

Dynamics of the isoenzyme composition of peroxidase and pigments in the needles of the introduced species of *Picea* (L.) Karst. in the taiga zone (Karelia)

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Abstract

The study was conducted at the Botanical Garden of Petrozavodsk State University (middle taiga sub-zone). The subjects of the study were an indigenous species (*P. abies* (L.) Karst.), and five introduced species (*P. pungens* Engelm. f. *glauca* Regel., *P. pungens* Engelm. f. *viridis* Regel., *P. glauca* (Mill.) Britt., *P. omorica* (Pane) Purk., *P. mariana* Britt., *P. obovata* Ledeb.). The study established high variability of the isoperoxidase spectrum in the *Picea* species needles during the circannual cycle. Molecular forms of peroxidase typical for growth and dormant periods were determined. Some *Picea* species were found to have isoenzymes appearing only during the deep dormant period. An increase in the heterogeneity of the needles isoperoxidase spectrum and appearance of molecular forms of the enzyme typical for the dormant period were observed in the indigenous and introduced *Picea* species in the course of adaptation to unfavorable winter conditions. The isoenzyme system rearrangement ensures plants tolerance to external factors and homeostasis regulation. The content of chlorophyll and carotenoids in the needles of the studied species undergoes significant seasonal changes and is largely determined by their biological characteristics. Pigments concentration naturally increases by the end of the vegetative period and decreases slightly in winter. The total number of pigments in the needles of the indigenous and introduced species is almost the same, indicating a similar rate of stock formation. By the dormant period, the ratio of chlorophylls to carotenoids increases and reaches approximately the same level in all *Picea* species. The *Picea* species introduced in Karelia adapt to low winter temperatures with the same physiological changes as the indigenous ones. These include changes in the isoenzyme composition of peroxidase, the dynamics of the pigments content in the needles, and the ratio of chlorophylls to carotenoids. Potential tolerance of the studied plant species to unfavorable environmental factors is affected by the extreme factor of tension that does not exceed the threshold value.

Keywords

Picea, peroxidase isoenzymes, pigments, needles, taiga, introduction

Introduction

The majority of indigenous species of woody plants in the taiga zone of Russia do not tolerate progressive environmental pollution. However, species of conifers, including the genus *Picea* in other geographical areas, are fairly tolerant to pollution of air with gas and smoke, they are long-lived and decorative throughout the year (Plotnikova 1983; Vstovskaya 1983). Furthermore, many of them are significantly more productive than the local ones, and often can be naturalized (Kalutsky and Bolotov 1983; Mamaev and Makhiev 1996). According to some researchers (Mamaev and Makhiev 1996; Budantsev 1999), increasing biological diversity of natural and artificial plant communities is possible only through the introduction of woody plants. Therefore, these findings indicate the necessity of conifers introduction and evaluation of its potential perspectives. The latter can be done only on the basis of a comprehensive study of adaptations occurring in the plants tested in new growing conditions (Voroshilov 1960; Bazilevskaya 1964).

In Karelia, the main environmental factor limiting the growth and development of plants is low air temperatures in winter. The research of many authors (Novitskaya 1971; Sergeeva 1971; Tumanov 1979; Petukhova 1981; Trunova 1990) showed that plants tolerance to low temperatures is achieved when they prepare for the deep dormant period through specific physiological and cytological rearrangements. Enzymes catalyzing oxidation and reduction reactions, as the most sensitive structures, can characterize the adaptive abilities of plants in new growing conditions (Klimachenko 1972). Peroxidase catalyzes the oxidation of a number of organic compounds and plays an important role in plants respiration, growing processes regulation, and lignin synthesis (Esterbauer et al. 1978; Larionova 1978; Semkina 1981). The diversity of these functions explains the presence of a large

number of molecular forms of the enzyme (Kavac and Rone 1975; Andreeva 1988; Sidorov et al. 1989). Previous studies (Osnitskaya 1965; Petrenko et al. 1970; Ozolina and Mochalkin 1972; Khodasevich 1982; Kopsell and Kopsell 2006; Yatsko et al. 2009; Jahns and Holzwarth 2012; Golovko et al. 2013; Latowski et al. 2014) reported that the state of the pigment system, the dynamics and ratio of its components can also serve as reliable indicators of the degree of plants adaptation to many factors, including low temperatures. However, peroxidases composition and needles pigment composition of the species introduced in Karelia have not been studied yet.

