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ANTHROPOGENIC TRANSFORMATION OF THE VEGETATION IN THE IMMEDIATE VICINITY OF THE SETTLEMENT COMPLEX AT POGANOWO (MRĄGOWO LAKELAND, NE POLAND)

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Abstract
The results of pollen, non-pollen palynomorph and microcharcoal particle analyses of deposits from a small pond in northeastern Poland are presented. The study focused on human-induced vegetation changes that occurred in a close vicinity of the settlement complex at Poganowo during the Middle Ages (*ca* 10th–16th centuries). We distinguished three phases of human impact. First and third phases correspond to intensified settlement activity. The second phase was a period when human activity decreased and woodland regeneration took place. The high incidence of the parasitic fungus *Kretzschmaria deusta* in a local forest stand during the third phase was simultaneous with numerous spores of coprophilous fungi (*Sordaria*-type and *Cercophora*-type). We consider that *Kretzschmaria deusta* inhabited the roots and bases of tree trunks damaged by digging and grazing animals.

Key words: human impact, pollen analysis, fungal spores, Masuria, Middle Ages.

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INTRODUCTION

A use of indicator characteristics of some plant taxa, as well as of other organisms, is a fundamental method in palaeoecology, enabling reconstruction of past environments (e.g. Birks, 2003; Latałowa *et al.*, 2013). Among the microfossils that are observed in pollen slides, fungi, algae and other non-pollen palynomorphs (NPP) have become particularly important, because of their potential to improve reconstruction of past ecosystems (van Geel, 2001; van der Linden *et al.*, 2012). Van Geel and Aptroot (2006) underlined that fungal remains are of high potential in this context. In particular, these authors emphasized the importance of fungal taxa with well-characterized biological and ecological requirements, e.g. *Sporormiella* sp. and *Sordaria* sp., which are indicators for dung, or *Kretzschmaria deusta*, a parasite on decaying wood, indicating presence of their host trees. However, a palaeoecological potential of fungal remains has not yet been fully explored. We present results of palynological analysis in the framework of interdisciplinary research project conducted in the settlement complex at Poganowo (Szal *et al.*, 2013; Wyczółkowski *et al.*, 2013). This settlement complex is located entirely in a forest, and nearby there are numerous small peat bogs and ponds suitable for local-scale vegetation reconstructions (compare Sugita *et al.*, 2007). Our main objective was to study transformation of vegetation caused by human activity. Moreover, by the application of NPP and microcharcoal particle analysis we tried to characterize farming models, assuming the possibility of attributing the presence of spores of coprophilous fungi (e.g. *Sordaria*-type, *Sporormiella*-type) to land-use practices, particularly husbandry.

ARCHAEOLOGICAL AND HISTORICAL BACKGROUND

The settlement complex at Poganowo is located in the northeastern part of the Mrągowo Lakeland. The earliest traces of human activity in the region have been dated to the Neolithic period. Nevertheless, generalization of permanent settlements occurred with the beginning of the West Balt Barrow culture in the early Iron Age (*ca* 7th century BC). The first settlement phase in the Poganowo hillfort is linked to this culture (Wyczółkowski *et al.*, 2013), and the charcoal and ash layer (perhaps from burnt timber constructions of ramparts or palisades) of this phase are dated to the 6th–4th century BC. Other sites, located a short distance from Poganowo, include the fortified settlement at Nakomiady, the settlement in Wólka, and the barrow cemeteries in Godzikowo and Nakomiady, also dated to the early Iron Age (Hoffmann, 1999; Wyczółkowski, 2011).

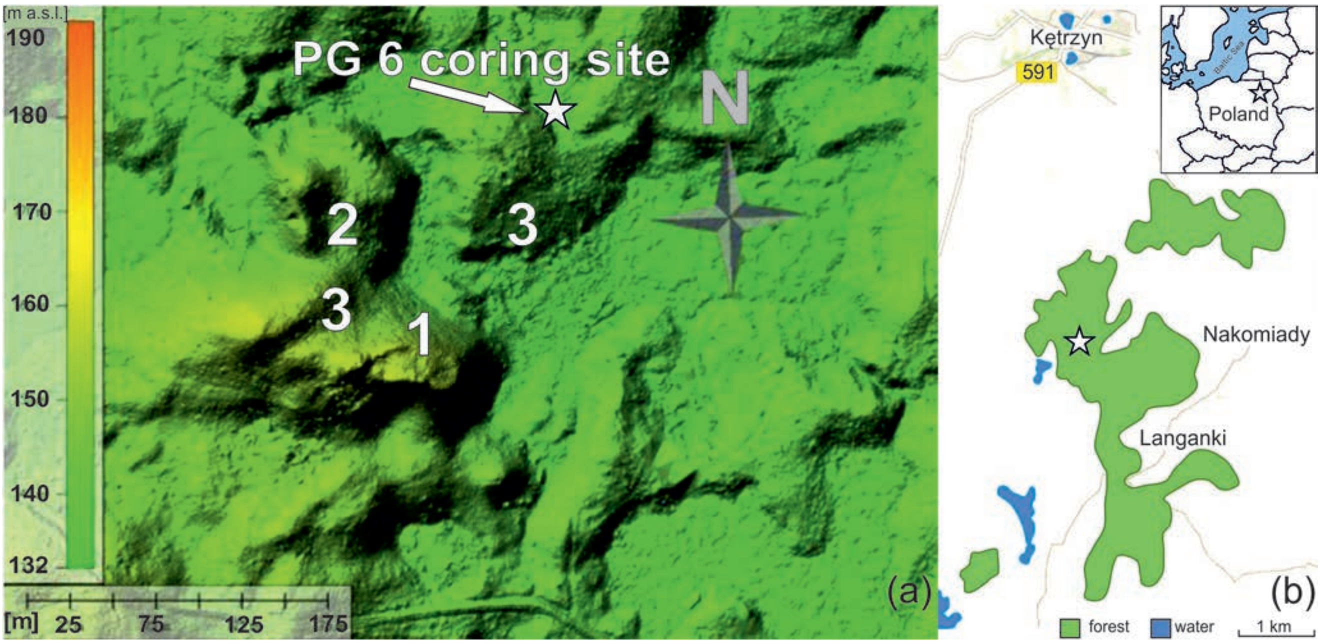

Fig. 1. Location of the study area produced by using the digital terrain model from LIDAR data (**a**) and Google Maps (**b**) with PG6 coring site (54°00'11.2"N 21°23'04.6"E); 1 –Poganowo hillfort, 2 – sacrificial place, 3 – settlements.

