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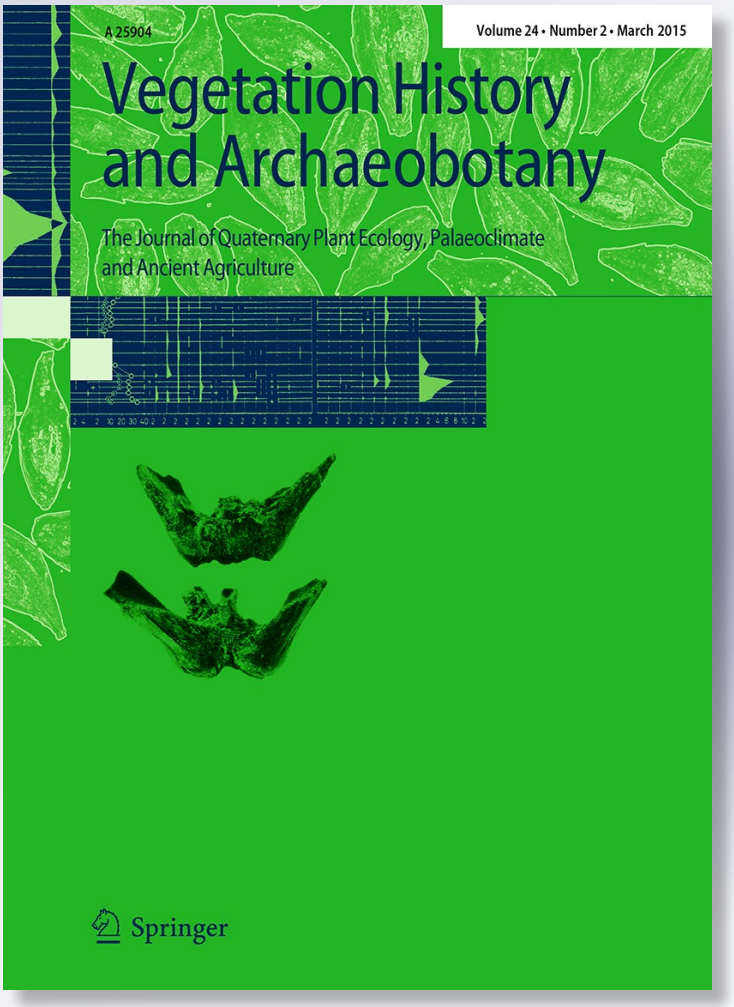

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ORIGINAL ARTICLE

Representation of *Picea* pollen in modern and surface samples from Central European Russia

Maria B. Nosova · Elena E. Severova · Olga A. Volkova · Jana V. Kosenko

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Abstract *Picea* pollen abundance (percentage and PAR) was investigated in 23 Tauber pollen traps located in the mixed coniferous-broadleaved forest zone, broadleaved forest zone and forest-steppe zone in the European part of Russia. Modern data were compared with fossil pollen diagrams. In the modern spectra of non-forest zones average *Picea* pollen percentage is about 1 %, the highest values (up to 3 %) are usually connected with open locations and reflect the regional component of pollen rain. Within the coniferous forest belt average pollen abundance is about 10 %, but this value varies considerably from 1 to 40 % depending on local characteristics of sampling points. The lowest *Picea* pollen percentages (1 % and less) are observed in the pollen spectra of oligo- and mesotrophic mires, thus the level of 1 % can be significant for *Picea* and can indicate the continuous range of *Picea*. For an appropriate interpretation of low *Picea* pollen abundance in fossil samples the abundance should be analyzed together with other components of the pollen spectra. Large areas of *Picea* forests are not always reflected in pollen spectra as a high *Picea* percentage/PAR, as in unfavorable climatic or hydrological conditions the pollen production of *Picea* forests can be very low. Comparison of fossil and modern pollen spectra shows that a modern analogue of Holocene *Picea* forests in Central European Russia has not yet been discovered.

Keywords *Picea* · Holocene · Modern pollen · Surface samples · Tauber trap · Russia

Introduction

Appropriate interpretation of Holocene pollen diagrams is impossible without a thorough understanding of the vegetation–pollen relationship. The investigation of modern (recent and subrecent) pollen deposition patterns in different vegetation types is an essential source of information in order to establish such a relationship. Special attention should be paid to the natural boundaries of vegetation zones (Hicks and Sunnari 2005; Jenssen et al. 2007; Poska and Pidek 2010) and to the distribution limits of the main forest forming taxa (Hicks 1999, 2001; Seppä and Hicks 2006; Hättestrand et al. 2008). In order to use the method of modern analogues for interpretation of fossil spectra we need to understand how the abundance of a taxon in the vegetation is reflected in sediment pollen spectra (Overpeck et al. 1985; Birks and Gordon 1985). Estimates of the pollen accumulation rate (PAR) can help to avoid the inherent mutual interference of percentage data and allow us to evaluate the independent contribution of each individual taxon (Seppä and Hicks 2006). Unfortunately, the fossil PAR data are very sensitive to many errors. For example, they require strong chronological control and in the case of insufficient numbers of datings, the accuracy of the results decreases. PARs are strongly dependent on basin location and size and do not always reflect the vegetation adequately.

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Pollen production near the boundaries of vegetation zones and close to the species distribution limits is more influenced by external environmental factors than in the centre of a range (Kuoppamaa et al. 2009). On the other hand, even pollen production within a distribution area is dependent on a combination of a number of climatic, soil and hydrological factors, light conditions, nutrient availability etc., which may vary in different parts of the area. Therefore, for estimating vegetation changes in the Holocene it is necessary to investigate modern pollen rain on large territories.

The most important ecotones in Central European Russia are the transitions from the southern taiga to coniferous-broadleaved forests, then to broadleaved forests and, finally, to the forest-steppe zone. *Picea* and broadleaved trees can be considered the most important indicators of these transitions.

Spruce (*Picea* A. Dietr.) is the dominant forest taxon in the taiga and in the coniferous-broadleaved forest zones of European Russia. Its northern range limit extends to just south of the tundra boundary in western European Russia and approximately along the Polar Circle east of the White Sea. The southern boundary is associated with the forest-steppe zone and is characterized by the aggregation of isolated patches (Kiseleva 1976). Continuous *Picea* forests are not found south of the Moscow region.