The objective of the study is to determine the specific aspects of seasonal dynamics in the peroxidase isoenzymes composition and the content of pigments in the needles of the introduced *Picea* species.

Materials and methods

The study was conducted at the Botanical Garden of Petrozavodsk State University, located in the taiga zone. The subjects of the study were an indigenous species and five introduced *Picea* species (Table 1).

Table 1. Description of the studied subjects

Species	Place of seedlings origin (Botanical garden – city)	Medium age, year	Average height, m	Seed production
<i>Picea abies</i> (L.) Karst.	Petrozavodsk	19	5.8	no
<i>P. abies</i> (L.) Karst.	Petrozavodsk	50	16.0	yes
<i>P. pungens</i> Engelm. f. <i>glauca</i> Regel.	St. Petersburg	36	12.7	yes
<i>P. pungens</i> Engelm. f. <i>viridis</i> Regel.	St. Petersburg	36	10.7	yes
<i>P. glauca</i> (Mill.) Britt.	St. Petersburg	33	11.2	yes
<i>P. omorica</i> (Pane) Purk.	Bucharest	27	5.7	no
<i>P. mariana</i> Britt.	Bucharest	19	4.7	no
<i>P. obovata</i> Ledeb.	Minsk	23	6.4	no

For biochemical analysis, one-year needles were taken from several trees of each species from different sides of the middle part of the crowns, with average weighed quantity being prepared for each species. Needles were sampled 5 times a year (2002–2003) during the periods of vegetative buds swelling (May), intensive growth of shoots (end of June), transition to the deep dormant period (mid-September), deep dormant period (late October), and forced dormancy period (February). The results of the previous studies (Kishchenko 2000) proved that the differences in the duration of these phenological stages in the studied species did not exceed one week, and, therefore, simultaneous sampling seemed to be appropriate. The states of deep and forced dormancy were established in the laboratory according to vegetative buds swelling.

The needle samples were frozen with liquid nitrogen and ground in an electric mill to determine the isoenzyme composition of peroxidase. The enzymes extraction from the plant material was carried out with tris-glycine buffer (pH 8.3) containing 0.1% EDTA, 1% Triton X – 100 (Larionova 1979). Dowex 1–8 ion exchange resin (200–400 mesh) was used for proteins purification from phenols. Extraction was performed for 1 hour in the refrigerator. A 10% acrylamide solution was used at current power of 2 W. Isoenzymes were separated by the method of polyacrylamide gel electrophoresis (Safonov and Safonova 1969; Mauer 1971). Zones with enzymatic activity were gel stained after Safonov and Safonova (1971). The mobility of individual isoforms in an electric field was measured as the value of relative electrophoretic mobility (R_f). It was calculated by dividing the distance covered by the fraction by the distance covered by the dye marker (bromophenol blue) from the start to finish. Peroxidase spectra consisted of low, medium, and high mobility fractions. Relative electrophoretic mobility R_f of fractions with low mobility ranged from 0 to 0.33, with the medium one from 0.34 to 0.66, and with the high one from 0.67 to 1.0 (Sadvakasova and Kunaeva 1987). The content of pigments was determined by the method of Limar and Sakharova (1973).

Results

The spectrum of peroxidase isoforms was characterized by a very high lability, which allowed designating it as a marker of a plant physiological state. (Polozova 1978; Gordey et al. 1988; Negru et al. 1988; Savich and Peruvian 1990). The study showed that the isoenzyme peroxidase spectrum of the studied *Picea* species was highly variable during a year and contained only 1–2 stable fractions in each species. In *P. abies*, *P. pungens*, and *P. glauca*, the heterogeneity of isoperoxidases composition increased with the transition from growth to dormancy periods, which is not typical of *P. omorica*, *P. mariana*, and *P. obovata*. The maximum number of enzyme isoforms (14) was determined in young *P. abies* trees during the deep dormant period (Table 2). R_f of isoforms depended on the size of the enzyme molecule and its charge: smaller and highly charged molecules moved faster through the molecular sieve of the polyacrylamide gel in the electric field.

