Studia Quaternaria, vol. 26: 25–39.

HISTORY OF THE BIAŁOWIEŻA PRIMEVAL FOREST, NE POLAND

Krystyna Milecka[1], Agnieszka M. Noryśkiewicz[2], Grzegorz Kowalewski[1]

[1] *Department of Biogeography and Palaeoecology, A. Mickiewicz University, Dzięgielowa 27, 61-680 Poznań, Poland; e-mail: milecka@amu.edu.pl; ichtys@amu.edu.pl*

[2] *Institute of Archaeology, Nicolaus Copernicus University, Szosa Bydgoska 44/48, 87-100 Toruń, Poland; e-mail: anorys@uni.torun.pl*

Abstract

Białowieża in Poland is a very famous region in Europe (because of its primeval forest and bison population), but its environmental history is poorly known. This article shows the results of palynological analysis, macrofossil analysis and geological settings of two mires in the Białowieża Forest. The pollen diagrams show changes of the vegetation cover from the younger part of the Late Glacial until the present time. The relative time scale is based on palynostratigraphy and comparison to published results of other sites from the adjacent regions. During the Late Glacial two stages of the vegetation succession were revealed: steppe and forest during the Alleröd period and tundra-like vegetation during the Younger Dryas. The Holocene history consists of five stages of plant cover development. The special features of the Białowieża Forest are conditioned by two main factors: low degree of anthropogenic impact and influences of continental climate and boreal zone, stronger than in the other regions of Poland.

Key words: pollen and macrofossil analysis, Białowieża Primeval Forest, NE Poland, peatland, Late Glacial, Holocene

INTRODUCTION

The Białowieża Primeval Forest (N 52°42' E 23°52') has been a very attractive area for man for many centuries. Natural features of this region, big area of forest and abundance of fauna were appreciated by Polish and Lithuanian kings and princes, who restricted the possibility of hunting there. After the First World War, law protection of the forest started and developed successfully and a nature reserve was installed in 1920. In 1977 Białowieża National Park was included to the World Biosphere Reserves of the UNESCO. The trial to recover the population of European bisons was successful in the twenties of the 20th century. Thanks to that, bison has become the symbol of Białowieża Forest, well known for all Polish people. Protection was one of the reasons for the low degree of anthropogenic changes in the forest communities, building probably the one of a few forest complexes in Europe, which can be called primeval forests. Three-leveled canopy of mixed deciduous forest with *Quercus*, *Ulmus*, *Tilia*, *Acer* and *Picea* is the main feature of this forest complex (Faliński 1986), a precious natural, scientific and touristic object, worth of many-directional studies substantiating the present state and directions of the development of the ecosystems. The most extensive research, made by Prof. J.B. Faliński and other scientists of the Geobotanical Station of Warsaw University provides scientific description of contemporary changes in the Białowieża Forest. This knowledge should be completed by palaeoecological research giving information about plant cover succession and climatic changes in the Late Vistulian (the last glaciation) and the Holocene.

Palaeoecological research at the Białowieża region was initiated in the 30-ties of the 20^{th} century (Paszewski, Poznański 1936; Paszewski 1937) and continued after the Second World War (Dąbrowski 1959; Borowik-Dąbrowska, Dąbrowski 1972). Unfortunately detailed palynological analyses have not been made for a long time in the area of NE Poland. Therefore chronological interpretation of events and their correlation between sites in this region was impossible. In the 80-ties and 90-ties of 20^{th} century new publications concerning some sites in Knyszyńska Forest (Kupryjanowicz 1991, 2000), Podlasie (Balwierz, Żurek 1987) and Polesie (Bałaga 1982, 1990) did appear. A considerable part of the research is still not published, *e.g.* of some sites in the Białowieża Forest and its surrounding (Kupryjanowicz 2003) and on the Late Vistulian (Weichselian) and Holocene vegetation history of the lake near Ełk (Milecka unpubl.).