The species composition of the genus *Picea* in European Russia is still unclear. Some authors recognize two species, *P. abies* (L.) Karst. and *P. obovata* Ledeb., which hybridize with each other on a broad belt (about 100 km wide) in central and northern parts of European Russia and form *Picea* × *fennica* (Regel) Kom. via introgressive hybridization (Bobrov 1970; Schmidt-Vogt 1977). A second point of view claims that there is one species *P. abies* (L.) Karst. with two subspecies: *P. abies* ssp. *abies* and *P. abies* ssp. *obovata* (Pravdin 1975; Goncharenko and Potenko 1991; Krutovskii and Bergmann 1995; Latałowa and Van der Knaap 2006). Palaeogeographic aspects of the resettlement of these taxa have been discussed by different authors (Bobrov 1970; Moe 1970; Serebrianiy 1974; Ilves and Sarv 1975; Huntley and Birks 1983; Hafsten 1986; Van der Knaap et al. 2005; Giesecke 2005; Latałowa and Van der Knaap 2006; Savelieva 2007; Kozharinov et al. 2010; Feurdean et al. 2011), but the situation in the eastern part of the *Picea* range needs further investigation.

The relationship between the abundance of *Picea* in vegetation and its reflection in pollen spectra has been broadly discussed in the literature (Grichuk and Zaklinskaya 1948; Mal'gina 1950; Kupriyanova 1951; Fedorova 1952a; Moe 1970; Jazvenko 1992; Blagoveschenskaya 1995; Van der Knaap et al. 2005; Filimonova 2005; Kozharinov et al. 2010; Lisitsyna et al. 2011). The minimum significant percentage value for modern samples is 2.5 % (Prentice 1978). For fossil samples the minimal values are lower: 1 % (Giesecke and Bennett 2004; Tanţău et al. 2006; Savelieva 2007) or 2 % (Kozharinov et al. 2010). Based on Soviet studies, within the continuous *Picea* range, the significant level can increase up to 10 % (Grichuk and Zaklinskaya 1948), and to the south of the continuous range it can vary from 1 to 5 % (Mal'gina 1950). According to the latter author, the abundance of *Picea* in pollen spectra within the forest zone varies from 12 to 40 %, in rare cases up to 50 %, and near the range boundary 8–9 % (up to 30 % in the Urals). Furthermore, the percentage of *Picea* depends on other components of the vegetation: for example, in Meschera, within the continuous range, percentage of *Picea* is about 1 % because of domination of *Pinus* forests with high pollen loading (Mal'gina 1950). On the other hand, Sugita et al. (2010) have shown that the absolute pollen productivity of *Picea* in northern boreal forest in Finland is actually higher than that of *Pinus*. However the pollen loading of *Pinus* is higher due to the fact that *Pinus* is usually more abundant and also its pollen is dispersed more easily. In Central Russia *Pinus* pollen is more abundant than *Picea* even in the regions with small areas of *Pinus* forests. The problem of *Picea* and *Pinus* loading and production in this region needs future investigations.

The nature of the relationship between the abundance of *Picea* in pollen spectra and its abundance in the vegetation became crucial for us when we compared surface and modern pollen spectra with the Holocene pollen diagram of the Central Forest State Natural Biosphere Reserve (Nosova 2009; Novenko et al. 2009). Despite the highly significant role of *Picea* in the vegetation, its percentage values in subfossil pollen spectra are only about 15–18 % in pure *Picea* forests, 11–12 % in swamp *Pinus* forest and less than 1 % in the middle of large mires (Novenko et al. 2011). Simultaneously, the percentage of *Picea* in the Holocene pollen diagram is 40 % (AP + NAP) or more (Nosova 2008, 2009; Novenko et al. 2009). This is not a unique situation: high percentages of *Picea* pollen (up to 50 %) were observed in the Subboreal in three lake sequences in NW Russia—Valdai, Kubenskoe and Vyshnevskoe (Davydova et al. 2001), in northern Belarus (Lozoviki, Osveyskoe—Zernitskaya and Mikhailov 2009) and eastern Estonia (Plaani, Raigasvere—Saarse et al. 2009).

What may be the possible reasons for differences between modern and Holocene percentages? What percentages and PAR values for *Picea* pollen can be used to characterize different vegetation zones in present conditions? What threshold values can we offer for *Picea* in Central European Russia? And how do local vegetation conditions affect the influx of *Picea* pollen? All of these questions are discussed in the present paper.

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Materials and methods

Modern pollen data were obtained from 23 Tauber pollen traps located in the mixed coniferous-broadleaved forest zone (four different variants), the broadleaved forest zone and the forest-steppe zone in the European part of Russia (6 model territories in 4 regions—Pskov Region, Tver Region, Moscow Region, Tula Region—Fig. 1). All these regions except Pskov Region are characterized by moderately continental climate; Pskov is located in the zone of transition from continental to marine climate. Trap locations within each zone reflect different habitats: open plant communities (mires, agricultural/abandoned areas), the forest edge and closed plant communities (gaps within a forest).