The variety of peroxidase isoenzymes resulted from changes in the amino acid composition of the protein part of the enzyme molecule, the composition of sugars in the carbohydrate part, or aggregation of low molecular weight forms (Sadvakasova and Kunaeva 1987). Most of the peroxidase isoforms in the needles of the studied species had an average mobility. During the period of forced dormancy in many species (except for *P. glauca* and *P. mariana*), the number of fractions of the enzyme increased (from 4 to 6 isoforms; Table 2) in the zone of low mobility.

From 15 to 20 different peroxidase isoenzymes were recorded during the year in each of the studied species. In general, for the *Picea* species, the highest frequency of occurrence was found for fractions with R_f of 0.43–0.46; 0.40–0.42; 0.53–0.56; 0.37–0.39, and 0.71–0.75.

The study revealed isoforms that appeared in the *Picea* species needles only during the periods of growth or dormancy. Thus, there were isoforms with R_f of 0.30–0.32, and 0.37–0.39 in the *P. glauca* needles during the vegetative growth. Their mobility slightly changed with the onset of dormancy and some isoenzymes appeared with R_f of 0.33–0.35, and 0.40–0.42.

Table 2. Peroxidase isoenzymes in the needles of different *Picea* species at different phenophases

R _f	No. of fractions	<i>Picea abies</i> (19 years)	<i>P. abies</i> (50 years)	<i>P. pungens</i> f. <i>glauca</i>	<i>P. pungens</i> f. <i>viridis</i>	<i>P. glauca</i>	<i>P. mariana</i>	<i>P. omorica</i>	<i>P. obovata</i>
Vegetative buds swelling (mid-May)									
0.03–0.05	1	+							+
0.07–0.09	2			+	+				
0.12–0.14	3			+			+		
0.20–0.22	4			+		+			
0.23–0.25	5			+	+				
0.28–0.29	6				+		+		
0.30–0.32	7	+	+		+	+			+
0.34–0.36	8			+	+				+
0.37–0.39	9	+		+	+	+	+	+	
0.41–0.42	10								+
0.43–0.45	11	+	+			+		+	+
0.47	12					+			
0.48–0.50	13					+	+	+	
0.51–0.53	14	+	+				+		
0.54–0.55	15			+				+	
0.58–0.59	16						+		
0.62–0.63	17								+
0.65–0.67	18					+			
0.68–0.70	19			+	+				
0.71–0.73	20	+	+				+		
0.75–0.76	21					+			+
0.80–0.82	22	+	+		+			+	
0.86	23								
Number of isoforms		7	5	8	8	8	7	5	7
Intensive shoot growth (mid-June)									
0.05–0.07	1		+		+			+	+
0.10–0.12	2			+			+		
0.17–0.19	3		+		+			+	+
0.20–0.22	4	+	+		+				+
0.27–0.29	5	+					+	+	+
0.30–0.32	6	+			+	+	+	+	+
0.34–0.36	7	+	+				+	+	
0.37–0.39	8			+	+	+			+
0.40–0.42	9	+	+				+	+	
0.43	10			+	+			+	
0.45–0.46	11	+	+						+
0.48–0.50	12	+		+	+	+		+	
0.53–0.55	13			+	+	+	+		+
0.58	14						+	+	
0.63–0.65	15	+	+	+					
0.70–0.72	16							+	+
0.73–0.75	17	+	+			+			
0.77–0.78	18	+		+			+		
0.82	19				+				
Number of isoforms		10	8	7	9	5	8	10	9
Transition to deep dormancy (end of September)									
0.03–0.06	1	+		+	+				+
0.10–0.12	2								
0.16–0.18	3			+	+	+		+	+
0.21–0.22	4		+	+	+		+	+	
0.25–0.27	5		+	+					