An increase in a number of sites related to the population of the Bogaczewo culture during the Roman Period (1^{st}–4^{th} century AD) has been observed (Szymański, 2005). At that time, two settlements existed in the vicinity of the Poganowo hillfort. There is a cemetery in Turwągi (Voß, 1886), and a settlement and sacrificial bog site at Wólka (Raddatz, 1992–1993).

A second settlement phase in the Poganowo hillfort has been dated to the late 10^{th}–12^{th} centuries AD. In northeastern Poland this period is called the Early Middle Ages or the Viking Age (e.g. Nowakiewicz, 2006, 2010; Nowakiewicz and Wróblewski, 2010). At that time, a sacrificial place existed, and an extensive settlement has been excavated (Wyczółkowski *et al.*, 2013). Radiocarbon dating (1338±58 AD) from the hearth of the sacrificial place may indicate a use of this place as late as in the 13^{th} and 14^{th} centuries.

In the second half of the 14^{th} century the forest where the Poganowo hillfort is located was given to the city of Kętrzyn (Rastenburg). From the first half of the 15^{th} century the villages began to develop (Beckherrn, 1880). Finally, in 1571 AD, the villages Pręgowo, Sławkowo and Poganowo, located in the northern and western part of the forest, included 93 hufen (1 hufe is *ca* 16.8 ha) that were managed by 43 farmers (Visitation, 1571). The number of farms existing on the edge of Poganowo did not change significantly until the end of the 18^{th} century (Goldbeck, 1785).

MATERIAL AND METHODS

Coring and lithology

The sediment core (PG6 profile) was collected in winter of 2012 from a small pond located *ca* 150 m to the northeast of the settlement complex at Poganowo (Fig. 1). Coring was performed by using an Instorf peat sampler. The core contained sandy peat (0.9–0.78 m depth) and fen shrub peat (0.78–0.2 m depth; D. Drzymulska, personal comm.). For technical reasons the highly hydrated topmost part of the deposit could not be retrieved.

Pollen analysis

Samples of 1 cm^3 were prepared using the standard procedure of Erdtman's acetolysis (Berglund and Ralska-Jasiewiczowa, 1986). Depending on the content of mineral matter the samples were treated with a heavy liquid (CdI_2+KI). The palynological analysis was performed on 35 samples from the PG6 profile. Pollen analysis was carried out with an Olympus BX43 light microscope with magnification of 600×; a larger magnification was used to identify problematic and small palynomorphs. The identification of cereal-type pollen was based on phase contrast studies under 1000× magnification. For taxonomical identification pollen keys (e.g. Beug, 2004) and a reference collection of modern pollen slides were used. On average 900 terrestrial pollen grains were counted and identified in each sample.

Analysis of non-pollen palynomorphs and microcharcoal

Non-pollen palynomorphs (NPPs) were counted along with the pollen analysis, and identified according to van Geel (1978, 2001), Bell (1983), Jankovská and Komárek (2000), van Geel *et al.* (2003) and van Geel and Aptroot (2006).

Microcharcoal particles were counted in the pollen slides and grouped into four size classes: 10–30 µm, 30–70 µm, 70–100 µm and >100 µm. According to Tinner and Hu (2003) the larger particles better reflect the incidence of local fires, whereas the smaller particles are more indicative of regional fires. Particles <10 µm were ignored, as they cannot be safely identi ed (Blackford, 2000). One tablet containing 20,848 marker spores of Lycopodium was added to each sample to enable a quantitative analysis of microfossil concentrations (Stockmarr, 1971). Charcoal particles were recorded with a light microscope at 400× magnification. Charcoal selection was restricted to fragments that were black, completely opaque and angular (Whitlock and Larsen 2001).

Calculations and the presentation of palynological and microcharcoal data were performed with POLPAL for Windows (Nalepka and Walanus, 2003). The AP+NAP sum was used for percentage calculations, both in the pollen and the NPP diagrams. The pollen diagram was stratigraphically ordered and zoned with Constrained Cluster Analysis (CONISS), and divided into local pollen assemblage zones (LPAZ), which were named according to the specific composition of pollen spectra. The human impact groups follow Behre (1981), Berglund and Ralska-Jasiewiczowa (1986), and Gaillard and Berglund (1988).

Principal component analysis (PCA) served for the detection of interspecies relationships. The analysis was based on data from all pollen samples; sporadically occurring arboreal taxa and non-arboreal taxa were excluded. PCA was carried out using XLSTAT 2014 trial version software.

Chronology

The age of one sediment sample from a depth of 0.48 m was determined by radiocarbon dating (^{14}C/AMS) in the Gliwice Radiocarbon Laboratory, Institute of Physics, Silesian University of Technology (Table 1).

RESULTS

Local pollen assemblage zones

The pollen diagram was divided into three LPAZ (from LPAZ PG6-1 to LPAZ PG-3), which correspond to the subsequent phases of vegetation development in the immediate vicinity of the sampling site (Fig. 2). The pollen zones are described (Table 2).

Principal Component Analysis (PCA)

It describes statistically possible relationships between arboreal pollen and the fungal spores record (Fig. 3). The results indicated that there may be a distinct positive correlation between the pollen record of forest species, e.g. *Quercus*, *Alnus*, *Picea abies*, *Carpinus betulus*, and the spores of the parasitic fungus *Kretzschmaria deusta* and the coprophilous fungi *Sordaria*-type and *Cercophora*-type.

INTERPRETATION AND DISCUSSION

Reconstruction of vegetation dynamics and human impact

The changes in the composition of the pollen assemblages recorded in the PG6 profile enabled to distinguish three phases of vegetation dynamics connected with human activity (Fig. 2).