Location of pollen traps (Fig. 1; Table 1)

1. Polistovsky Natural Reserve (RU-PL) is situated in the Pskov Region in north-western European Russia, in the northern part of the coniferous-broadleaved forest zone. The main part of the Reserve is occupied by meso- and oligotrophic bogs of the Polistovo-Lovat Mire System. The dominant vegetation types are deciduous and mixed secondary forests with *Betula* and *Alnus*. Four pollen traps were established (2 bog margins—meso- and oligotrophic, a mineral island with mixed forest and an open bog) in 2007, but these were regularly damaged due to various circumstances, so we have only fragmentary data for this point.
2. Biological Station "Chisty Les" (RU-TR) is located in the sandy soil type of coniferous-broadleaved forest zone in the Tver region, Toropets district. Three pollen traps (near the bog edge, on the open bog and in the centre of a small open mire surrounded by *Pinus* forest) were placed in 2009.
3. Central Forest State Natural Biosphere Reserve (RU-CF), Tver Region, is situated on the south slope of the Valdai Hills, at the watershed of the main rivers of the Russian Plain—the Volga, Western Dvina and Dnieper. This territory is a good example of an area with low disturbance. Seminatural *Picea* and secondary *Betula*/*Populus* forests are the dominant vegetation types, so the vegetation of the territory looks like southern taiga despite the fact that it formally belongs to the coniferous-broadleaved forest zone. Four pollen traps were established in 2007 (in the gap within the mixed forest, in the bog-pine forest, on the open mire and at the bog margin near the abandoned village).
4. Zvenigorod Biological Station of Moscow State University (RU-ZV), Moscow Region, is located in the densely populated suburban belt of Moscow. The dominant vegetation types on the watershed are secondary *Picea*, *Pinus–Picea* and *Picea–Betula* forests of 80–100 years old. In 2011–2012 the *Picea* forests were greatly damaged by the European *Picea* bark beetle (*Ips typographus*). The banks of the Moscow River are covered by coniferous-broadleaved forests. Six pollen traps were established in *Betula*, *Picea* and mixed forests, in the cutting area, in the centre and near the edge of the oligotrophic bog.
5. Tulskie Zaseki, in the surroundings of Tula (RU-TU), 190 km south of Moscow, in the broadleaved forest belt. This region has been under very intensive agricultural activity since the Neolithic age. The vegetation today consists of fragmentary old broadleaved forests (the remains of the forest belt which possessed defensive value in the Middle Ages), surrounded by agricultural lands and suburban areas. Three traps were established in 2009 on the mires in karst sinks (2 mires surrounded by broadleaved forests and another one near the settlement in open landscape).
6. The southernmost sampling point is also situated in Tula Region in the territory of the Military History and Natural Reserve "Kulikovo Field" (RU-KP) in the forest-steppe zone. The territory of the Reserve is covered by arable and abandoned lands, steppe-faced meadows, small areas of natural steppes and mixed

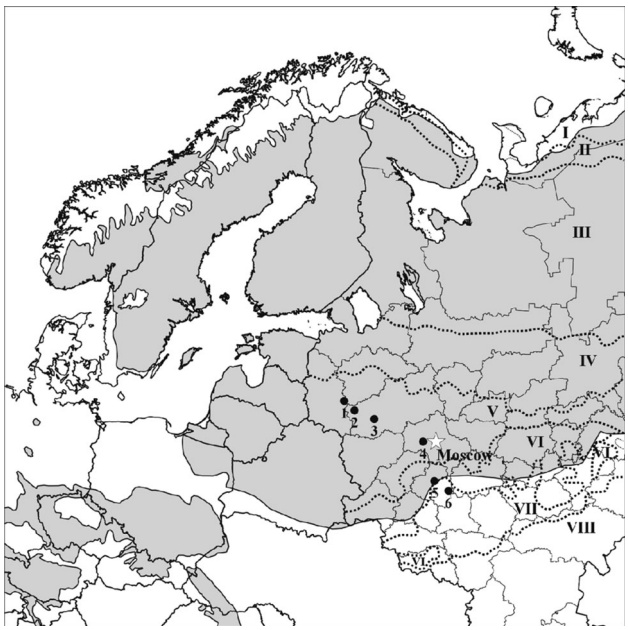

Fig. 1 Distribution of *Picea* and PMP-sites (points *1–6*) within the European part of Russia based on: Distribution map of Norway spruce (*Picea abies*) EUFORGEN 2009, www.euforgen.org. Vegetation zones: *I* tundra; *II* forest-tundra; *III* northern and middle taiga; *IV* southern taiga; *V* broadleaved-coniferous forests; *VI* broadleaved forests; *VII* forest-steppe; *VIII* steppe (based on Gribova et al. 1980); *1–6* PMP sites (see Table 1 for detailed information)

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Table 1 Location and regional vegetation of PMP points in Central European Russia *Picea* and mixed forests within a 5 km radius of trapping site (% of area)

Point No, code, location	Coordinates	Regional vegetation	Years examined	No of traps	% of 5-km radius area	
					Picea forests and plantings	Mixed forests with *Picea*
1. RU-PL* Pskov Region, Polistovsky Reserve	57°04′ N 30°40′ E	Coniferous-broadleaved forests, Polistovo-Lovatskaya mire system	2008-2012	4	0.22	14.84
2. RU-TR Tver Region, Chisty Les Biology station	56°44′ N 31°31′ E	Coniferous-broadleaved forests on sands	2010-2012	3	0	17.48
3. RU-CF* Tver Region, Central Forest Natural Reserve	56°28′ N 33°02′ E	Southern taiga – coniferous-broadleaved forests transition	2008-2012	3 (4 after 2010)	27.12	23.73
4. RU-ZV* Moscow Region, Zvenigorod Biology Station	55°40′ N 36°42′ E	Coniferous-broadleaved (mixed) forests	2008-2012, 2010-2012	3*+3	8.07	34.62
5. RU-TU Tula Region, Tulskie Zaseki	54°03′ N 37°35′ E	Broadleaved forests	2010-2012	3	0.32	0
6. RU-KP Tula Region, Kulikovo Field	53°40′ N 38°38′ E	North forest-steppe	2010-2012	4	0	1.34

* 5-year series of observations

forests. Four Tauber traps were placed on the steppe slope, at the eutrophic mire in the floodplain, at the abandoned field and at the steppe-faced meadow.

Vegetation maps

Vegetation maps based on satellite images were created for all territories within a 5 km radius of the trap locations (Fig. 2). The dominant taxa of the key areas were determined by visual decryption of satellite images using Quantum GIS 1.7. In addition, data from forest surveys were used for the decryption. Five types of vegetation with different levels of *Picea* abundance were determined for each model territory:

- *Picea* forests (>50 % of *Picea*)
- *Picea* plantations (>50 % of *Picea*)
- mixed forests with *Picea* (20–50 % of *Picea*), *Pinus* and/or small-leaved trees (*Populus*, *Betula*, *Alnus*)
- small-leaved deciduous forests with young *Picea* in undergrowth
- other forests (mixed deciduous of *Betula* and broad-leaved trees, or *Pinus*, or *Alnus glutinosa*)

All these vegetation types are shown on the maps for each model territory (Fig. 2) The total area of *Picea* forests (including *Picea* plantations) and forests with an admixture of *Picea* was calculated as a percentage of the 5 km radius area around the trap locations (Table 1).