The need for detailed description of the Białowieża Forest ecosystem history was the main reason for taking up the research in cooperation between the Geobotanical Station of Warsaw University and the Department of Biogeography and Palaeoecology AMU in Poznań. In summer 2000 two cores for sediment description and pollen and macrofossil analyses were taken. The cores were collected in the SE part of Białowieża National Park in the spring area of the Orłówka stream (left tributary of Narewka) in forestry section 373 (Fig. 1). The first core is located in the central part of Dziedzinka mire, the second one was a repetition of Dąbrowski's research (1959) at Kletno, but unfortunately the spot with the largest thickness of sediments could not be found.

Fig. 1. Location of the cores Kletno and Dziedzinka in the Białowieża Forest, NE Poland.

This article documents the results of pollen analysis of the Kletno and Dziedzinka peatbog (preliminary results also in Noryśkiewicz, Milecka 2002), the results of macrofossil analysis of the Kletno peatbog (results of macrofossil analysis of Dziedzinka peatbog in Noryśkiewicz, Kowalewski 2002, 2003) and presents the palaeoecological interpretation of the results and their comparison with other published diagrams of NE Polish sites.

MATERIALS AND METHODS

A geological survey was conducted on the Dziedzinka peatbog. Two coring transects (NS and WE) crossing the center were made (Fig. 2). Core S-20 (0–124 cm), located in the central part of the peatbog was taken for palynological and macrofossil analyses.

In Kletno one core (315 cm lengh) was taken in the central part of the peatbog using an Instorf corer with a diameter of 45 mm. The sediments were described following the Troels-Smith system (Troels-Smith 1955; Tobolski 2000) (Fig. 2).

The samples for pollen analysis were taken every 5 or 10 cm along the core, 1 cm^3 from the limnic part and 3 cm^3 from the peat. A standard preparation procedure and then acetolysis (3 min) was applied (Berglund, Ralska-Jasiewiczowa 1986) and the samples were mounted in glycerine and just before making a microscope preparation, stained with safranine or basic fuchsine for easier examination of pollen grains sculpture. The total of 1000 sporomorphs was counted (trees, shrubs, herbs, telmatophytes, aquatics and *Pediastrum*). In some parts of the cores, especially in the Late Glacial and early Holocene, the frequency was too low, and the counted sums were lower.

Percentage diagrams (Figs 3, 4) were prepared in Tilia and Tilia-Graph programmes (Grimm 1990), based on AP+NAP=100% (aquatic and wetland species excluded). The pollen types were divided into ecological groups and the zonation into local pollen assemblage zones (L PAZ) made on the basis of trees and NAP percentage curves, was confirmed by CONISS (Grimm 1987). Charcoal values are given in percentages of the total pollen sum.

Parts of 1–5 cm thickness (*ca.* 10–50 cm^3) were washed with running water through sieves of mesh diameter 250 and 120 µm. Some compacted samples were heated for 5 minutes in 10% potassium hydroxide (KOH). The remains were examined under a stereo-microscope Stemi 200-C Zeiss under 10–100× magnification and some selected remains in light microscope using 400× magnification. For determinations, keys and the reference collection of the Department of Biogeography and Palaeoecology were used (Bertsch 1941; Aalto 1970; Katz *et al.* 1965, 1977; Grosse-Brauckmann 1972, 1974, 1992; Tobolski 2000).

The macrofossil diagram was prepared with the programme C2 ver 1.4 (Juggins 2003). On the basis of the dominating plant components four local macro assemblage zones (L MAZ I-IV) were defined.

RESULTS

Stratigraphy

Kletno

Limnic sediments such as detritus gyttja mixed with macrofossils of Bryales (mainly *Drepanocladus* sp.) and *Sphagnum* peat are dominant in the Kletno mire (Fig. 2). Detritus gyttja was recorded at the bottom part (315–295 cm). It contains some roots of sedges (Cyperaceae) growing later at this place. Gyttja was accumulated in relatively shallow (*ca* 2 m) and stagnant water, whereas the overlying layer (295–235 cm) was deposited in a more shallow water body forming poorly decomposed peat characteristic for telmatic part of the lake (cf. Tobolski 2000). It contained some wood remains probably floating in water. The upper part of the core consists of normal peat. Poorly decomposed peat consisting of remains of *Carex* radicells and wood was recorded at 235–150 cm depth. More decomposed herbaceous peat dominated the next layer (150–50 cm). In the bottom part of this layer, poorly decomposed peat was recorded with dominating *Eriophorum* and *Sphagnum* remains. Description of sediment components according to Troels-Smith formula is shown below (Ld *Limus detrituosus*; Dh *Detritus herbosus*; Th *Turfa herbacea*; Dl *Detritus lignosus*; Tl *Turfa lignosa*; Sh *Substantia humosa*; Tb *Turfa bryophytica*):