Table 1

AMS radiocarbon dates from the PG6 core used for chronology

Depth (cm)	Lab. No.	Age ^{14}C (BP)	Calibrated age range 68% (calendar age, AD)	Calibrated age range 95% (calendar age, AD)
48	GdA-3545	695±25	1274 (68.2%) 1296	1266 (78.4%) 1308 1362 (17.0%) 1385

First phase (LPAZ PG6-1)

Vegetation changes in the study area at the beginning of this phase represent a period of strong human impact. Pollen spectra illustrate occurrence of a pine-birch forest, where the undergrowth was dominated by hazel. The existence of open surfaces and/or good light conditions on the forest floor is indicated by the presence of *Juniperus communis* pollen. Moreover, *Juniperus communis* indicates that dry and moderately moist soils occurred near the study site, what can be deduced from edaphic requirements of this species (Zarzycki, 2002). The abundant occurrence of microcharcoal particles, in all size classes, may re ect human impact on the environment. The presence of *Melampyrum* and *Pteridium aquilinum*, which are considered indicators of soil enrichment by ash (Latałowa, 2007), additionally confirms the occurrence of fires in the area. Most probably, it was intentional use of fire, pointing to activity within the settlement and to woodland clearing. The palynological data reveal the existence of large open areas near the sample site, as indicated by nearly 20% of NAP. A considerable area was covered by meadows and pastures, represented mainly by Poaceae, Cyperaceae, *Filipendula* and *Centaurea nigra*-type, and ruderal communities with *Artemisia* and Chenopodiaceae. Only small plots were used as fields.

In the investigated water body aquatic macrophytes like *Potamogeton, Nymphaea alba*, *Nymphaea candida* and *Nuphar* occurred. Along the lakeshore reed swamp communities with *Typha latifolia* and *Typha angistifolia* occurred. Numerous green algae, including *Tetraedron*, *Pediastrum* and *Botryococcus*, developed in the water body. These algae, as well as cyanobacteria of the *Gloeotrichia*-type, play an important role in inferring past lake conditions, and almost all are known to be dominant in more eutrophic systems (e.g. van Geel and Grenfell, 1996; Jankovská and Komárek, 2000). Moreover, *Gloeotrichia* is one of the most important organisms today causing so called ‘water blooms’, linked to the enrichment of the aquatic environment with phosphorus and nitrogen (Burchardt and Pawlik-Skowrońska, 2005). We may assume that the relatively high trophic status of the investigated water body was probably due to a large supply of nutrients in response to the intensive settlement activity in this area.

Linking the first phase of anthropogenic vegetation changes with a de nite cultural event is not possible due to the availability of only one radiocarbon date from a depth of 0.48 m in this section. However, it could be related tentatively to the second phase of occupation of the hillfort at Poganowo, dated to the early Middle Ages (10th–12th centuries AD). Archaeobotanical analysis of the early medieval layers and hearths

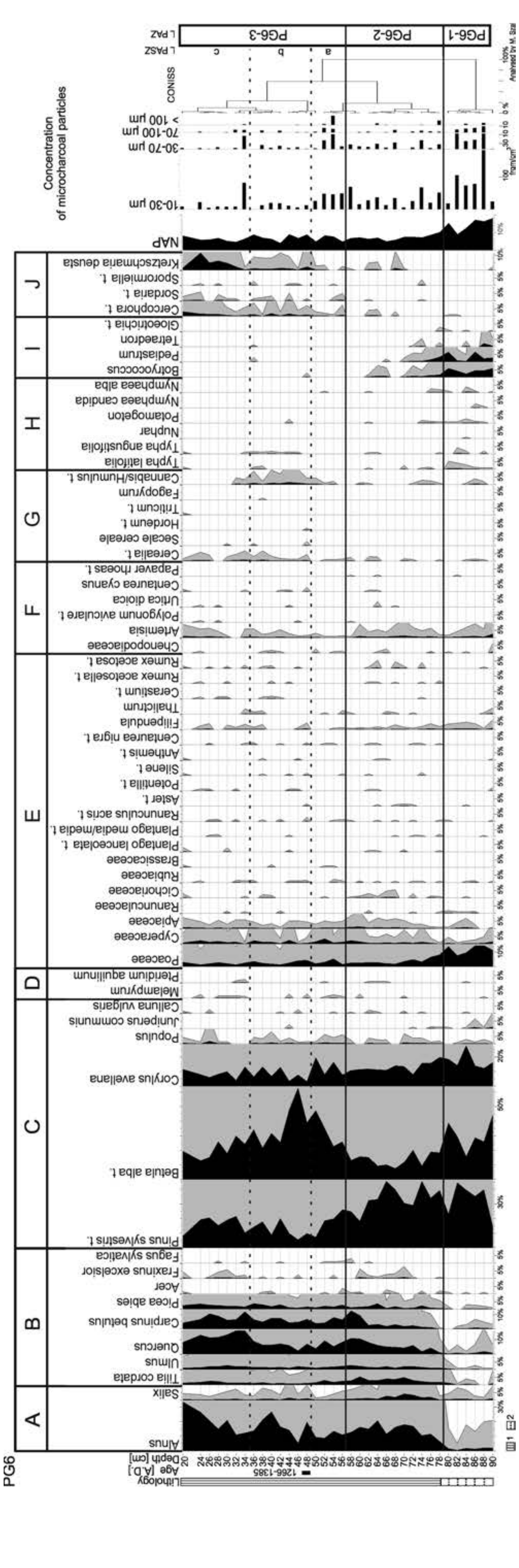

Fig. 2. Pollen percentage diagram with selected herb and woody taxa, non-pollen palynomorphs and charcoal record from the PG6 core. Trees and shrubs: A - plants of wet and fresh habitats; B – shade-loving plants, C – heliophilous plants; herbs and dwarf shrubs: D – plants of disturbed forest, E – meadow and ecologically undefined plants, F – ruderals and weeds; G – cultivated, H – water-loving plants; NPPs: I – green algae, J – fungi. Lithology: 1 – fen shrub peat, 2 – sand with peat.

within the settlement complex at Poganowo confirmed a cultivation of cereals in this time. Remains of barley (*Hordeum vulgare*), millet (*Panicum miliaceum*), wheat (*Triticum*), rye (*Secale cereale*) and oats (*Avena*) were found (K. Pińska, personal comm.). According to Wyczółkowski and Makowiecki (2009), it can be claimed that the inhabitants of the early mediaeval settlement at Poganowo raised cattle and horses.

