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Holocene Dynamics of Vegetation and Ecological Conditions in the Center of the East European Plain

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Abstract—Changes in the vegetation and fire regimes in the central East European Plain during the second half of the Holocene have been reconstructed based on the results of paleobotanical analysis and radiocarbon dating of material from a section of peat deposit in the Mordovia State Nature Reserve. It has been shown that birch–pine forests were widespread in the region between 7000 and 5000 yr BP, with the frequency of fires in that period being high (the fire return interval ranged from 10–20 to 100 years). Beginning from 5000 yr BP and to the early 20th century, broadleaf forests were dominant, with the fire return interval increasing to 300–500 years or longer.

Keywords: the Holocene, palynological spectrum, botanical analysis of peat, paleoecological reconstruction, vegetation dynamics, peat bog

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The Holocene evolution of landscapes in central regions of European Russia is an important and interesting scientific problem that requires a detailed study. Due to the high landscape diversity and natural potential of these regions, their economic development began long ago and has resulted in profound anthropogenic transformation of natural vegetation [1–3]. Therefore, paleogeographic reconstructions at local and regional levels are important for gaining an insight into the dynamics of natural geosystems and recovery of natural vegetation.

The Mordovia State Nature Reserve is of special interest in this context, since it lies on the boundary between two landscape regions—the forest and forest–steppe zones of the East European Plain—and its natural complexes are therefore especially sensitive to changes in environmental conditions. Reconstruction of the history of vegetation and fire regimes based on detailed paleoecological data is important for the conservation of forest and bog ecosystems and prediction of their dynamics under conditions of recent climate change.

Despite major interest in research on the anthropogenic Holocene dynamics of vegetation, the territory of Mordovia has not been studied sufficiently in this respect. In the 1950s, paleobotanical studies of several peatlands in the republic were performed by P'yavchenko [5]. The first data on the Holocene dynamics of vegetation in the neighboring regions of Penza oblast were obtained by Chiguryaeva [6] in the study on the group of so-called Ivanovskie peatlands. Unfortunately, these reconstructions are not supported by radiocarbon dating. Blagoveshchenskaya [6, 7] reviewed a large amount of paleobotanical data on the Volga region near Ulyanovsk and described the main stages of vegetation development in the Volga Upland during the Late Glacial and Holocene. However, the available data on the vast territory of the Middle Volga basin are deficient in detailed paleoecological reconstructions based on the use of several indicator groups and series of radiocarbon dates.

Research on the plant and soil cover of the Mordovia reserve was initiated in the 1920s. Detailed studies by Gaffenberg [8] and Kuznetsov [9] on the vegetation of the reserve are of special interest for understanding its spatial organization. Important publications concern the description of Quaternary deposits and soils [10], characteristics of the flora [11], vegetation dynamics [12], and relationships between edaphic and forest site conditions [13]. Bog geosystems in the reserve were studied in detail by Grishutkin [14].

In this study, we performed for the first time a paleoecological analysis and detailed radiocarbon dating of a peat section in the Klyukvennoe bog located in

Table 1. Results of radiocarbon dating of peat deposit in Klyukvennoe bog

Laboratory no.	Sampling depth, cm	Radiocarbon age, yr BP	Calendar age, yr BP (2σ)
IG RAN 4585	34–40	104.78 ± 3.04%	Current activity
IG RAN 4586	75–80	2660 ± 70	2800 ± 50
IG RAN 4587	125–130	3680 ± 80	4030 ± 100
IG RAN 4588	176–180	4910 ± 90	5680 ± 100
IG RAN 4593	220–225	5850 ± 90	6670 ± 110
IG RAN 4589	170–175	5980 ± 100	6850 ± 120

the Mordovia reserve and, on this basis, reconstructed changes in the natural environment during the Middle and Late Holocene at the levels of local bog paleocommunities and the vegetation of the region as a whole. The results also allowed us to estimate the impact of fires and human activities on the vegetation of the reserve.