315–295 cm – Ld2, Dh2; detritus gyttja;
295–235 cm – Th3, Dh1, Dl+; herbal peat;
235–150 cm – Th3, Tl1, Sh+; herbal peat with pieces of wood;
150–50 cm – Th2, Sh2; moderately decomposed herbal peat;
50–27 cm – Th3, Sh1; poorly decomposed herbal peat;
27–0 cm – Tb3, Sh1; poorly decomposed moss peat.

Dziedzinka

The coring transect shows the extent of the basin with a flat mineral bottom (Fig. 2). N–S extent of the basin is 280 m and in W–E direction 320 m, depth rarely exceeds 130 cm. A

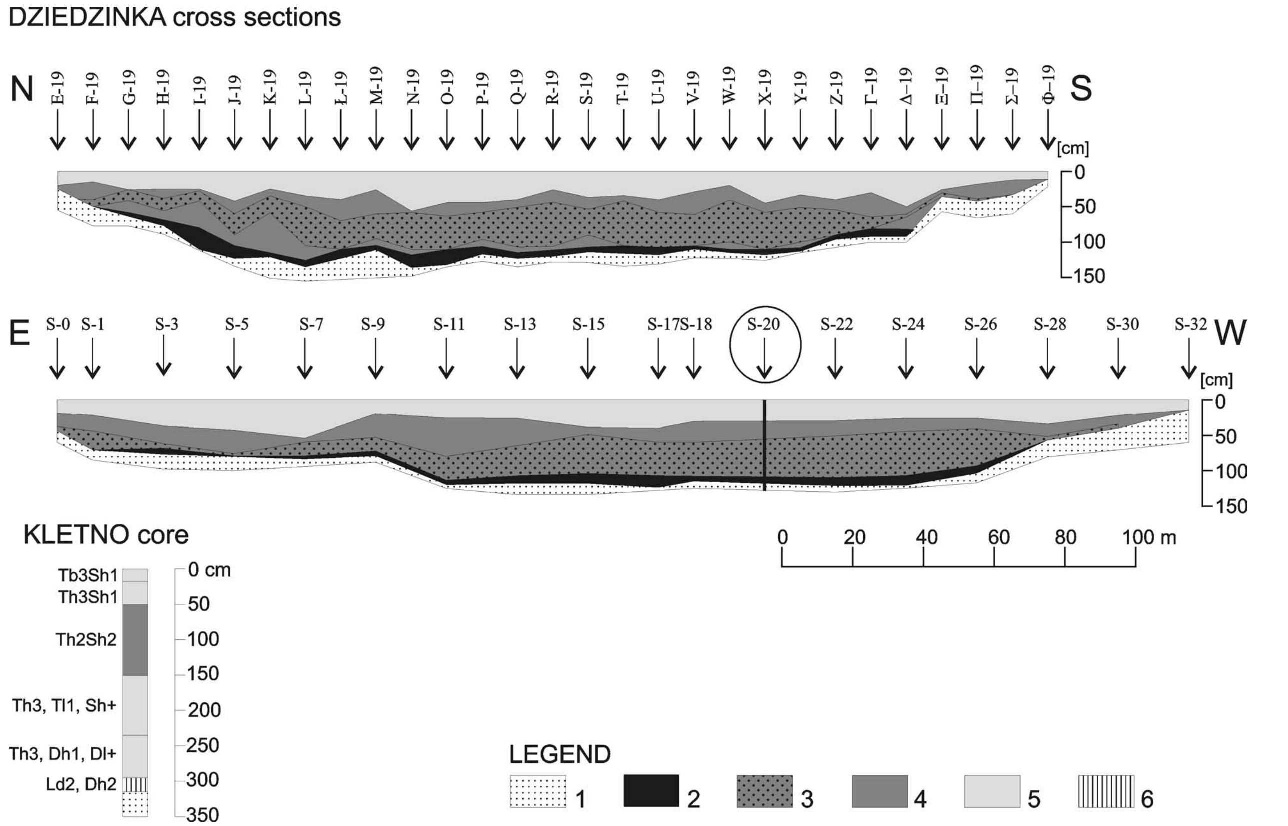

Fig. 2. Stratigraphy of sediment in the accumulation basins Kletno and Dziedzinka. *1* – mineral bedding, *2* – strongly decomposed organic matter, *3* – medium decomposed peat with charcoals, *4* – medium decomposed peat (mainly *Eriophorum* in Dziedzinka), *5* – slightly decomposed peat (mainly *Sphagnum-Pinus* in Dziedzinka, *Eriophorum* peat in Kletno), *6* – detritus gyttja.

similar pattern of layers was found in the entire peatbog. Strongly decomposed organic sediments with a significant content of mineral material (20–50% well rounded sand grains) occur at the bottom. In the core S-20 this layer is about 30 cm thick (124–94 cm), and contains quite a large amount of water and marsh plant macrofossils. The layer of moderately humified peat is overlying. It contains charcoals in addition to mineral material (94–60 cm). Numerous parts of vascular plants, with *Eriophorum angustifolium* roots in them, were the main components of this peat. Fruits and seeds were lacking, only single stems of *Sphagnum* sect. *Cuspidata* were found (80–75 cm). *Eriophorum vaginatum* dominated at the bottom as well as *Sphagnum* and *Pinus sylvestris* at the top (60–0 cm). Detailed description of sediments is given below (Gmin *Grana minora*; Dg *Detritus granosus*; anth *anthrax*; cort *cortex*):