Second phase (LPAZ PG6-2)

The period of intensive exploitation of the environment during the first phase was followed by a phase of decreased human activity (decrease in NAP frequency and concentration of microcharcoal particles) leading to the forest regeneration. Then, considerable changes in forest composition occurred. An increase of *Quercus* pollen is synchronous with an increase in pollen of the other main arboreal taxa: *Tilia*, *Ulmus*, *Carpinus*, *Picea*, *Fraxinus*, and expansion of *Salix* shrubs. The vicinity of the studied site became almost completely forested. Dry morainic hills were overgrown by mixed pine forests. Patches of fertile, fresh soils were covered by oak-hornbeam forest, with an admixture of spruce. Considerable areas in the lakeshore zone and in other wet places were covered by alder woods and carrs. At this phase, forest regeneration relates to a very low level of human exploitation of the landscape and possibly reflects the time when the Poganowo settlement complex was abandoned. There is an assumption that this could have happened in the early 13th century (M. Wyczółkowski, personal comm.). According to historical sources (Saage and Woelky, 1860), in the surroundings of the Poganowo hillfort there was a large forested area called Tauro ("Walt Tauro"), which was mentioned in documents dated to 1231–1340 AD. Nevertheless, pollen spectra from the PG6 section indicate that some pastoral agriculture seems to have been practiced at this time, as well as arable farming. According to Vuorela (1973), Cerealia-type pollen grains are not well dispersed in airstreams, and therefore their poor representation cannot be considered as a guide to the importance of crop farming in the area. Admittedly, some weeds of arable fields were present in the pollen record, but in low frequencies only. The appearance of *Centaurea cyanus* was probably connected with the cultivation of winter crops. Other weeds documented in the PG6 pollen profile include Chenopodiaceae, *Papaver* and *Polygonum aviculare*. *Cannabis*/*Humulus*-type pollen most probably indicates that *Humulus lupulus* grew in this area as a native plant on damp soils.

The area of meadows significantly decreased, but a low-level presence of *Plantago lanceolata*, *Rumex acetosella*-type, *Rumex acetosa*-type and Cichoriaceae pollen grains indicates that some open

Table 2

Local pollen assemblage zone description from PG6 core diagram

Name of L PAZ and depth	Description
PG6-1 *Pinus-Betula-Poaceae* 90-80 cm	Dominance of *Pinus sylvestris*-type (14-43%) and *Betula alba*-type (15-45%). High values of *Corylus avellana* (to 19%) with short-lasting peak (27%) in the middle part of zone. Several percentage frequency of *Alnus* (to 2%) and *Quercus* (to 1.5%). Sporadic presence of other tree taxa. Relatively frequent Juniperus communis. Considerable participation of NAP (9–18%). The herbaceous spectra dominated by Poaceae (to 15%). Regularly present *Filipendula*. Among the anthropogenic indicators, systematic presence of *Artemisia*, Chenopodiaceae and Cerealia-type. Frequent pollen grains of limnophytes, such as *Potamogeton* and *Typha latifolia*. Regular occurrence of green algae (*Botryococcus*, *Pediastrum*, *Tetraedron*) and single remains of cyanobacteria (sheaths of *Gloeotrichia*).Very high concentration of microscopic charcoal particles.
PG6-2 *Alnus-Pinus-Quercus-Tilia* 78–58 cm	Increase of *Alnus* above 20%. Significant decrease of *Betula alba*-type. Dominance of *Pinus sylvestris*-type (20–47%). High values of *Corylus avellana* (to 14%). Increasing curves of *Tilia cordata* (to 7%), *Ulmus* (to 3%), *Quercus* (to 12%), *Carpinus betulus* (to 12%), *Picea abies* (to 4%) and *Salix* (to 4%). Less numerous NAP (6–9%). Gradual decrease of Poaceae (to 3%). Frequent *Filipendula*, Cyperaceae, Apiaceae and Cichoriaceae. Regular occurrence of *Artemisia*. In several spectra, presence of Cerealia-type, *Centaurea cyanus*-type, *Plantago lanceolata*, *Rumex acetosella*-type, *Rumex acetosa*-type and Chenopodiaceae. Decreasing values of green algae. Single occurrences of coprophilous fungi (*Sporormiella*-type, *Sordaria*-type and *Cercophora*-type). Sporadic *Kretzschmaria deusta*. Relatively low concentration of microscopic charcoal particles.
PG6-3 *Betula-Quercus-Carpinus-Alnus* 56–20 cm	Dominance of *Betula alba*-type, *Pinus sylvestris*-type and *Alnus*. Constant presence of *Tilia cordata*, *Quercus, Carpinus betulus* and *Ulmus*. The PG6-3 LPAZ was divided into three subzones.
PG6-3a *Betula-Corylus* 56–50 cm	Fast increase of *Betula alba*-type (to 48%). High values of *Corylus avellana* (to 20%). Frequent *Populus*. Gradual decrease of *Pinus sylvestris*-type (to 8%). Relatively high values of *Alnus* (10–13%), *Quercus* (4–10%) and *Carpinus betulus* (5–11%). More frequent Poaceae (to 7%) and Cyperaceae (to 4%). Decreasing values of Apiaceae, *Filipendula* and Cerealia-type. Lower frequency of *Artemisia*. Relatively frequent *Cercophora*-type. Sporadic occurrence of *Sporormiella*-type, *Sordaria*-type and *Kretzschmaria deusta*. Relatively high concentration of microscopic charcoal particles.
PG6-3b *Betula-Alnus* 48–36 cm	Strong increase of *Betula alba*-type to 63%, then decrease to 24%. Increasing percentage values of *Pinus sylvestris*-type (to 21%). Lower values of *Corylus avellana* (4–12%) and *Populus* (to 1%). Fluctuating increase of *Alnus* (to 28%). Gradual decrease of Poaceae. More frequent *Artemisia* and *Cannabis/Humulus*-type. Regular occurrence of Cerealia-type and single occurrences of *Secale cereale* and *Hordeum*-type. Sporadic *Centaurea cyanus*-type, *Plantago lanceolata*, *Rumex acetosella*-type, *Rumex acetosa*-type. More frequent *Cercophora*-type and *Kretzschmaria deusta*. Sporadic *Sporormiella*-type and *Sordaria*-type. Much lower concentration of microscopic charcoal particles. The age of the sediment at 0.48 m depth was estimated at 1266–1385 AD (Table 1).
PG6-3 *Quercus-Carpinus-Kretzschmaria* 34–20 cm	High values of *Quercus* (to 16%) and *Pinus sylvestris*-type (to 20%). Increasing tendency of *Alnus* (to 34%). Gradual decrease of *Betula alba*-type (to 15%). *Carpinus betulus* oscillating around 7–11%. Constant presence of *Corylus avellana* (to 12%). Higher values of *Artemisia*. Regularly occurring Poaceae, Cyperaceae and Apiaceae. More frequent *Plantago lanceolata*, *Rumex acetosa*-type and Ranunculaceae. Sporadic *Rumex acetosella*-type. Temporary decreasing tendency of Cerealia-type. Strong increase of *Kretzschmaria deusta* to 12%. Increasing tendency of *Cercophora*-type. Sporadic occurrence of *Sporormiella*-type and *Sordaria*-type. Low concentration of microscopic charcoal particles.