R_f	No. of fractions	<i>Picea abies</i> (19 years)	<i>P. abies</i> (50 years)	<i>P. pungens</i> f. <i>glauca</i>	<i>P. pungens</i> f. <i>viridis</i>	<i>P. glauca</i>	<i>P. mariana</i>	<i>P. omorica</i>	<i>P. obovata</i>
0.29–0.30	6			+	+	+			
0.31–0.32	7		+	+	+				+
0.34–0.36	8			+	+	+	+		
0.37–0.39	9	+	+						+
0.40–0.41	10			+	+	+	+	+	
0.42–0.44	11	+	+		+	+			
0.45–0.47	12						+	+	
0.48–0.49	13	+							
0.51–0.52	14							+	
0.53–0.55	15	+	+					+	+
0.56–0.58	16					+	+		
0.60	17								+
0.63–0.65	18			+	+	+	+	+	
0.66–0.69	19	+	+					+	
0.71–0.73	20			+	+	+			+
0.74–0.76	21	+					+		+
0.77–0.79	22	+	+			+			
0.82–0.84	23	+						+	+
Number of isoforms		9	8	10	10	9	7	9	9
Deep dormancy (October)									
0.03–0.05	1	+	+			+	+	+	
0.07–0.09	2	+		+	+				+
0.11	3							+	
0.14–0.15	4			+	+				
0.33–0.35	5		+	+		+	+		+
0.37–0.38	6	+	+				+		+
0.39	7								+
0.40–0.42	8	+	+	+	+	+	+	+	+
0.43–0.45	9	+		+	+				+
0.46	10	+					+		
0.47–0.49	11	+		+	+	+		+	+
0.51–0.52	12	+	+	+					
0.53–0.54	13	+		+	+	+			
0.55–0.56	14	+						+	
0.58–0.59	15	+	+					+	
0.63	16					+			
0.68–0.69	17	+		+	+				
0.70–0.71	18					+		+	
0.76–0.78	19	+	+			+	+		
0.80–0.81	20			+	+				+
0.82–0.84	21	+	+				+	+	+
Number of isoforms		14	8	10	8	8	7	8	9
Forced dormancy (February)									
0.04–0.05	1		+						+
0.08–0.10	2	+	+	+	+	+		+	
0.14–0.15	3		+	+	+				
0.17–0.18	4	+			+			+	+
0.21–0.22	5	+		+	+			+	
0.24	6	+	+						+
0.26–0.27	7				+	+	+		
0.29–0.30	8	+	+	+					+
0.31–0.32	9			+	+				
0.33–0.35	10		+			+	+	+	+

R_f	No. of fractions	<i>Picea abies</i> (19 years)	<i>P. abies</i> (50 years)	<i>P. pungens</i> f. <i>glauca</i>	<i>P. pungens</i> f. <i>viridis</i>	<i>P. glauca</i>	<i>P. mariana</i>	<i>P. omorica</i>	<i>P. obovata</i>
0.37–0.39	11	+		+	+		+		+
0.40–0.42	12	+	+			+			
0.44–0.46	13						+	+	+
0.47–0.49	14	+		+	+				
0.50–0.52	15		+			+	+	+	+
0.57–0.60	16			+	+	+	+	+	
0.61–0.63	17	+	+			+			+
0.64–0.66	18		+	+	+		+		
0.69	19					+			
0.71–0.73	20	+	+					+	+
0.75	21						+		
The number of fractions		10	11	9	10	8	8	8	10

P. mariana fractions with R_f of 0.12–0.14 and 0.28–0.29 were characteristic for the period of growth, and fractions with the R_f of 0.45–0.46 were characteristic for the dormancy period. In the needles of some *Picea* species isoperoxidases were determined as appearing only in the period of deep dormancy. For example, in *P. abies* these were fractions with R_f of 0.58–0.59; 0.76–0.78 and 0.82–0.84; in *P. obovata*, this isoform had R_f of 0.37–0.38 and 0.39 (two instead of one with R_f 0.37–0.39), 0.47–0.49 and 0.80–0.81. In addition to other characteristics, molecular forms of peroxidase differed by the optimal conditions necessary for the of catalytic activity manifestation (Sadvakasova and Kunaeva 1987). Different environmental conditions during the periods of growth and dormancy affected the activity of various peroxidase isoforms. This explains the change in the spectrum of isoperoxidases when phenological phases change.