124–119 cm – Gmin4, Dg+, Dh+; inflow wood, roots from the upper (younger) layers, endocarps of *Potamogeton* spp., proportion of mineral material up to 90%;

119–100 cm – Sh2, Th1, Dg+, Gmin1; rhizoderms, mostly determined as Cyperaceae, endocarps of *Potamogeton*, nuts and utricles of Cyperaceae *e.g. Carex* spp. 2- and 3-stigmata, proportion of mineral material up to 25%;

100–95 cm – Sh2, Th2, Dg+, Gmin+; rhizoderms, mostly determined as Cyperaceae, frequent endocarps of *Potamogeton natans* and *P. obtusifolius*, fruits of *Sparganium minimum*, seeds of *Menyanthes*, very frequent nuts of *Carex nigra* and *C. vesicaria*;

95–80 cm – Sh2, Th2, Dg+, Gmin+, anth.+; medium decomposed peat with traces of charcoals, mineral part up to 10%, frequent nuts of *Carex* cf. *vesicaria*, seeds of *Menyanthes*;

80–60 cm – Sh3, Th1, cort.+, anth.+; highly decomposed peat (the most in the bottom), undetermined rhizoderms dominate, charcoal, single parts of epiderms (with stomata), single parts of dicotyledonous leaves, *Pinus* bark, single branches of *Bryales*, single grains of sand;

60–55 cm – Th2, Sh2, Dg+, cort.+, anth.+; dominance of leaf vaginae of *Eriophorum vaginatum*, a seed of *Menyanthes*, traces of *Pinus* bark, a lot of charcoal, single covers of *Sphagnum* capsules, single leaves of *Sphagnum*;

55–50 cm – Th2, Sh2, Dg+, Dl+, cort.+; *Eriophorum* peat: epiderms of leaf vaginae of *Eriophorum* (60%), single leaves of *Calliergonella cuspidata*, pieces of wood, frequent seed testae of *Andromeda*, *Pinus* bark;