herbaceous plant communities occurred as fodder for domesticated herbivores.

LPAZ PG6-2 represents a period of generally low anthropogenic activity in the catchment area and, based on decreased percentages of *Botryococcus*, *Pediastrum*, *Tetraedron* and *Gloeotrichia*, eutrophication diminished. However, the decrease of algae and some aquatic plants coincides also with sedimentological changes. It should be underlined that local terrestrialization, a transition from wetland to drier peat, could be an alternative explanation for the decline in algae and cyanobacteria.

Third phase (LPAZ PG6-3)

The pollen record from this core interval enabled to determine three sub-phases that indicate response of local vegetation to a variability of human activity dated to 13th–16th centuries AD.

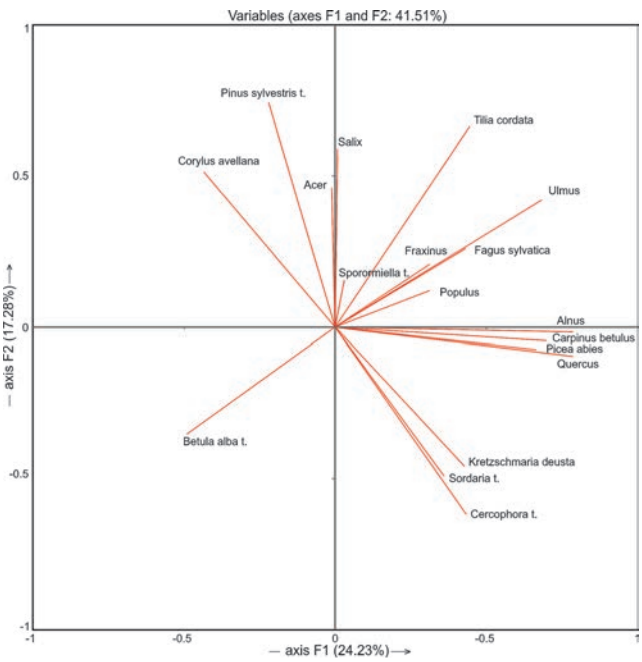

Fig. 3. PCA plot illustrating the interspecies relationships in the pollen spectra from the PG6 core.

In the oldest part (LPAZ PG6-3a) the most characteristic phenomenon was woodland clearance and the expansion of birch. Microscopic charcoal concentrations steeply increased, indicating the presence of fire events in the vicinity. Moreover, the presence of spores of *Pteridium aquilinum,* which easily colonizes disturbed ground, including burnt areas (Hartig and Beck, 2003), may also point to fires. The fires could have served as a silvicultural tool for deforestation, or just to create openings in a tree canopy. Local development of birch woodland and shrubs is perhaps associated with *Betula,* featuring as a prominent pioneer species after fires (Connor *et al.*, 2012; Lindbladh *et al.*, 2003). Moreover, at the beginning of this phase *Alnus* also increases, which plausibly illustrates its fire-related behaviour. Alder was classified by Tinner *et al.* (2000) to the group of taxa whose abundance largely depends on fire. The rapid increase in the pollen values of the light-demanding *Corylus*, accompanied by the more frequent *Populus,* is evidence for forest opening. *Corylus* as an understory species produces little pollen under a heavy tree canopy, and large quantities of hazel pollen may result from bushes growing at the woodland margin and in clearings (Rackham, 1988). In our investigation high frequencies of *Corylus* pollen, up to 22%, suggest that hazel had a dominant position in the vegetation, indicating that pollen dispersal was hardly hindered by trees. However, there were more changes in the woodland composition that occurred as consequence of forest fires. A reduction of deciduous tree pollen was observed, particularly of *Tilia*, *Quercus* and *Carpinus*, which grew on more fertile soils and this may indicate that more land was needed for arable fields. The importance of *Pinus* and *Ulmus* gradually decreased. However, elm was still present on fresh, fertile and moderately mesotrophic soils. Locally, wet alder woods may have grown in depressions, around the lake and on mires. There were slightly larger areas covered by meadow vegetation, in the PG6 pollen profile mainly represented by Poaceae, Cyperaceae, Apiaceae, Brassicaceae, Rubiaceae, *Silene*-type*, Thalictrum* and *Centaurea nigra*-type*.* Probably, there were also relatively small-cultivated areas and grazed grasslands situated close to the lake. It is also possible that deforestation took place because of the need to acquire new residential areas. However, it is difficult to determine the causes of forest destruction, especially because there is no archaeological evidence for construction materials and no anthracological data from the Poganowo settlement complex.