MATERIAL AND METHODS

The Mordovia State Nature Reserve named after P.G. Smidovich lies in the southwestern part of Oka–Klyazma Polesye [10], also known as Moksha Polesye [4], which is in the center of the East European Plain, in the conifer–broadleaf forest subzone bordering on forest–steppe. The territory of the reserve is at the junction of two landscape provinces, the Volga forest–steppe province and the Meshchera forest province [4], with the Moksha River marking the boundary between them.

The territory of the reserve in the right-bank part of the Moksha valley lies at five topographic elevation levels: the floodplain (105–110 m a.s.l.), three floodplain terraces (110–132 m), and moraine-fluvioglacial plain (132–186 m) [15]. In places, the moraine of Don glaciation and pre-Quaternary deposits (karst limestones) occur close to the surface, which accounts for spatial heterogeneity of habitat conditions for the vegetation [13]. Forest types specific for its territory include pine–oak, pine–linden, and steppificated pine forests; broadleaf linden–oak forests; moist spruce forests in waterlogged habitats; and black alder swamp forests in the floodplain [12].

The mesotrophic Klyukvennoe bog occupies 3.6 ha in the southeastern part of the reserve. Its vegetation consists mainly of cottongrass–*Sphagnum* communities with a large proportion of bog dwarf shrubs (primarily *Chamaedaphne calyculata* (L.) Moench) and, in places, sparse birch stands. The peat deposit has a maximum depth of 245 cm and is underlain by fluvioglacial sands. In the territory surrounding the bog, aeolian fluvioglacial ridges under sparse *Sphagnum* pine forests alternate with moraine-fluvioglacial plains where pine–broadleaf forests prevail.

The description of peat section and sampling were carried out in the course of field research in 2014. Peat samples were taken at intervals of 2–5 cm with an Eijkelkamp hand sampler and processed by standard methods [16, 17] to determine the degree of peat decomposition and prepare the samples for detailed botanical and palynological analysis and radiocarbon dating. Ash content was measured determined after dry incineration at 450°C. The absolute age of the samples was determined in the Laboratory of Radiocarbon Dating and Electron microscopy of the Institute of Geography, Russian Academy of Sciences (Moscow). On the whole, six radiocarbon dates were obtained (Table 1). The rate of peat accumulation was calculated based on the age–depth model using the Clam package in R [18].

To reveal the impact of fires on the vegetation of the reserve, the pattern of charcoal layers in peat cores was analyzed. As shown in studies on fire histories in bog ecosystems, such layers (fire horizons) are preserved in peat deposits and provide indisputable evidence for strong fires in the surrounding area [19]. The location depth and thickness of all charcoal layers in the peat core from the Klyukvennoe bog were measured and recorded in the field, in the course of sampling, since their contrasting color is retained for a short period of time. Their age was determined using the model of peat accumulation rate (Fig. 1) plotted on the basis of radiocarbon dates (Table 1). It was assumed that each charcoal layer corresponds to one fire, with the period of time between the formation of neighboring layers being equal to the fire return interval. The observed layers corresponded only to strong fires, i.e., those that spread to the center of the bog (where the cores were collected). It may well be that the number of fires in the surrounding area was greater, but these could be forest fires that affected only the margin of the bog.

RESULTS

The age–depth model (Fig. 1) was plotted to estimate the rate of peat accumulation at different stages of bog development. Based to this model, the rate of peat accumulation was found to be very high (up to 1.2 mm/year) at the initial stage, 6850 ± 120 to 6660 ± 110 calendar years ago (cal. yr BP), which corresponded to the second half of the Holocene thermal maximum (relatively warm and humid). This rate subsequently decreased to 0.5 mm/year in the late Atlantic phase of the Holocene (6660 ± 110 to 5680 ± 100 cal. yr BP) and varied between 0.4 and 0.1 mm/year during the Subboreal and Subatlantic phases.