50–45 cm – Tb2, Sh2, Th+, anth.+; *Sphagnum* peat dark brown (60%), *Pinus* remains (40%), seed testae of *Andromeda*, single fibres of *Eriophorum*, single stems of *Aulacomnium palustre*, charcoal;

45–40 cm – Th2, Sh1, cort.1, Tb+, Dg+; herbal peat, dark brown, 70% epiderms of leaf vaginae of *Eriophorum vaginatum*, *Pinus* bark 25%, single leaves and stems of *Sphagnum*, single seed testae of *Andromeda*;

40–32 cm – Th2, Tb1, Sh1, Dg+, cort.+; *Eriophorum* peat (50%) dark brown, *Sphagnum* 10% (sect. *Cuspidata*, unfrequent stems, dominance of leaves), *Pinus* remains;

Table 1

Names, boundaries and short description of Kletno LPAZ (Fig. 3)

Depth [cm]	Number of LPAZ	Name of LPAZ	Description
45-0	Kl 9	*Carpinus-Picea*	High content of *Carpinus betulus* and *Picea abies* pollen; low curves of deciduous trees; NAP reaches 12%; Chenopodiaceae, *Rumex a/a* type, *Secale cereale* and cereals are present
65-45	Kl 8	*Quercus*	Low content of *Betula* and *Pinus* pollen; *Quercus* and *Corylus avellana* are the most numerous species in the deciduous trees group; *Alnus* curve exceeds 20%; single pollen grains of pasture indicators, *Cannabis* type and cereals
95-65	Kl 7	*Corylus-Betula*	The last increase of *Betula* curve, low content of *Pinus* grains; *Ulmus*, *Tilia* and *Fraxinus* declined; *Carpinus betulus* curve is low, but stable; continuous curve of *Picea abies*; presence of Ericaceae (*Calluna*, *Ledum palustre* and *Vaccinium* type) and *Secale cereale*
125-95	Kl 6	*Ulmus-Tilia-NAP*	*Pinus* curve stable, *ca.* 40%. *Betula* low; pollen grains of deciduous trees are dominant; *Fagus sylvatica* and *Carpinus betulus* appeared; *Pteridium aquilinum* spores are recorded; *Sphagnum* spores are abundant
155-125	Kl 5	*Alnus-Corylus*	Lowering of *Pinus* pollen grains; higher proportion of *Quercus*, *Ulmus*, *Tilia* and *Fraxinus*; *Corylus avellana* exceeding 5%; single pollen of *Viscum*; stable presence of *Pteridium aquilinum*, absence of aquatics and *Pediastrum*
195-155	Kl 4	*Pinus-Corylus*	High percentage of *Pinus* pollen grains; *Corylus avellana* curve reaches 5%; low and uncontinuous curves of *Quercus*, *Tilia* and *Fraxinus* excelsior are present; low, stable content of *Ulmus* grains; beginning of stable content of *Sphagnum* spores
273-195	Kl 3	*Pinus*	Dominant presence of *Pinus*, *Betula* curve decreases; beginning of presence of mesophilous trees like *Quercus*, *Tilia* and *Fraxinus* excelsior; stable, but low content of *Alnus* pollen grains; low NAP curve; presence of sporomorphs of *Typha latifolia*, *Utricularia* and *Menyanthes trifoliata*
294-273	Kl 2	*Betula-Pinus*	A lot of *Betula* pollen grains (max. 60%); *Pinus ca.* 35%; at 287 cm a continuous curve of *Ulmus* appears; decrease in NAP, especially heliophytes like *Artemisia* and Poaceae; increase in concentration of pollen grains
315-294	Kl 1	*Salix-Juniperus*	High percentage of herbaceous plants, *ca.* 30%; stable curves of *Pinus* and *Betula*; presence of *Dryas octopetala*, *Scleranthus perennis*, *Linnaea borealis* and *Selaginella selaginoides*

Table 2

Names, boundaries and short description of Dziedzinka L PAZ (Fig. 4)