Pollen spectra from LPAZ PG6-3b indicate the predominance of forest communities, with *Betula* playing the most significant role, as suggested by its pollen values of up to 60%. Huntley and Birks (1983) assumed that *Betula* pollen values larger than 50% indicate *Betula*-dominated woodlands in the landscape. Szal *et al.* (2014) discussed the problem of the long-lasting dominance of *Betula* in the Iron Age and in the Migration Period, particularly in the area of Lake Salęt, situated close to the site investigated here. It was concluded that *Betula* expansion was connected with agricultural practices within the settlement region. In the case of the Poganowo area, the high *Betula* participation may indicate that this land was cleared repeatedly in order to prevent the re-growth of woodland and to enable effective crop farming. Cereal cultivation indicators recorded in the PG6 profile show that *Secale*, *Hordeum* and *Fagopyrum* were among the cultivated plants. However, the spectrum of herbaceous taxa mainly points to the existence of meadows (pollen of Poaceae, *Centaurea nigra*-type, *Filipendula*). In the surroundings of the investigated site, there occurred also ruderal plants, such as *Artemisia, Urtica* and Chenopodiaceae, which, according to Behre (1981), are associated with nitrogen-rich habitats. They may also have grown along the nitrogen-rich banks of the lake. In tree-less parts of the landscape grazed grasslands were present, as indicated by *Plantago lanceolata*, *Plantago major/media*, *Potentilla*-type, *Cerastium*-type, Rubiaceae, and Cichorioideae, which are considered to indicate pastoral activities (Mazier *et al.*, 2006; Hjelle, 1999). Moreover, Mazier *et al.* (2006) concluded that *Plantago lanceolata*, *Plantago major/media* and Chenopodiaceae could be also treated as indicators of woodland grazing. This may indicate that domesticated herbivores grazed close to the sampling site. In addition, pollen grains of *Polygonum aviculare* and *Rumex acetosella*-type were recorded. These weeds thrive on trampled, disturbed ground, and were classified by Pokorná *et al.* (2014) as reliable indicators of trampled vegetation.

In the youngest sub-phase (LPAZ PG6-3c) a significant spread of *Quercus* was observed. This process was accompanied by an increase of *Carpinus betulus* and *Pinus sylvestris* contemporaneous with a decrease in *Betula* and *Picea abies.* The pollen record shows that the surroundings of the study site were overgrown by mixed pine-oak forests and by rich, deciduous lime-oak-hornbeam forests. Areas occupied by hygrophilous *Alnus* increased, suggesting the development of swampy alder forest with *Fraxinus excelsior*. We suppose that the observed changes in species composition, mainly the dominance of *Quercus*, developed under the substantial in uence of human activity, and to some extent were associated with moderate livestock grazing in woodland. The occurrence of trampled and grazed areas near the study site is illustrated by presence of *Polygonum aviculare*, *Plantago lanceolata*-type, *Potentilla*-type, *Cerastium*-type, *Rumex acetosa*-type and *Rumex acetosella*-type. It is worth mentioning that in mediaeval documents related to the study area there are several place names indicating open oak woods with wood-pasture practices. For example, the name of the village Nakomiady (‘Eichmedien’) (eiche – an oak tree; median – the Prussian forest), may indicate the existence of oak wood (Gerullis 1922). Additionally, Beckherrn (1885) mentioned the area named ‘Damerau’, situated close to the study site since 1393. Gross (1935) claimed that in medieval times this name was commonly used to describe deciduous forest, mainly with oak trees, where domesticated pigs were fattened on acorns, a practice known as pannage. Moreover, according to Beckherrn (1889), and Wyczółkowski and Makowiecki (2009), it can be claimed that the inhabitants of the medieval Poganowo settlement complex raised cattle and horses.

It is not clear to what degree herbivores can influence long-term patterns of plant abundance, dynamics and distribution (Maron and Crone, 2006). Despite this, some scientists (e.g. Flannery, 2003) claim that there is a clear correlation between oak forest and the introduction of grazing herds into the primeval forests in medieval times. Faliński (1986) described the dominance of *Quercus* in Białowieża Forest as a result of grazing. However, different animal species are likely to have different effects, with larger animals likely to cause more physical damage by breaking branches, eating saplings and seedlings, or trampling the herbaceous vegetation. Cattle and other large herbivores may have created clearings, or at least more open woodland, allowing light to reach the ground and to support a growth of herbaceous plants on the woodland floor. In the PG6 section there are clear signs of small landscape openness and reductions in a tree canopy, leading to understory development with light-demanding *Pteridium aquilinum* and *Calluna vulgaris*. Moreover, in some areas where livestock grazing was suspended increased flowering/re-sprouting of *Corylus avellana* and *Populus* could occur.

Faliński (1986) noticed that in Białowieża Forest changes in species composition occurred that were associated with a reduction in grazed areas. The species of open habitats gradually declined and mesophytic *Carpinus* replaced *Quercus*. This led to the loss of species assemblages typical for subcontinental oak woods (Kwiatkowska *et al.*, 1997). The maintenance of oak woodlands in the past was also discussed by Szabó (2013). According to this author, traditional forest management was not a driving factor in a distribution of various forest types, while oak wood might be an exception. Because of the economic potential of acorns, woodland owners may have decided to conserve oak woods or even to transform other types of forests into oak woods. In addition, if such oak woods were used as pastures, such management led to subsequent changes in woodland composition and structure, connected with the prevention of forest succession. It is worth mentioning that according to Bobiec (2012), very high grazing pressure by large ungulate herbivores substantially limits oak regeneration. His observations of contemporary feeding stations located in Białowieża Forest indicate that high concentrations of bison effectively prevent oak recruitment. Moreover, López-Sánchez *et al.* (2014) observed reduction in density of oak seedlings and saplings, but not of adult trees in areas grazed by cattle. They concluded that the long-lasting presence of ungulates negatively affected oak regeneration, especially in pastures with a high stocking rate density.

Palaeoecological context of the fungal spores record

In central Europe, many human activities, e.g. deforestation, forest grazing and agriculture, significantly altered landscape structure and forest composition in the past (e.g. Behre, 1988). An important anthropogenic environmental change at or near settlement sites is eutrophication, resulting from the production of dung by high densities of domesticated herbivores (van Geel *et al.*, 2003). Furthermore, man and domesticated animals are responsible for a range of new habitats, also, the mycoflora of settlement sites and the surrounding arable land, pastures and hay-meadows will have had different fungal assemblages relative to natural habitats.