The sample located at a depth of 35–40 cm in the peat core from the Klyukvennoe bog was characterized by a high ^{14}C radioactivity, which indicated that the age of deposit was less than 100 years. Therefore, the rate of peat accumulation in the upper horizon of the deposit increased by an order of magnitude, to 3.5 mm/year.

Botanical analysis of peat from the Klyukvennoe bog (Fig. 2) showed that the deposit at depths of 250 to 55 cm (6850–1400 cal. yr BP) basically consisted of eutrophic herbaceous peat formed mainly from the remains of *Calamagrostis* sp., *Carex* sp., *Scirpus* sp., *Menyanthes trifoliata*, etc. and brown mosses, except for the lower 15-cm layer that contained a significant proportion of *Sphagnum*. The degree of peat decomposition was 25–35%. The peat at depths of 55 to 20 cm (1400–50 (70) cal. yr BP) had an increasing content of woody plant remains (*Pinus* and, in lesser amount, *Betula*), with the proportion of *Calamagrostis* sp. and other herbaceous remains being still high. In addition, *Sphagnum obtusum* and *Sp. angustifolium/fallax* appeared in the peat. The degree of its decomposition was 20–30%.

The upper 20-cm peat horizon formed at the recent stage of bog development (during the past 50–70 years) was characterized by increase in the contents of moss remains (*Sphagnum* of section *Cuspidata (angustifolium/fallax)* and other species of the genus). It also contained a substantial proportion of the remains of *Eriophorum vaginatum* and of *Oxycoccus* sp. (first detected in this horizon), which indicated that the transitional peat type was being formed. The degree of its decomposition was decreased to 15%.

Analysis of the pattern of charcoal layers in the peat core from the Klyukvennoe bog (Fig. 2) showed that their number reached a maximum of 16 between 6850 and 5600 cal. yr BP. The fire return interval in this period did not exceed 100 years and in many cases, was only 10–20 years (Fig. 3). The frequency of fires between 5000 and 3000 cal. yr BP was much lower, with large fires occurring at intervals of 300–500 years, and traces of only one such fire were found in the sample corresponding to the period of 3000–1500 cal. yr BP. During the past millennium, the fire return interval decreased to 150–200 years. Several large fires occurred around 1000 cal. yr BP, and two fire horizons were formed approximately 50–70 years ago.

Analysis of loss on ignition showed that the content of organic matter increased more than twofold, from 35 to 79% in the basal peat horizon (Fig. 2), reached 96–98% at depths of 230 to 75 cm, gradually decreased to 85% at a depth of 40–30 cm, and increased again to 93–95% in the upper 20-cm layer.

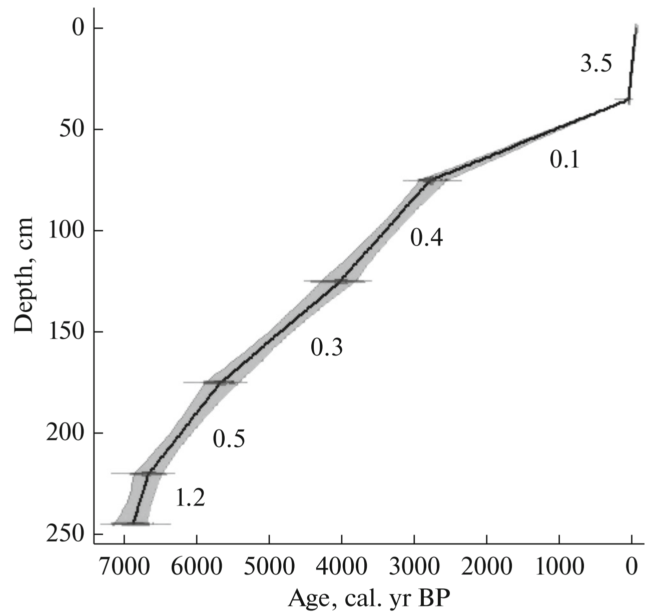

Fig. 1. Age–depth model of peat deposits in Klyukvennoe bog during periods between datings (figures on the curve, mm/year).