Trap treatment

All modified Tauber traps were installed and treated according to PMP guidelines (Hicks et al. 1996; Hicks 1999). The traps operated throughout the year; the final collection of the traps was in October–November. *Lycopodium* tablets were added to each sample before laboratory treatment for calculation of annual PARs (Stockmarr 1971). The slides were analyzed under a light microscope (400×–1000×). At least 500 pollen grains were counted for each sample. Percentage diagrams and diagrams of PAR were produced with the programs TILIA and TGVIEW 2.0.2 (Grimm 1991). Pollen sums include arboreal and non-arboreal pollen and spores, and exclude pollen of aquatic plants and *Sphagnum* spores.

Numerical methods

Pearson's correlations were calculated in Statistica 7.0 for comparison of pollen abundance (PAR average and PAR maximum) in the spectra with the total area of *Picea* forest or the sum of *Picea* and mixed forests.

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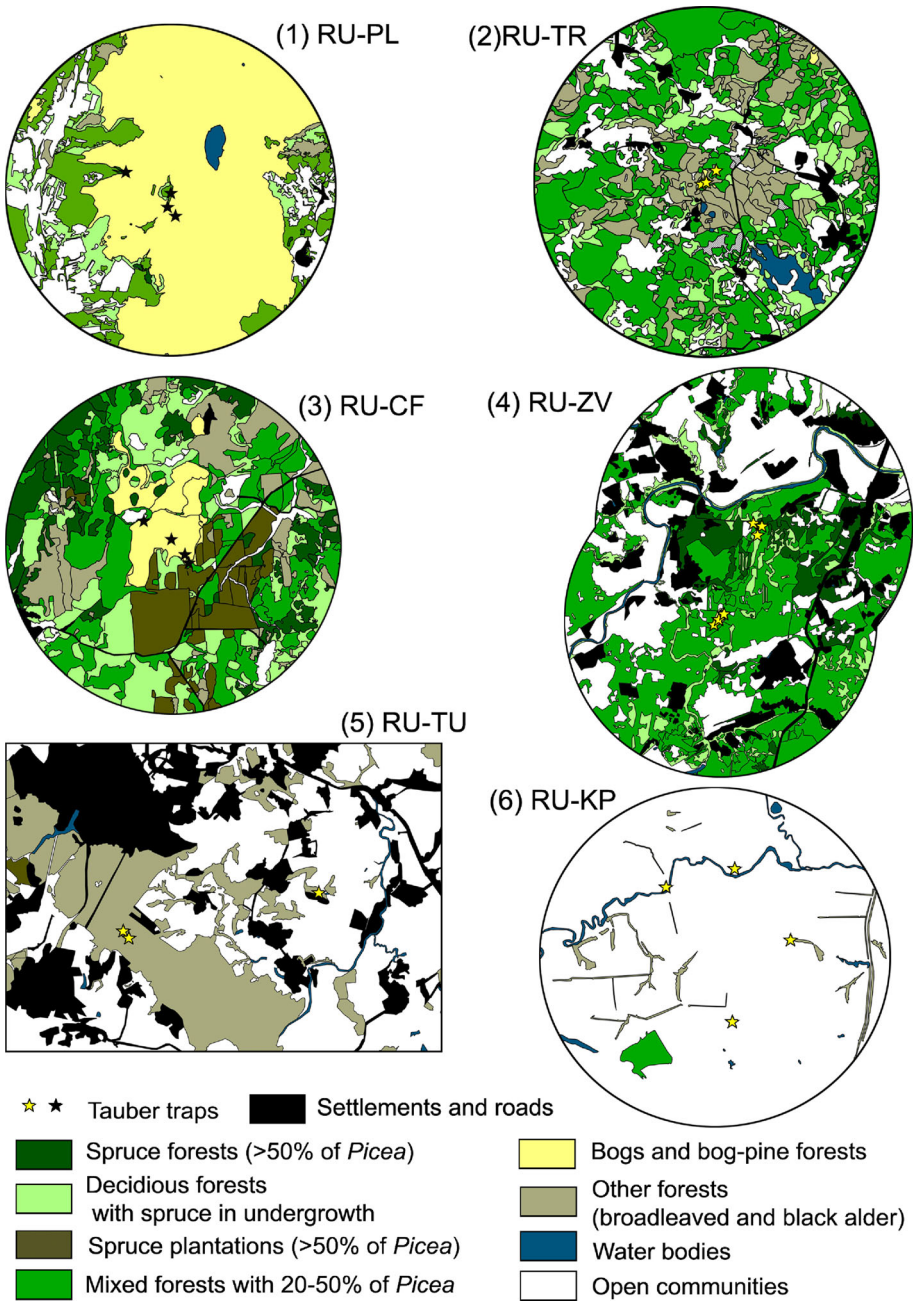

Fig. 2 Vegetation maps of a 5 km radius around six PMP sites of Central European Russia

Surface pollen data

In addition, pollen data from the Russian Palynological Database (www.pollendata.org) was used for discussion of possible threshold values for *Picea* pollen percentage in Central European Russia. The database includes the results of pollen analysis of surface and upper fossil samples. Pollen spectra were analyzed by different authors. Information about landscape, vegetation at sampling points and all references is included into the database. For analysis of the fluctuations of percentages of *Picea* pollen at different local conditions, we used data from vegetation zones where the Tauber traps were installed. A total of 102 samples were included in the analysis.

