pollination. Therefore, the hypothesis about the genetic load leading to the formation of empty seeds seems highly probable. According to I.I. Kharova (1989) and M.F. Surso (2017), degenerative processes in non-pollinated ovules and blocking the development of the female gametophyte in *P. sylvestris* also occur under conditions of free self-pollination. According to M.F. Surso (2017), pollination, absence of pollination, and pollination with non-viable pollen lead to a destructive type of ovule development at the early stages in most coniferous species, which is one of the reasons of underdeveloped seeds formation. The author showed that low growth energy of pollen tubes, sterility of male gametophyte, as well as death of embryos in early embryogenesis cause ovules necrosis at the later stages of their development, resulting in empty seeds formation. Consequences of self-pollination and self-fertilization in *Pinaceae* begin to appear in pro-embryogenesis and early embryogenesis due to the physiological incompatibility of the tissues of the embryo and the female gametophyte (Mergen et al., 1965; Forshell, 1974; Williams, 2009). These disturbances lead to an increase in the yield of empty seeds (Zavada, Taylor, 1986; Kormuták, Lindgren, 1996; Slobodník, 2002). All this leads to a sharp decrease in seed germination of the introduced species of coniferous plants (Sedaeva et al., 2008; Tretyakova, Voroshilova, 2014). Such deviations in indigenous species are much less common (Bazhina et al., 2018; Surso, 2015).

Thus, of all studied species of the genus *Picea*, the maximum delay in the passage of all main stages of morphogenesis, as well as the highest percentage of empty seeds, was observed in *P. pungens*, which indicates the least degree of adaptation of the generative sphere of this introduced species to new conditions.

CONCLUSIONS

The general scheme of meiosis in microsporocytes of the indigenous and introduced *Picea* species is basically the same. In all studied species, microsporogenesis begins almost simultaneously (early May). The appearance of microspore tetrads in *P. abies* is observed 5–9 days earlier than that in the introduced species. Formation of the male gametophyte lasts about 10 days. Pollen dispersion in *P. abies* and *P. canadensis* begins a week earlier (end of May) than that in *P. pungens*. The duration and timing of all stages of microsporo- and microgametogenesis are determined by the weather conditions of the current growing season. In *P. abies* and *P. canadensis*, the sum of positive temperatures of 250°C is required for the full development of pollen grains, whereas, in *P. pungens* – 360°C. At all stages of pollen formation of the introduced species, no deviations from the norm were found.

The processes of megagametogenesis and embryogenesis in the indigenous and introduced species are characterized by similar stages. In mid-May, the female gametophyte is still at a free stage, and by early June it already has a cellular structure. Embryogenesis begins at the end of July and ends in the second ten-day period of August. There are various kinds of deviations in the development of the female generative sphere and in the course of embryogenesis of the introduced species. The main ones are the degeneration of the female gametophyte at the free-nuclear stage and archegonia destruction at the stage of proembryogenesis. As a result, from 37 to 51% of seeds lack an embryo, although they often have an endosperm.

The latest dates of the main morphogenesis stages, as well as the highest percentage of empty seeds, was observed in *P. pungens*, which indicates the least degree of adaptation of the generative sphere of this introduced species to new conditions.

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РАЗВИТИЕ ГАМЕТОФИТОВ ИНТРОДУЦИРОВАННЫХ ВИДОВ *PICEA* (PINACEAE) В ТАЕЖНОЙ ЗОНЕ (КАРЕЛИЯ)

И. Т. Кищенко^{a, #}, В. В. Тренин^a

^a Петрозаводский государственный университет
пр. Ленина, 33, Петрозаводск, 185910, Россия

[#]e-mail: ivanki@karelia.ru

Исследования проводили в средней подзоне тайги. Цель настоящих исследований – установить особенности прохождения отдельных стадий спорогенеза, гаметогенеза и эмбриогенеза у аборигенного и интродуцированных видов *Picea* A. Dietr. в таежной зоне (Карелия). Объектами исследования служили аборигенный вид и два интродуцированных вида рода *Picea*. Оказалось, что общая схема мейоза в микроспороцитах у аборигенного и интродуцированных видов *Picea* в основном совпадает. У всех изученных видов он начинается почти одновременно (начало мая). Появление тетрад микроспор у *P. abies* наблюдается на 5–9 сут. раньше, чем у интродуцентов. Онтогенез мужского гаметофита исследуемых видов длится 3–8 сут. Пыление у *P. abies* и *P. canadensis* начинается (конец мая) на неделю раньше, чем у *P. pungens*. Исследованиями установлено, что продолжительность и сроки прохождения всех этапов микроспоро- и микрогаметогенеза определяются температурным режимом воздуха текущей вегетации. Для полного развития пыльцевых зерен у *P. abies* и *P. canadensis* требуется сумма положительных температур (>+5°C) 250°C, а у *P. pungens* – 360°C. На всех этапах формирования пыльцы отклонений от нормы не обнаружено. Исследованиями установлено, что в середине мая женский гаметофит находится еще на свободной стадии, а к началу июня он уже имеет клеточное строение. Эмбриогенез начинается в конце июля и заканчивается во второй декаде августа. У интродуцированных видов в развитии женской генеративной сферы и в ходе эмбриогенеза наблюдаются различные отклонения. От 37 до 51% семян интродуцентов лишены зародыша. Наибольший процент пустых семян и наиболее поздние сроки прохождения основных этапов морфогенеза отмечается у *P. pungens*.

Ключевые слова: гаметогенез, женский гаметофит, интродукция, пыльцевое зерно, спорогенез, хвойные, эмбриогенез, *Picea*

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