Depth [cm]	Number of LPAZ	Name of LPAZ	Description
35-0	DZIE 8	*Carpinus-Picea*	There are absolute maxima of *Carpinus betulus* (20.4%) and *Picea abies* (10.1%); local peaks of *Tilia* and *Quercus*; *Alnus* and *Ulmus* decrease; increasing proportion of anthropogenic indicators: *Rumex*, *Plantago lanceolata*, *Secale* and cereals
62-35	DZIE 7	*Carpinus-Corylus-Betula*	Peak of *Carpinus betulus* (3.1%); single pollen grains of *Fagus sylvatica*; continuous curve of *Picea abies*; decrease of proportion of deciduous trees pollen; single grains of cereals and *Plantago lanceolata*
70-62	DZIE 6	*Corylus-Ulmus-Tilia*	Low proportion of pine; peaks of *Corylus*, *Alnus*, *Ulmus* and *Tilia*; pollen grains of *Viscum* appear; NAP doesn't exceed 4%, *Pteridium aquilinum* spores are still present; increasing content of *Carpinus betulus* pollen in the upper part
75-70	DZIE 5	*Corylus-Ulmus*	Peaks of *Corylus avellana* (8%) and Alnus (19%); increasing proportion of *Ulmus*, *Tilia*, *Quercus* and *Fraxinus* pollen; NAP declines; single spores of *Pteridium aquilinum*; decrease of *Sphagnum* spores
82-75	DZIE 4	*Pinus-Betula II*	Dominance of *Pinus* (26–49%) and *Betula* (31–55%); continuous curves of *Corylus avellana* and *Alnus*; *Sphagnum* average 22%, *Menyanthes trifoliata* and *Comarum palustre* are present
102-82	DZIE 3	*Pinus*	*Pinus* pollen grains are dominant (ca 50%); continuous curve of *Ulmus* appears; Poaceae and *Filipendula* are the most abundant herbs; *Typha latifolia*, *Menyanthes trifoliata*, *Sphagnum* and *Equisetum* are permanently present
115-102	DZIE 2	*Salix-Juniperus-NAP*	High proportion of *Pinus* (up to 61%) and *Betula* (up to 37%); maximum of *Juniperus* and *Salix*; there are heliophytes like: *Artemisia*, Poaceae, Chenopodiaceae; *Helianthemum*, *Linnaea borealis* and *Selaginella selaginoides*; increasing proportion of aquatics: *Alisma*, *Myriophyllum*, Nymphaea and *Pediastrum*
124-115	DZIE 1	*Pinus-Betula I*	*Pinus* pollen grains are dominant (61–75%), *Betula ca.* 20%; continuous curve of *Salix*; single grains of *Juniperus*, *Hippophaë*, *Betula nana* type, *Linnaea borealis* and *Helianthemum*; low curve of *Pediastrum*