The spore–pollen diagram of the peat section (Fig. 4) can be divided into four major palynozones corresponding to the stages of change in the vegetation of the reserve during the Middle and Late Holocene.

In the spore–pollen spectra of palynozone 1 (245–165 cm, 6850–5300 cal. yr BP), tree and shrub pollen account for about 95%, with predominance of *Pinus* and *Betula* pollen (up to 30–40 and 60–70%, respectively). The amount of broadleaf tree pollen (*Tilia, Quercus, Ulmus*) is relatively small.

The lower boundary of palynozone 2 (165–115 cm, 5300–3800 cal. yr BP) is marked by an increase in the proportion of *Quercus* pollen. The contents of *Tilia*, *Ulmus*, *Corylus,* and *Alnus* pollen in the spectra also increase, with those of *Pinus* and *Betula* pollen remaining high. In the spectra of palynozone 3 (115–35 cm, 3800–50 (70) cal. yr BP), pollen of broadleaf tree species and *Corylus* reaches a peak (in total, up to 50%), with the proportion of pine and birch pollen varying from 10–20 to 50%; the amount of *Picea* pollen is small (0.5–3%). The proportion of herbaceous pollen increases to 10%.

In palynozone 4 (35–0 cm, the past 50–70 years), the proportion of broadleaf tree pollen decreases to 1–2%, while that of pine and birch pollen reaches 40–50%. The content of spruce pollen also increases to 5–7%. An increase is also observed in the proportion of pollen from herbaceous species that grow in the forest zone but are more typical of overgrown fields (*Artemisia*, Chenopodiaceae, Asteraceae, Poaceae) and from meadow forbs.

In the peat deposit as a whole, spore–pollen spectra sporadically include pollen of Cerealia, *Fagopyrum,*