Fungi that inhabit or are associated with the dung of animals are known as coprophilous fungi (Krug *et al.*, 2004). These fungi are uniquely adapted to herbivore dung. Bell (1983) concluded that the spores of many coprophilous taxa are ingested by animals feeding on the plants, and then germinate after passing through the herbivores' digestive track. The spores not only survive passage through the digestive system of animals, but also in most cases the mechanical and chemical digestion processes also benefit the germination of the spores on the dung substrates (Bell, 1983). Krug *et al.*, (2004) underlined that germination, growth, and sporulation occur on freshly deposited dung. In the next phase, the spores are discharged forcefully into the air and readily adhere to nearby vegetation. Then, they will be consumed by herbivores, pass through their intestines, and again will be deposited with faeces (Bell, 2005). According to Krug *et al.* (2004), most of the coprophilous fungi are found on mammalian dung from domesticated farm animals, such as cattle, horses, and sheep; from wild mammals, both herbivorous and carnivorous; and from birds.

From the various studies of fossil and modern spores of coprophilous fungi (e.g. van Geel, 2001; Blackford and Innes, 2006; Graf and Chmura, 2006; van Geel and Aptroot, 2006) it became clear that the recorded spores in most cases were of strictly local occurrence. They were fossilized at, or near, the place where they had been produced, or the spores were deposited only a short distance from the place where sporulation took place. Consequently, spores of coprophilous fungi indicate nearby the former presence of dung produced by herbivores (van Geel *et al.*, 2003). According to Lundqvist (1972), representatives of the Sordariaceae (Ascomycetes) are mostly coprophilous, particularly the genera *Sporormiella*, *Podospora*, *Sordaria*, and *Cercophora*, which are the most common ones among dung fungi (e.g. Krug *et al.* 2004; van Geel *et al.*, 2007). Moreover, these fungi produce thick-walled spores that are well preserved in palynological preparations, and can be identified and counted alongside pollen, and this makes it feasible to use them in the category of secondary anthropogenic indicators (van Geel *et al.,* 2003; López-Sáez and López-Merino, 2011).

Ejarque *et al.* (2011) analysed modern assemblages of pollen and NPP, and found useful relationships with vegetation and environmental patterns, as well as with grazing activities. The study included samples from herbivorous excrement in order to identify potential grazing indicators. These authors emphasized the significant role of coprophilous taxa, particularly of *Sporormiella*-type and *Sordaria*-type, as local indicators of herbivores. The spore cells of *Sporormiella* species, which include obligate coprophilous species growing on herbivore dung (Ahmed and Cain, 1972), are actually most often used to study the mid-to- late Holocene history of pastoral activities (e.g. Mighall *et al.*, 2006; Currás *et al.*, 2012).

Recently, López-Merino *et al.* (2014) indicated that *Cercophora*-type spores should be also regarded as good indicators of dung and grazing pressure. Fossil ascospores of the coprophilous *Cercophora*-type were first recognized by van Geel (1978). According to Ralska-Jasiewiczowa and van Geel (1992), the occurrence of *Cercophora*-type may be related to increased populations of large wild, and possible domesticated, herbivores. *Cercophora* species occur not only on dung, but also on decaying wood, culms, stems and leaves (Lundqvist, 1972). Moreover, Cugny *et al.* (2010) reported that *Cercophora*-type is more frequent in forested sites than elsewhere, and thus can be used as an indicator of grazing in a woodland.

In our study the record of spores of coprophilous fungi (*Sporormiella*-type, *Sordaria*-type and *Cercophora*-type), in combination with pollen data, was used to identify animal-related agricultural practices in the vicinity of the studied site. In the first phase of human impact on the vegetation (LPAZ PG6-1, Fig. 2) frequently noted pollen of human impact indicators coincided with evidence of deforestation. The relatively high peaks of Poaceae, Apiaceae, Ranunculaceae, as well as numerous *Filipendula* and *Centaurea nigra*-type pollen (Fig. 2), document a large area of meadows rather than pastures. There were no *Plantago lanceolata*, *Rumex acetosella*-type, and almost no *Rumex acetosa*-type pollen, considered by Gaillard *et al.* (1992) as characteristic of grazed and mown grasslands, and indicators of animal husbandry. However, the presence of numerous charred particles, high frequencies of *Artemisia,* which is an indicator of ruderal communities and certain amounts of Chenopodiaceae point to significant activity within the settlement. In spite of the fact that human activity was intense at this phase, fungal spores were very scarce. Only *Cercophora*-type was present, but in small numbers and in only a few samples. It should be taken into consideration that wet local conditions may have limited both the local development of fungi and the frequentation of the site by animals (therefore, almost no dung may have been deposited). However, based on the pollen and fungal spore record from the first phase, it is possible that agriculture and animal husbandry did not play a key role in the close vicinity of the PG6 site. This is understandable if this first phase relates to the second phase of occupation of the hillfort at Poganowo, when an early medieval sacrificial place existed there, and mainly magical-religious rituals were performed. Agriculture was the most important human activity in the medieval period, and therefore we can say with a high degree of certainty that farmlands occurred at some distance from the investigated site. This interpretation is in agreement with the archaeological evidence of an early medieval human habitation in the Poganowo area.

The first phase was followed by a phase of decreased human activity (second phase, Fig. 2). However, pollen data from the PG6 profile indicate that some new land-use practices appeared in the second phase, but on a small local scale. The occurrence of *Plantago lanceolata, Rumex acetosella*-type, *Rumex acetosa*-type and Cichoriaceae pollen grains indicates that some open plant communities spread, probably as a result of grazing. Moreover, presence of spores of the coprophilous *Cercophora*-type, *Sporormiella*-type and *Sordaria*-type may confirm this type of activity in the close vicinity of the studied site. However, it remains an open question whether grazed plots were located in a forest or in areas outside the forest.