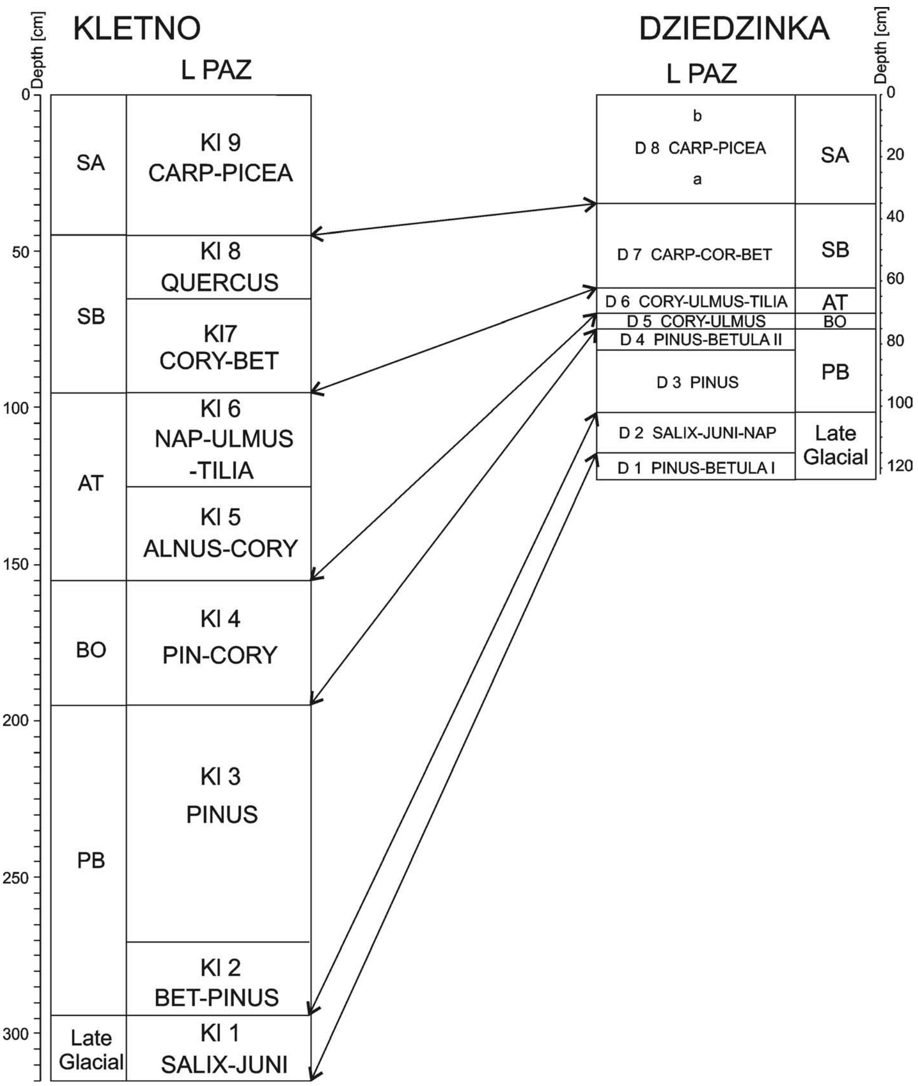

Fig. 5. Correlation of Local Pollen Assemblage Zones (LPAZ) of the Kletno and Dziedzinka S-20 cores. Positions of chronostratigraphical boundaries are uncertain because of lack of independent, absolute dating.

32–28 cm – Tb3, Sh1, Dg+, cort.+; *Sphagnum* peat (90%), *Pinus* remains;

28–25 cm – Tb3, Th+, Sh1, cort.+; *Sphagnum* peat (80%), *Pinus* bark, small roots of conifers;

25–20 cm – Tb1, Dg2, cort.1, Sh+; *Pinus* peat (70%): many pieces of bark;

20–0 cm – Tb4; *Sphagnum* peat.

Results of pollen analysis

On the basis of the main trees and NAP curves, pollen diagrams have been differentiated into nine (Kletno) or eight (Dziedzinka) local pollen assemblage zones (Tables 1, 2). Correlation of Kletno and Dziedzinka LPAZes is shown in Fig. 5.

Results of plant macrofossil analysis

Kletno

Macrofossil remains analysis was made for the bottom part of the sediment core (315–200 cm). It allowed to describe the succession of telmatophyte and aquatic plant communities and to specify the time of the lake overgrowing and mire formation. Four local macro assemblage zones (LMAZ) were defined (Fig. 6). They are correlated with the pollen zones Kl 1–Kl 3 (Fig. 7).

Kletno LMAZ I, *Chara-Scorpidium*, 315–295 cm

Chara is dominant in the sediments of this MAZ, 516 oospores/50 cm^3 were found at the depth of 305–300 cm. There was also *Potamogeton* identified mainly as epiderms of the leaf stalks. In the bottom sample of this layer endocarps of *Potamogeton filiformis* and *P. praelongus* were recorded. There were also fruits of *Ranunculus* sect. *Batrachium* and *Myriophyllum*. Since the beginning of the sedimentation process *Nymphaea* remains were present as seed testae. *Drepanocladus* and *Scorpidium scorpioides* (some leafless stems) represent the Bryales group. Animal remains were identified as well. Cladocera (ephippia), Bryozoa (statoblasts), Chironomidae (head capsules) and Oribatida have been present since the beginning of the accumulation process.