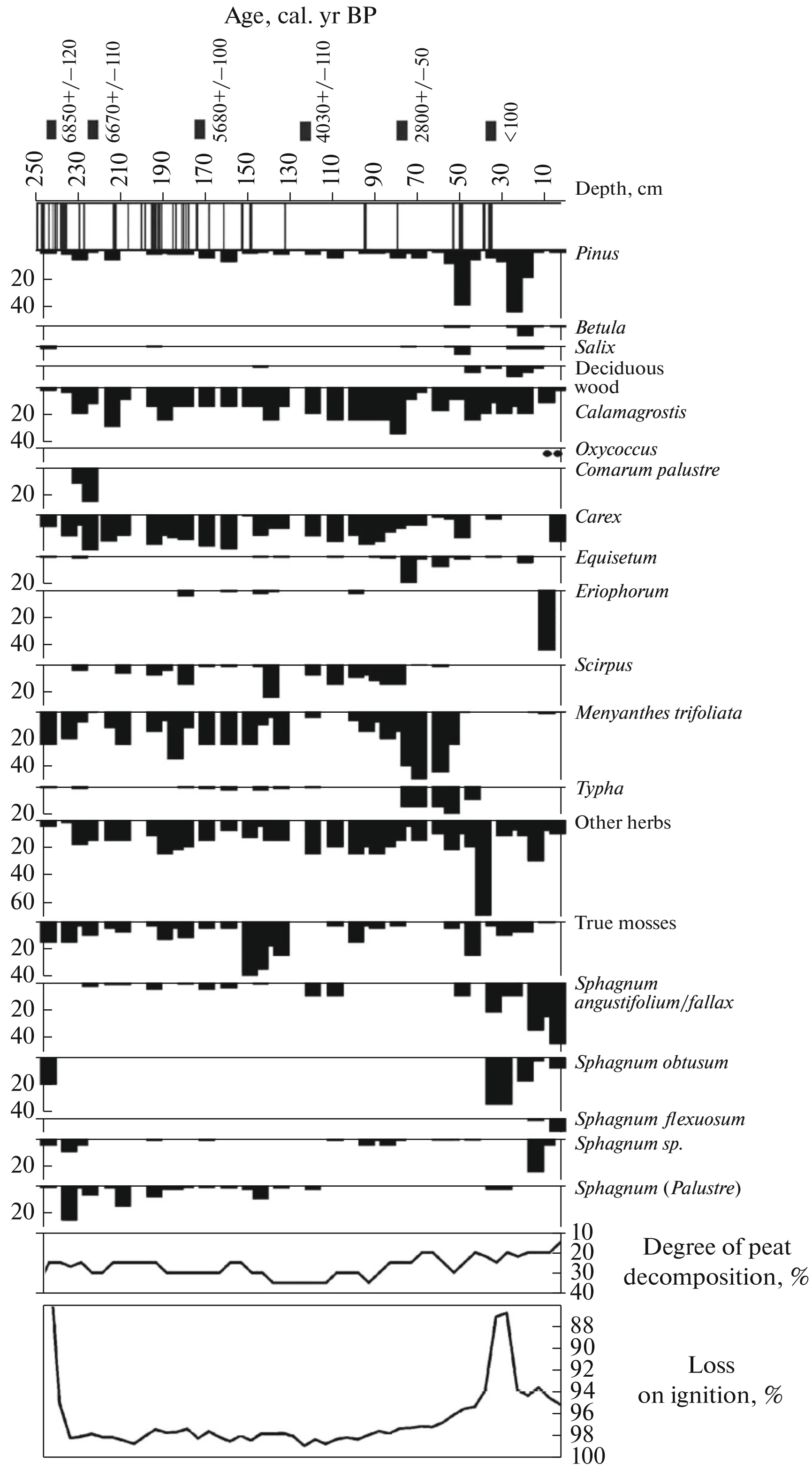

Fig. 2. Botanical composition of peat in Klyukvennoe bog. Black bars at the lithological column indicate charcoal layers.

Cannabis, and *Centaurea cyanus*, a typical weed in grain fields. Species indicative of anthropogenic impact on the vegetation—*Plantago, Rumex, Polygonum aviculare-type, Ranunculus acris-type*—are permanent components of the spectra, but the content of their pollen does not exceed a fraction of one percent, except in palynozone 4. However, the proportion of these components sharply increases in the upper peat

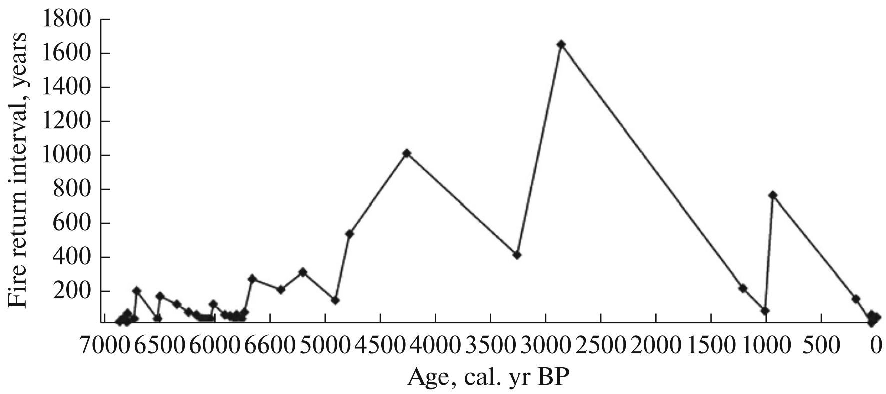

Fig. 3. Reconstruction of changes in fire return interval based on the numbers of charcoal layers in peat.

horizon. The proportion of pollen from cultivated cereals in palynozone 4 reaches a maximum (up to 7%).