Results

Data from Tauber traps along the Central European Russia transect

Modern PARs: *Picea* shows great inter-annual fluctuations of pollen accumulation rates (PAR) at each site along the transect (Figs. 3, 4). Minimum PAR-values

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(0–237 grains cm^{-2} $year^{-1}$) are registered in the broadleaved forest zone (TU). In the northern part of the coniferous-broadleaved forests PARs vary from 64 to 3,848 grains cm^{-2} $year^{-1}$. Polistovsky Reserve (RU-PL) with its large mires shows higher values than the sandy soil type of coniferous-broadleaved forests in the Tver Region (RU-TR). The lowest PAR values in the coniferous forest belt are registered in the Central Forest Natural Reserve (RU-CF), especially on the open mires. The highest *Picea* PAR values were observed in the southern coniferous-broadleaved forests in the Moscow Region (point 4—RU-ZV), with an absolute maximum of 4,880 grains cm^{-2} $year^{-1}$. The fluctuations of PAR are higher at open locations than at sampling points within the forest.

Percentages: The lowest percent values are typical for the broadleaved forest zone (RU-TU—0.2 %) and the forest-steppe zone (RU-KP—0.26 %). Within the forest belt, the lowest values are registered in the samples from the pine-dominated forests (RU-TR) (2.13 %), and the highest—in the samples from coniferous-broadleaved forests in the Moscow region (RU-ZV—3.75 %). The minimal values at all sampling locations are less than 1 % (Fig. 4).

Analysis of vegetation maps: The highest percentages of *Picea* and mixed forests are observed in the coniferous-broadleaved forest zone in the Central Forest Natural Reserve (RU-CF—27.12 and 23.73 %) and the Zvenigorod Biological Station (RU-ZV—8.07 and 34.62 %). The area of pure *Picea* forests within the northern part of the coniferous-broadleaved forest zone is very small due to significant anthropogenic disturbances during the last centuries (RU-PL 0.22 %, RU-TR 0 %), and mixed forests occupy no more than 15–18 % of the area. Outside of the forest belt (RU-TU, RU-KP), the total area of *Picea* and mixed forests does not exceed 1.5 % (Fig. 2; Table 1).

Picea pollen data from the Russian palynological database

Picea pollen data from the Russian Palynological Database (www.pollendata.org) were used to create the percentage pollen diagram which reflects *Picea* abundance in different vegetation zones. All samples were divided into groups based on the conditions at the location: 1. Open oligotrophic/mesotrophic mires; 2. *Picea* forests; 3. Mixed forests with *Picea*; 4. *Pinus* forests; 5. Grass communities (agricultural lands and steppe); 6. Broadleaved forests; 7. Small-leaved forests. For each group minimum and maximum *Picea* pollen percentages were calculated. The results are presented in Fig. 5 and Table 2.

Picea abundances in open oligo- and mesotrophic mires range from a minimum of 1 % to a maximum of 13 % within a continuous *Picea* range. The pollen spectra of *Picea* forests in the southern taiga zone are characterized by considerably high *Picea* percentages, ranging from 12 to 40 %. Similar maximum values (35 %) are typical for coniferous-broadleaved forest, but the minimal percentages are much lower (about 1 %). *Picea* pollen abundance in mixed forests varies within very broad limits: maximum abundance can reach 6 % even in broadleaved forest zones, while minimal percentages are about 0.6 % in the coniferous-broadleaved forest zone and 0.1 % in the broadleaved forest zone. *Pinus* forests show very small minimal numbers (0.1–1 %), maximal abundance varies from 7.7 % in the southern taiga zone to 18 % in the coniferous-broadleaved forest zone. Open communities outside the forest zone (agricultural lands, steppes, meadows etc.) are characterized by very low *Picea* abundance in the pollen spectra.

Discussion

Comparison of relative and absolute *Picea* pollen abundance in the spectra with the total area of *Picea* forests shows that relationship between these two parameters is not always clear (Figs. 3, 4; Table 3). No correlation is found for combinations of PAR average or PAR maximum with % area of *Picea* forests or % area of *Picea* + % area of mixed forests (p values >0.05). In RU-CF, which contains the largest area of *Picea* forest (27 % *Picea* forests and 23.7 % mixed forests with *Picea*), pollen abundance is very low (average 2 % and 431 pollen grains cm^{-2} $year^{-1}$). In more southern locations (RU-ZV) and in locations with a more marine climate (RU-PL), which have smaller areas of *Picea* forests, both the percentages and the PAR pollen spectra contain *Picea* abundances that are three or more times higher. It is possible that modern climatic and hydrological conditions in RU-CF are less favorable for *Picea* and lead to the decrease in pollen production.

Picea PARs in fossil samples from the Central Forest Natural Reserve, Tauber point RU-CF (Fig. 6), varied within a very broad range (6–47,000 pollen grains cm^{-2} $year^{-1}$) and reached a maximum in the middle of the Atlantic and in the Subboreal period. Although we consider extreme peaks to be a result of insufficient chronological control, PAR during Holocene was several times higher than in the modern pollen samples, which suggests that the climate during these periods was milder than its modern state; these periods can be considered as the most favorable for *Picea*. One possible explanation for this phenomenon is the concept of genetic differentiation of *Picea* in different parts of the area, as suggested by Latałowa and Van der Knaap (2006). We assume that today the southern phenotype of *Picea* dominates the southern part of Valdai Uplands, where the CFNR is located. While this phenotype may be not as well adapted to the modern climatic conditions, it was sufficiently well