Comparison of isoenzymes sets of different species and forms of the genus *Picea* showed similarities between related forms, especially in the dormancy period. Therefore, during the growth period (June) *P. pungens* f. *glauca* and *P. pungens* f. *viridis* were found to have four or five identical fractions out of seven or nine; during the dormancy period they had eight or nine forms out of ten. In *P. abies* trees of different ages, the sets of isoenzymes contained five –seven similar forms when the number of fractions was changing from five to thirteen during May – October, and during the period of forced dormancy in February they were almost the same: nine out of ten or eleven.

Discussion

Thus, the high variability of the spectrum of peroxidase isoenzymes in the needles of the studied species during the year was established. Only 1–2 components of the spectrum in each species or form remained stable. Molecular forms of peroxidase present in the needles only during the periods of growth or dormancy were determined. They obviously performed different functions in the plant: some of them were involved in the growth process, while the others played the protective function by ensuring the plants ability to procure the energy necessary for life-sustaining activity during the winter period (Voronkov 1967; Polozova 1978; Negru et al. 1988).

Peroxidase is considered to be the main winter respiratory system (Okuntsov and Aksenova 1960). In the local species, as well as in some introduced species (*P. pungens*, *P. glauca*), the number of peroxidase isoenzymes in the dormant period is greater than during the growing season. The number of fractions in the spectrum of isoforms in *P. mariana*, *P. omorica* and *P. obovata* does not increase during the period of transition from growth to dormancy, only their qualitative change takes place. The studies of the Pinus species (Semkina 1985), the *Picea* species (Kavac and Rone 1975; Kavac 1978), and the Larix species (Larionova 1979) showed that the growth period during spring-summer is characterized by an impoverished spectrum of peroxidase isozyme fractions, and during autumn-winter – by the enriched one.

The study of an important physiological indicator of tolerance resistance – the composition of peroxidase isoenzymes – revealed the similarity of adaptation mechanisms in different species and forms of the genus *Picea*. During the adaptation to unfavorable winter conditions indigenous species as well as the introduced ones showed the tendency to increase the heterogeneity of the isoperoxidases spectrum in the needles and to appearance of molecular forms of the enzyme typical for the dormant period. The isoenzyme system rearrangement ensured plants tolerance to external factors and homeostasis regulation (Redkin 1974).

Environmental changes were primarily reflected in chloroplasts, where green and yellow pigments play a major role in carbon dioxide assimilation. It was established that the content of plastid pigments in the leaves of relatively frost-resistant species and varieties of fruit crops was much higher (Novitskaya 1967). Therefore, the study of adaptation mechanisms of woody plants in the areas with harsh climatic conditions should include the determination of the pigment system state in comparison with that of the sustainable indigenous species.

The results of the studies allowed us to establish that the amount of plastid pigments in the needles of the studied *Picea* species underwent significant seasonal fluctuations (from 0.45 to 1.30 mg/g of raw material). Their content naturally increased (more than twofold) during the growing season, reaching a maximum in autumn, and then decreased slightly (by 20–25%) in winter. The content of the total plastid pigments in the needles of *P. mariana* and *P. obo-*

vata throughout the year was by 20–40% higher than that of the other studied species. A similar trend was observed in the dynamics of separate components of the pigment system: in chlorophyll ‘a’ and ‘b’, as well as in carotenoids.

The ratio of content of chlorophyll ‘a’ to that of chlorophyll ‘b’ in the needles of the studied plant species gradually decreased from spring to winter (from 3 to 2, Table 3). The ratio of the green pigment amount to the yellow pigment amount increased by the dormant period (Table 3). In the autumn-winter period, the value of this indicator in all studied *Picea* species reached approximately the same level (about 3). This indicates a significant similarity in the pigment stock formation in the needles of indigenous and introduced species. Consequently, the photosynthesizing apparatus of the introduced *Picea* species can rebuild its pigment system in order to adapt it to harsh winter conditions just as the indigenous species, *P. abies*, do. The research results of Protsenko and Sirenko (1964) (cited after Novitskaya 1967) and Khodasevich (1982) indicate that the concentration of pigments in the needles can be considered as an indicator of plant resistance to unfavorable environmental factors.