DISCUSSION

The onset of Klyukvennoe bog formation dates from 6850 ± 120 cal. yr BP, which corresponds to the Atlantic climatic phase of the Holocene [20]. For a very long time, this was a grass peatland at the eutrophic stage of development. The establishment of pine on the bog began around 1400 cal. yr BP, with consequent formation of woody-herbaceous eutrophic peat. As shown by comparing the results of botanical analysis of peat with data on the pattern of charcoal layers and loss on ignition, tree vegetation spread to the bog after a series of relatively strong fires. It may well be that periodic fires affecting the bog ecosystem and (later) timber harvesting in the surrounding territory contributed to the input of nutrients into the peat deposit, thereby providing for eutrophic habitat conditions.

Drastic changes in the peatland geosystem—transition to the mesotrophic stage, a decrease in the degree of peat decomposition, and an increase in the rate of its accumulation by more than an order of magnitude—occurred 50–70 years ago. This is in agreement with the general trend toward intensification of peat accumulation observed for the southern taiga subzone and conifer–broadleaf forests of the Eat European Plain during the past 100 years [21–23]. Published data provide evidence that the rates of bog growth during the past century exceed the average rates of peat deposition during the Holocene.

In the deposit of Klyukvennoe bog, the upper horizon of slightly decomposed mesotrophic peat is separated from underlying horizons by a distinct charcoal layer. Apparently, the aforementioned drastic increase in the rate of peat accumulation may also be due to change in local conditions of the bog ecosystem caused by burning of the upper layer of the deposit, which provided for an increment of organic matter content against the background of additional input of ash elements.

The results of palynological analysis make it possible to reconstruct changes in the vegetation of the territory surrounding the bog. Birch–pine and pine forests prevailed there between 6850 and 5300 cal. yr BP. As found by comparing our results with palynological data from neighboring regions, the period of their prevalence in this territory was longer than other regions: such forests were widespread in the East European Plain during the Boreal phase of the Holocene, but broadleaf forest formations replaced than as soon as in the Atlantic phase. Thus, the expansion of broadleaf forests on the Smolensk–Moscow Upland and Central Russian Plain took place around 8000 cal. yr BP [24, 25]. In the Meshchera Lowland and on the northwestern Volga Upland, the proportions of linden, elm, oak, and hazel in tree stands was found to increase around 7000 and 6000 cal. yr BP, respectively [6, 26]. The survival of pine–birch forests in the region of Mordovia reserve could probably be facilitated due to frequent fires, as follows from our reconstruction based on the count of charcoal layers in the peat core from the Klyukvennoe bog (Fig. 2). It so, the dynamics of vegetation in the period of 6850 to 5300 cal. yr BP can be interpreted as a series of successional changes.

Significant changes in the vegetation of the reserve around 5300 cal. yr BP (the Subboreal phase) were associated with increase in the proportion of broadleaf species in plant communities. Climatic reconstructions for the second half of the Holocene provide evidence for climate cooling and increasing humidity beginning from 5700 cal. yr BP [27], which probably accounted for a decrease in the frequency of fires (see Fig. 2). The pattern of vegetation during the Subboreal phase was a combination of broadleaf and pine forests with an undergrowth of hazel, birch–pine forests, and floodplain forests with alder; the role of broadleaf tree species in the communities increased in the second half of that phase. Our data on the composition and ratio of main components in the spore–pollen spectra and significant differences in pollen production and dis-