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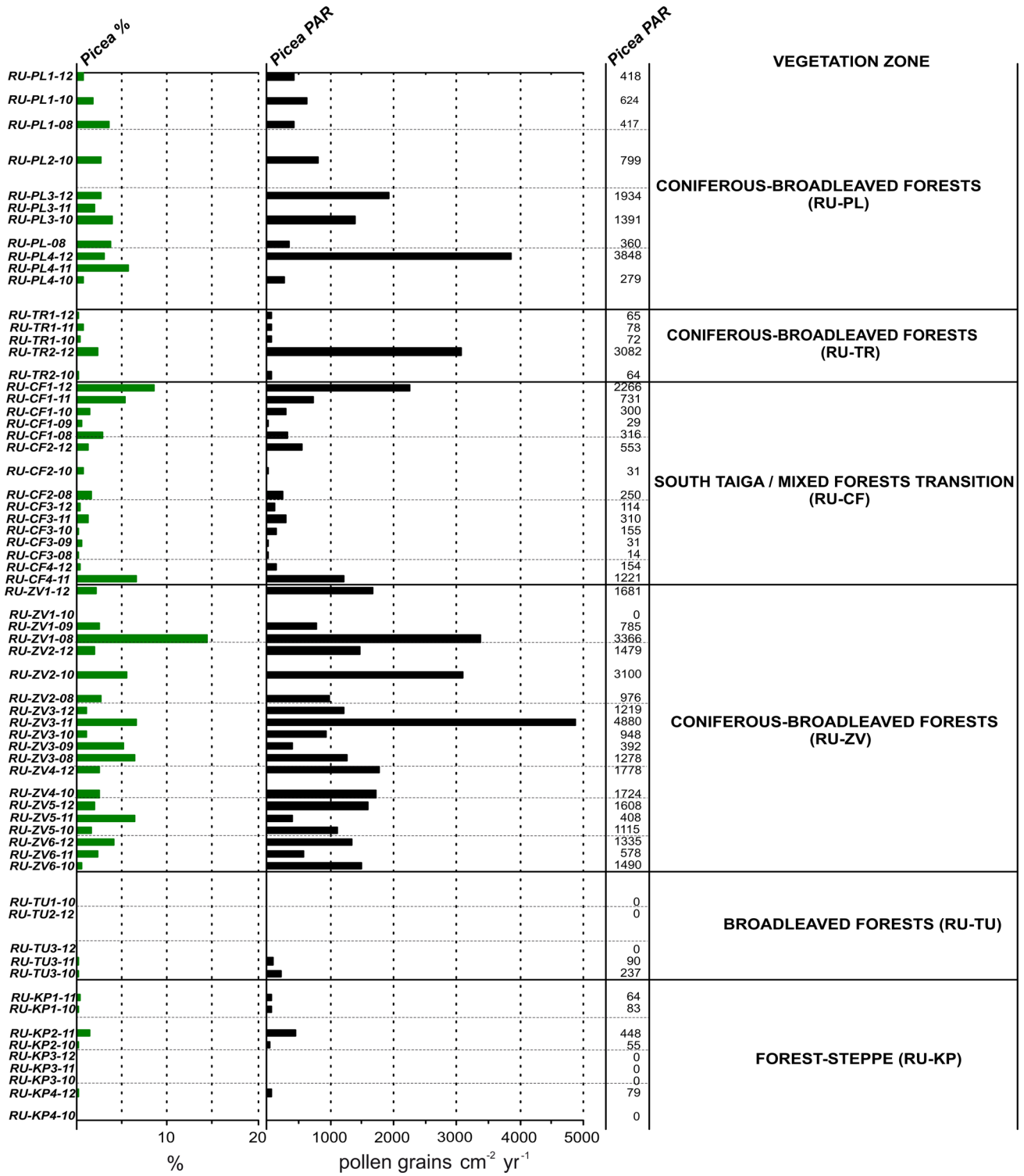

Fig. 3 All available PAR and percentages for the 5 years of observations along the Central European Russia transect (see site names in Table 1). Empty spaces indicate lost traps, null values for *Picea* are showed as "0" in "Picea PAR" column

adapted during the Atlantic and Subboreal. In the subfossil samples of the Holocene core (Fig. 6) *Picea* PAR is similar to the highest values in modern samples from Tauber traps. None of the modern samples register as high a *Picea* pollen influx as was measured for the past. This suggests that modern analogues of ancient *Picea* forests typical for the central part of European Russia in the Atlantic and Subboreal have not been discovered yet.

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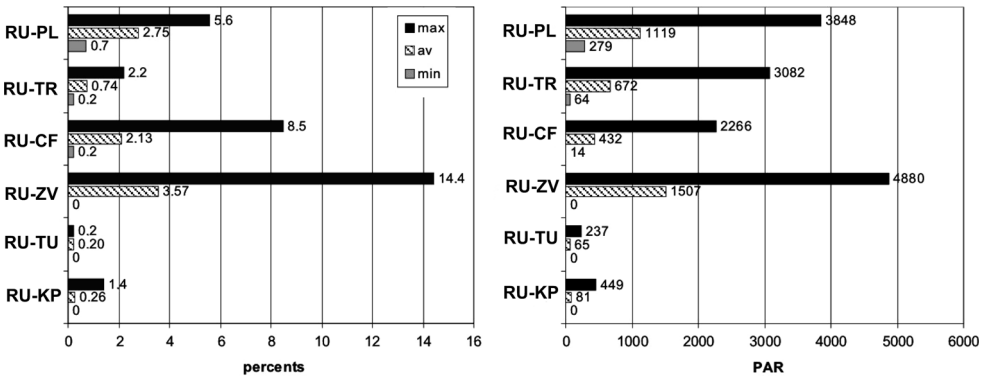

Fig. 4 Minimum, maximum and mean percentages (%) and PAR for 6 PMP sites in Central European Russia (showed as *bars* and *digits*)

Table 2 Maximum and minimum percentages of *Picea* pollen (surface and subfossil samples) in different vegetation zones based on data from the Russian Palynological Database (www.pollendata.org)

Local vegetation of sample points	Vegetation zones				
	South taiga	Coniferous-broadleaved forests	Broad-leaved forests	North forest-steppe	Forest-steppe
(1) Oligotrophic/mesotrophic bogs	1–13	0.7–13	0–1	–	–
(2) Spruce dominated forests	12–40	1–35	–	–	–
(3) Mixed forests with spruce	11	0.6–14	0.1–6	–	0.8
(4) Pine forests	1–7.7	1–18	0.1–0.6	–	–
(5) Agrolandscapes, steppes and meadows	4–5	1–40.4	0.1–1	0.2–3	0–0.4
(6) Broadleaved forests	–	0.3–1.4	0.4–2	–	–
(7) Small-leaved forests	–	3–14	0	–	–
Average percentage for zone	11.5	8.62	0.89	1.12	0.32

"0" no *Picea* pollen, "–" no data

The assumption that *Picea* PAR values are influenced by distance from the trap to the nearest *Picea* trees is true only in part. On one territory (for example, Fig. 3, pollen spectra from the CFNR where RU-CF1 is in the forest gap, RU-CF3 is on the open mire), the PAR value clearly depends on that distance. However, traps in closed habitats show much lower values in RU-CF than the traps in the Moscow Region RU-ZV (the local vegetation is similar; mixed forest with *Picea*, *Betula* and *Pinus* in both cases).