Plastid pigments are known to be involved in many physiological and biochemical processes of the plant organism (Ozolina and Mochalkin 1972; Sofronova et al. 2016). In addition, it was established (Osnitskaya 1965; Petrenko et al. 1970) that the effect of unfavorable factors on plants can cause protective-adaptive reactions, consisting in pigments transition to the function of oxidant or stimulator of oxidative phos-

Table 3. Dynamics of some indicators of pigments content in the needles of various *Picea* species (2002–2003)

Species	The ratio of chlorophylls ‘a’ to ‘b’					The ratio of the amount of chlorophylls to the amount of carotenoids				
	13 V	15 VI	21 IX	19 X	4 II	13 V	15 VI	21 IX	19 X	4 II
<i>Picea abies</i> (19 years)	3.27	2.98	2.94	3.11	2.00	2.44	2.71	3.24	3.24	3.00
<i>P. abies</i> (50 years)	3.25	2.74	3.11	3.19	2.29	2.46	2.75	3.00	3.14	3.29
<i>P. pungens</i> f. <i>glauca</i>	2.44	2.72	2.31	2.53	2.33	2.64	2.85	3.42	3.33	3.00
<i>P. pungens</i> f. <i>viridis</i>	3.05	2.66	2.78	2.66	2.22	2.76	2.72	3.07	3.15	3.45
<i>P. glauca</i>	2.79	2.94	2.70	3.09	2.25	2.72	2.71	3.15	2.79	3.59
<i>P. omorica</i>	2.74	2.57	2.92	2.72	2.40	2.38	2.53	3.17	3.13	3.28
<i>P. mariana</i>	2.88	2.86	2.60	2.77	2.30	2.28	2.54	3.04	3.14	3.50
<i>P. obovata</i>	2.61	3.10	2.63	2.50	1.80	2.67	2.64	3.12	2.84	2.92

phorylation and ATP formation, and, therefore, their content increases. Probably, this fact could explain the increase in the content of pigments in the needles of *P. mariana* and *P. obovata* during the whole year as compared with other introduced species.

Conclusion

The study established high variability of the isoperoxidase spectrum in the *Picea* species needles during the annual cycle. Molecular forms of peroxidase typical for growth and dormant periods were determined. Some *Picea* species were found to have isoenzymes that appear only during the deep dormant period. Different isoforms of peroxidase seem to be active in different environmental conditions, and, therefore, in different phases of tree development: during the vegetative growth or the dormant period.

During the dormant period the local species and some introduced species have a greater number of peroxidase isoenzymes than during the growing season. In *P. omorica*, *P. mariana*, and *P. obovata* the number of fractions in the isoforms spectrum does not increase during the transition from growth to dormancy but only their qualitative change takes place. Thus, in the course of adaptation to unfavorable winter conditions indigenous and introduced *Picea* species demonstrate the increase in the heterogeneity of the isoperoxidases spectrum in the needles as well as the appearance of molecular forms of the enzyme typical of the dormant period. The isoenzyme system rearrangement ensures plants tolerance to external factors and homeostasis regulation.

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The content of chlorophyll and carotenoids in the needles of the studied species undergoes significant seasonal changes and is largely determined by their biological characteristics. The concentration of pigments naturally increases by the end of the vegetative period, and decreases slightly in winter. The total number of pigments in the needles of indigenous and introduced species is relatively the same, indicating a similar rate of their stock formation. By the onset of the dormant period, the ratio of the amount of chlorophyll to the amount of carotenoids increases and reaches approximately the same level in all *Picea* species.

Plants adaptation to extreme environmental impact is a complex system of processes controlled by the self-regulation system of the organism. Introduced species in new climatic conditions use the same adaptation mechanisms as the indigenous ones. Thus, the *Picea* species introduced in Karelia adapt to low winter temperatures in the same ways as the local species do. They have similar physiological changes including the changes in the isozyme composition of peroxidase, the dynamics of the pigment content in needles, and the ratio of chlorophylls to carotenoids. Potential tolerance of the studied plant species to unfavorable environmental factors is affected by the extreme factor of tension that does not exceed the threshold value.

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