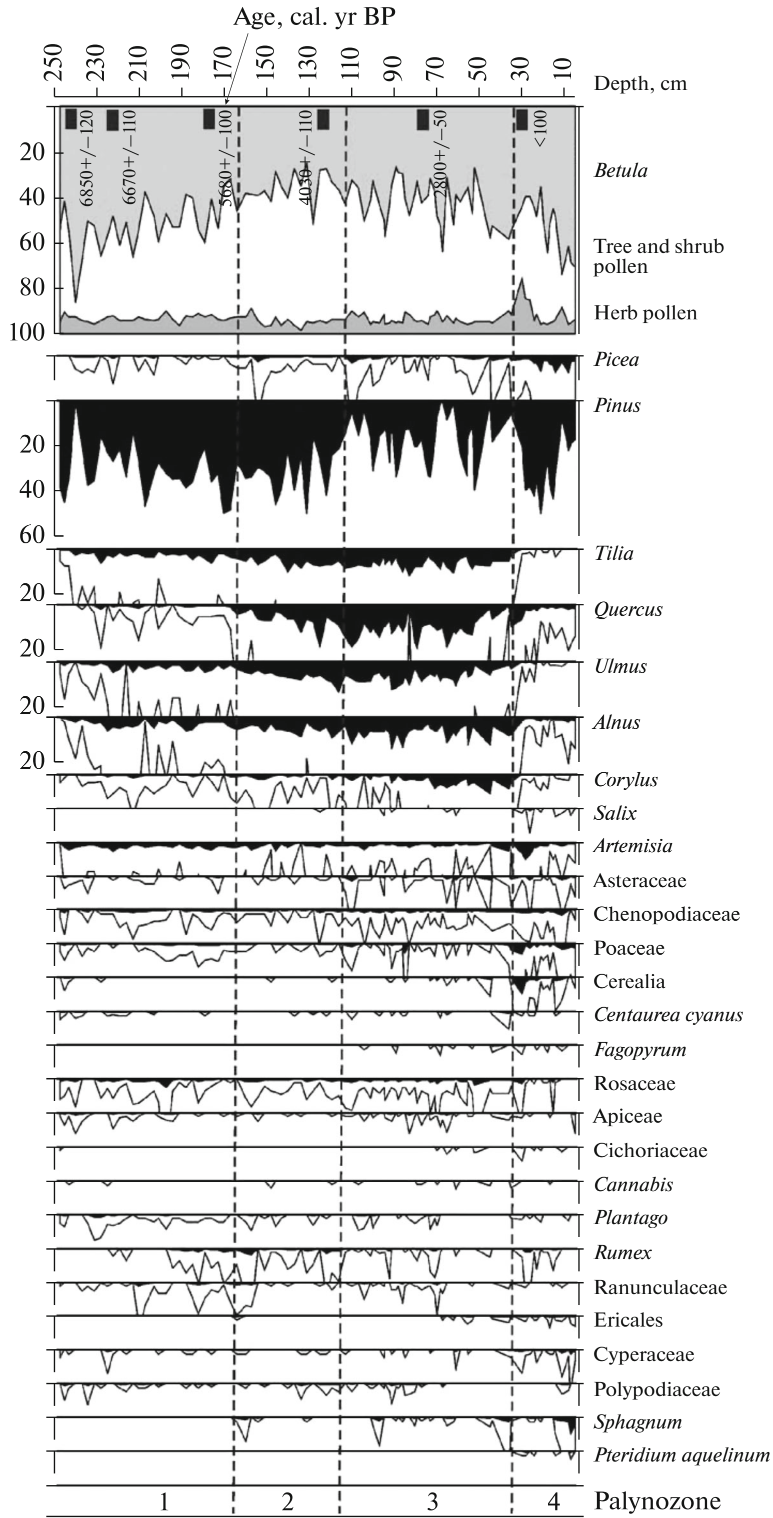

Fig. 4. Spore–pollen diagram of peat section in Klyukvennoe bog (AP + NAP = 100%; the additional contour shows a tenfold increase in the proportion of basic taxon).

persal range between pine, birch, and broadleaf species provide sufficient grounds to conclude that broadleaf forests were growing in the study area during the period of 3800 to 100 cal. yr BP, with pine and birch forming forest communities in the most suitable ecotopes, such as bogs, waterlogged depressions, or on tops of ancient aeolian landforms with thick sand deposits.

As shown in studies on the history of vegetation in the Meshchera Lowland, the spread of broadleaf tree species in landscapes of Polesye type (such as in the Mordovia reserve) is limited mainly by soil overmoistening rather than by insufficient heat supply [28, 29]. This is why broadleaf forests reached a peak of development in a relatively dry period (around 3800 cal. yr BP) [27] and subsequently retained their position in the plant cover.