What percentages of *Picea* pollen are typical for different vegetation zones under modern conditions? What are the possible threshold values for *Picea* in Central European Russia? In non-forest and broadleaved zones, the average *Picea* pollen abundance is about 1 % and the upper limits do not exceed 3 % (Table 2). The highest values are usually attributed to more open locations and reflect the regional component of pollen rain, whereas in forested locations *Picea* pollen abundance is usually close to zero. Within northern forest areas (coniferous-broadleaved and south taiga zones) the average pollen abundance is about 10 %, as discussed by Grichuk and Zaklinskaya (1948), but this value varies considerably depending on local characteristics of sampling points (open/closed location, vegetation structure, pollen production of dominant taxa etc.). The lowest pollen *Picea* percentages (1 % and less) are observed in the pollen spectra of open oligotrophic and mesotrophic mires. This is due to the poor aerodynamic qualities of *Picea* pollen (Fedorova 1952b; Sugita et al. 1999 after Eisenhut 1961) and the huge areas of mires within the continuous coniferous forest belt. These results indicate that the level of 1 % can be significant for *Picea* and may reflect not only the presence of *Picea* in distant locations or the presence of just a few trees, but may also indicate continuous *Picea* forests. To interpret low *Picea* abundance correctly in fossil spectra, it is important to analyze it together with the other components of the pollen spectra. Low *Picea* pollen percentages together with pollen of broadleaved taxa are typical for a broadleaved forest zone with patches of *Picea*. Low *Picea* pollen percentages with low arboreal pollen and high non-arboreal pollen indicate the forest-steppe zone. The combination of low *Picea* pollen percentages with pollen of *Pinus*, *Betula* and a minimum of broadleaved taxa can indicate the northern part of coniferous-broadleaved forests. High percentages of *Picea* pollen with the pollen of broadleaved taxa, *Betula* and *Pinus* are characteristic of the southern part of the coniferous-broadleaved forest zone.

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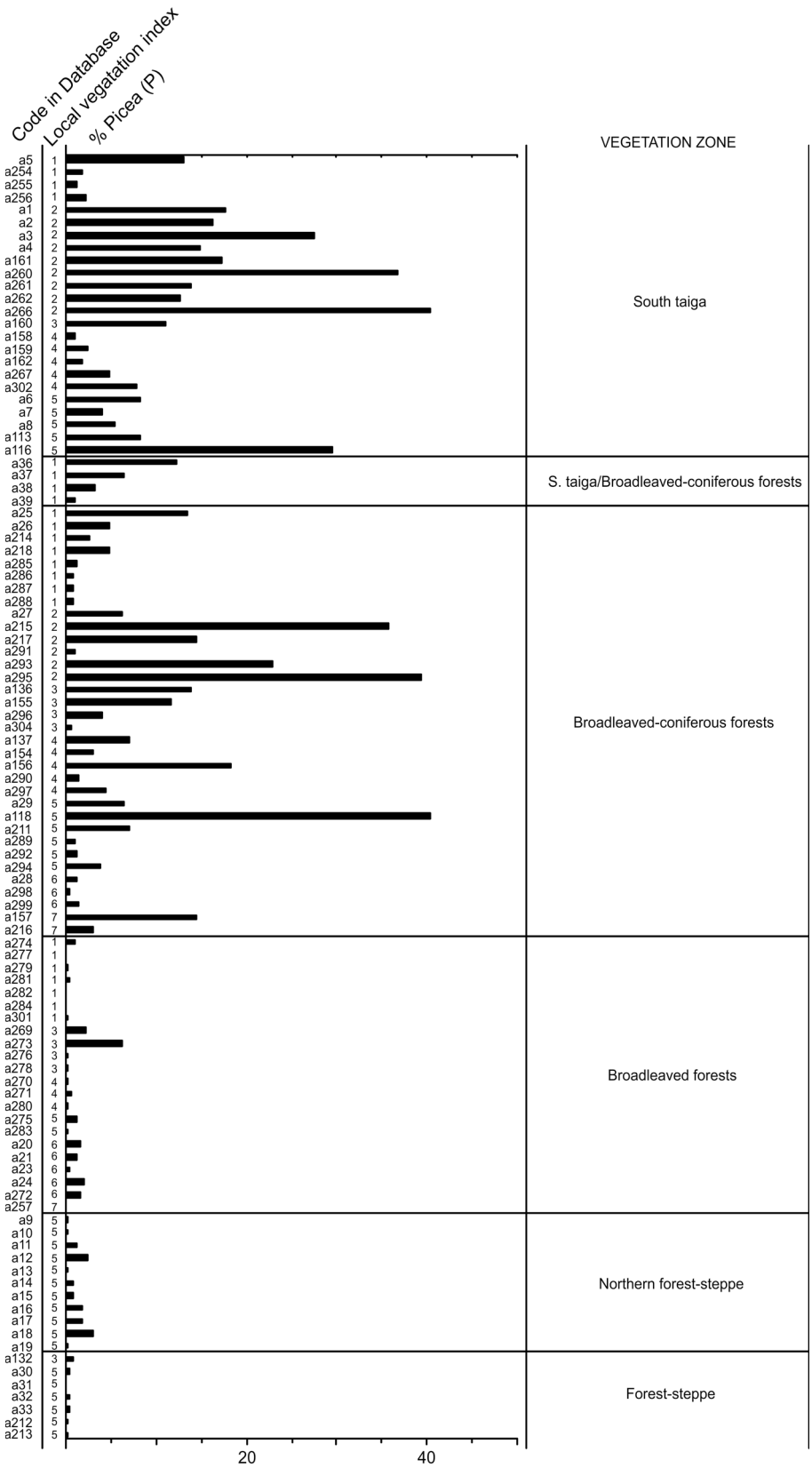