The third phase (LPAZ PG6-3) corresponds to the period of intensification of settlement processes that probably started from the late 13th century AD onwards. Pollen data indicate changes in the woodland composition and show the frequent occurrence of human impact indicators. To some extent, the anthropogenic forest disturbances were probably related to the pasturing of livestock and firewood collecting. The increase of coprophilous fungi suggests that the livestock frequented the wetlands and fens located close to the sampling site, probably more often than before. It should be taken into account that over 4,500 fragments of animal bones were found during the archaeological investigations of the medieval sacrificial place at Poganowo (Wyczółkowski and Makowiecki, 2009) which might have functioned here even in the 13th and 14th centuries AD (M. Wyczółkowski, personal comm.). Almost 90% were horse bones and about 10% cattle bones. The authors estimated the minimum number of horse individuals at 60. We suppose that cattle and horses were the dominant domesticated species in the study area. Moreover, in written sources (Beckherrn, 1885), a place called 'Stiermarkt' (bovine/cattle market) is mentioned and it is located a few kilometres from the sampling site. This toponym may confirm that grazing cattle played a significant role in this area in the past, but we cannot exclude an influence of game populations on the vegetation. However, typically, the spores of coprophilous fungi are occasionally present in the sediments and become very common only after the introduction of domesticated pasture animals (Graf and Chmura, 2006). According to Ejarque *et al.* (2011), dung-related fungi appear in much higher abundance in the excrement of domesticated animals than in the faeces of wild species, but the experimental research by Richardson (2001) showed that it is not possible to differentiate between fungal spectra from domestic (cattle, sheep, goat and horse) and wild (deer, elk) species.

It seems logical that the increase in *Cercophora*-type, *Sordaria*-type and *Sporormiella*-type that occurs in LPAZ PG6-3 (Fig. 2) implies a significant enhancement in grazing intensity and thus an increased population density of livestock near the investigated site. The higher frequencies of the spores of coprophilous fungi coincide with a noticeable increase of the spores of the parasitic fungus *Kretzschmaria deusta*, reaching a maximum frequency of ca. 12%. The data from Poganowo may show that animals damaged the root system and the lower part of the trees by scraping bark away, hence allowing infection by this parasitic fungus. Moreover, the results of the PCA (Fig. 2) show that there is a correlation between dung-related fungi (*Sordaria*-type and *Cercophora*-type), the wood-rot fungus *Kretzschmaria deusta* and tree species such as *Alnus*, *Carpinus betulus*, *Picea abies* and *Quercus*. This may indicate that animals browsed mainly in woodland dominated by the above-mentioned tree species. Moreover, based on data from the topmost part of the PG6 pollen diagram (Fig. 2), where frequencies of *Kretzschmaria deusta* and *Quercus* change simultaneously, it could be concluded that this fungus might infected oaks more often than other trees. However, it should be taken into account that from the beginning of the LPAZ PG6-2 the local environment has changed, and the establishment of a local riparian and deciduous forest occurred, which permitted the presence of animals and, subsequently, spores of coprophilous fungi, as well as *Kretzschmaria deusta*.

Ascospores of *Kretzschmaria deusta* were previously identified as *Ustulina deusta* or as non-pollen microfossil 'Type HdV-44' by van Geel (1978), who also recognized that those spores were produced by a representative of the Xylariaceae. The fungus *Kretzschmaria deusta* (Hoffm.) P.M.D. Martin (*Ustulina vulgaris* Tul. and C. Tul; *Ustulina deusta* Hoffm.) is a tree pathogen that is also called brittle cinder, and it is found in temperate regions of the northern hemisphere (Rogers and Ju, 1998; van Geel *et al.*, 2013). It causes soft-rot in wood, breaking down both cellulose and lignin, and it decays the trunk and roots of living trees. The fungus continues to decay wood after the host tree has died, making *Kretzschmaria deusta* a facultative parasite (Rogers and Ju, 1998). This fungus has a wide host range among broadleaved trees in Europe, including *Acer*, *Aesculus*, *Alnus*, *Betula*, *Carpinus*, *Castanea*, *Fagus*, *Fraxinus*, *Populus*, *Quercus*, *Salix*, *Tilia* and *Ulmus.* It has been rarely noted on *Abies* and *Taxus* (Wilkins, 1934). Although there is no evidence that *Kretzschmaria* occurs on *Picea abies*, potentially it can invade this tree (J. Rogers, personal comm.). Moreover, Schwarze (2007) showed experimentally the ability of *Kretzschmaria deusta* to cause decay in living spruce trees. Chlebicki (2008) reported that some xylariaceous fungi occur on *Picea abies* in Poland. Wilkins (1934) summarized many papers dealing with the pathogenicity of *Kretzschmaria*. It is an opportunistic parasite that takes advantage of already significantly damaged trees (Rogers and Ju, 1998). Open wounds on tree trunks are needed to account for major expansions of the fungus. Moreover, attacks by *Kretzschmaria* are usually associated with infections by some other fungi (Wilkins, 1934).

CONCLUSIONS

Integration of data from pollen, non-pollen palynomorph and microcharcoal particle analyses proved to be a useful tool for assessing human occupation of the Poganowo area. It is possible to distinguish three phases of vegetation dynamics connected with local human impact dated to the Middle Ages (*ca* 10^{th}–16^{th} c.). The oldest, first phase, corresponds to very intensive human activity within the Poganowo settlement complex and relates to relatively large open areas created by regular human-caused burning. This region was, to a considerable extent, covered by meadows and ruderal communities, and only small plots were used as fields and pastures. The second phase was a period when human activity decreased and woodland regeneration took place. Finally, the third phase reflects response of a local vegetation to human activity dated to the 13^{th}–16^{th} centuries AD. Increasing ruderalisation and intensification of human impact were manifested by indicator species of trampled and grazed vegetation. The medieval management most probably promoted oaks and pastured oak woods. During the youngest part of this phase, a significant spread of *Quercus* was accompanied by an increase in spores of coprophilous fungi and the parasitic fungus *Kretzschmaria deusta*. We suppose that grazing animals caused damage to the roots and trunks of oak trees, thus triggering infections with *Kretzschmaria deusta*.

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