In the second half of the Holocene, spruce forests began to gradually displace broadleaf formations from the central East European Plain. Although small amounts of spruce pollen occurred in the spectra throughout the Holocene, the role of this species in forest communities was insignificant. Beginning from 2200 cal. yr BP, spruce forests gained predominance in the vegetation of the Smolensk–Moscow Upland [24]. The role of spruce as an admixture in broadleaf forests increased at the boundary of their range, in the Central Russian Plain and Volga Upland [7, 26, 25]. The proportion of spruce in forests of the study region also increased in that period.

There is no information on archaeological findings within the Mordovia reserve, but four sites of the Early and Middle Bronze Age were discovered close to its boundaries (10–25 km from the peat section) in the Moksha River valley, east and southeast of the reserve [30]. In addition, nine sites dating from the Neolithic, Mesolithic, and Bronze age and also two sites of the Early Iron Age in the valley of the Satis River, a tributary of the Moksha, were discovered northwest and northeast of the reserve, within a radius of about 30 km from the peat section [31]. Obviously, the vicinities of the reserve were human populated during the second half of the Holocene. This also follows from the regular representation of species indicative of human economic activities and occurrence of pollen from cultivated cereals in the pollen spectra. Both archaeological and palynological data provide evidence that geosystems of the reserve were exposed to anthropogenic impact over 7000 years, but this did not result in any significant transformation of the vegetation until the last century.

The past 100 years were marked by active economic development in the surrounding territory, forest cutting for timber and cropland, and fires. According to historical records and observations by the staff of the reserve, large fires occurred in 1889, 1932, 1972, and 2010 [8, 9, 14]. Large-scale felling operations were carried out in the early 20th century and in 1954–1956, when the functions of the reserve were suspended. These factors resulted in damage to the vegetation and soils of aeolian fluvioglacial ridges surrounding the Klyukvennoe bog, which are currently characterized by high drainage and poorly developed soil cover. Disturbances of soil and plant cover facilitated the input of mineral components into the peat deposit, which was reflected in an 8–10% increase in the ash content of peat at a depth of 25–45 cm (Fig. 2).

Thus, broadleaf forest markedly decreased in area under anthropogenic impact, having been replaced by pine–birch forests with spruce. The content of spruce pollen in the upper 20-cm peat layer is the highest over the Holocene period. Spruce was probably growing in the reserve during the Middle and Late Holocene (small amounts of its pollen were found in the spectra of peat formed beginning from 5000 cal. yr BP), but its active expansion started after the removal of broadleaf forests and alleviation of competition with broadleaf tree species, primarily oak.

CONCLUSIONS

An integrated paleobotanical analysis of peat deposit in the Klyukvennoe bog made it possible to reconstruct the dynamics of vegetation and changes in fire regimes during the past approximately 7000 years. According to the resulting data, birch–pine and pine forests were widespread in the territory of the reserve in the second half of the Atlantic phase of the Holocene (6850–5300 cal. yr BP). This period was characterized by the highest frequency of fires (with a fire return interval of 10–20 to 100 years), which probably contributed to long-term prevalence of these forest formations in the plant cover. Climate cooling and increasing humidity during the Subboreal phase provided for reduction in fire frequency, which allowed broadleaf species to gradually improve their position in tree stands. Broadleaf forest dominated in the territory of the reserve from about 5300 cal. yr BP until the past century, when active economic development began in the region. As a consequence, the frequency of fires increased, broadleaf forests were markedly reduced in area and replaced by pine–birch forests actively infiltrated by spruce.

The results of studies on the botanical composition and properties of peat deposit show that, from 6850 cal. yr BP until the past century, the Klyukvennoe mire was at the eutrophic stage of development. Drastic changes in the geosystem and transition to the mesotrophic stage and increase in the rate of peat accumulation by more than an order of magnitude (to 3.5 mm/year) occurred approximately 100 years ago.

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