Fig. 5 Pollen percentages in different vegetation zones of Central European Russia based on data from the Russian Palynological Database (www.pollendata.org). Local vegetation indices which mark different habitats are: *1* open oligotrophic/mesotrophic mires; *2 Picea* forests; *3* Mixed forests with *Picea*; *4 Pinus* forests; *5* Grass communities (agricultural lands and steppes); *6* Broad-leaved forests; *7* Small-leaved forests

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Table 3 Pearson's correlations between area of *Picea* forests and maximum or average PARs

Correlation between	*p* value
Squares of *Picea* forests and PARav	0.9491
Squares of *Picea* forests and PARmax	0.7947
Squares of *Picea* + mixed forests and PARav	0.2753
Squares of *Picea* + mixed forests and PARmax	0.1865

Conclusions

Large areas of *Picea* forests are not always reflected in pollen spectra as high *Picea* percentages/PARs since in unfavorable climatic or hydrological conditions pollen production of *Picea* forests can be very low. Comparison of fossil and modern pollen spectra shows that a modern analogue of fossil *Picea* forests (characterized by a very high PAR and typical of the central part of European Russia in the Atlantic and Subboreal) has not yet been discovered in the centre of European Russia. *Picea* did not only play a more significant role in the past vegetation, but was also characterized by higher pollen productivity than is observed in its modern state.

In modern spectra of non-forest zones the average *Picea* pollen abundance is about 1 %, and the highest values (up to 3 %) are usually connected with open locations and reflect a regional component of the pollen rain. Within the coniferous forest belt, the average pollen abundance is about 10 %, but this value can vary considerably from 1 to 40 % and depends on local characteristics of sampling points (open/closed locations, vegetation structure, pollen production of dominant taxa etc.). The lowest *Picea* pollen percentages (1 % and less) are observed in the pollen spectra of oligo- and

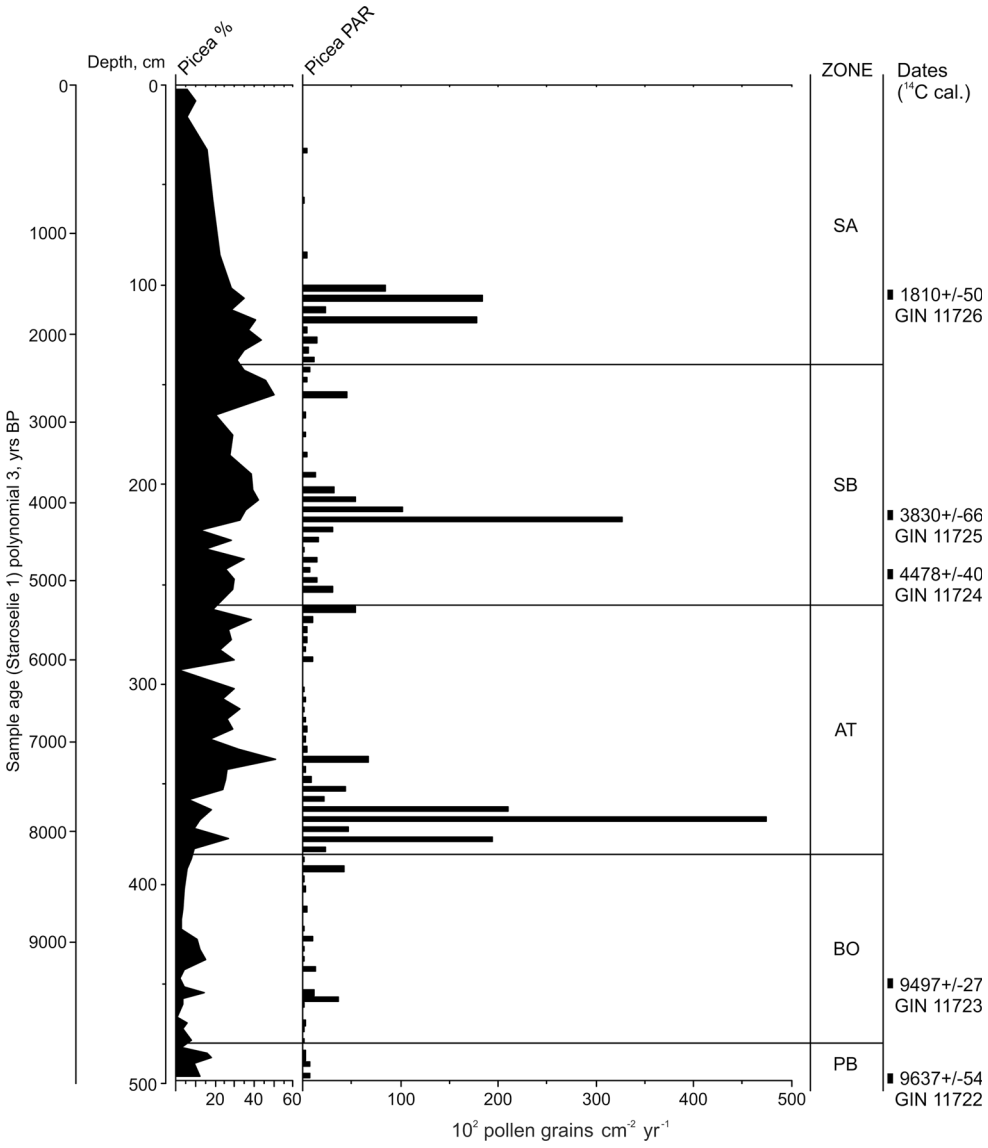

Fig. 6 Fossil *Picea* percentages and PAR-values from Stariselskiy Mokh mire in the Central Forest Natural Reserve (3), trapping point RU-CF (modified results from Nosova 2009)

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mesotrophic mires; thus, the level of 1 % is significant for *Picea* and can indicate its continuous range. For an appropriate interpretation of low *Picea* pollen abundance in fossil samples, this abundance should be analyzed together with the other components of the pollen spectra.

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