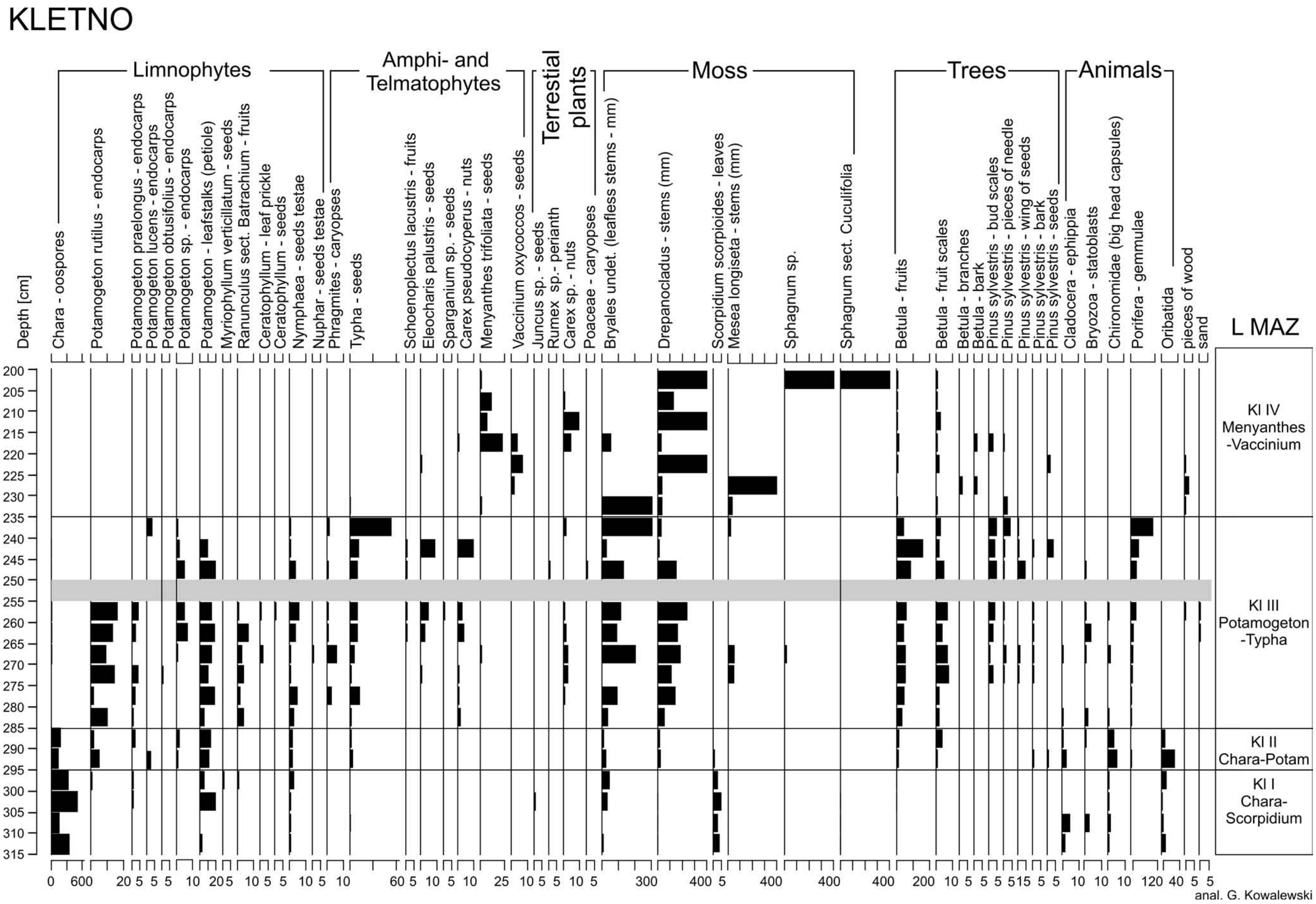

Fig. 6. Macrofossil diagram of a deeper part of the Kletno core. Numbers are given per 50 cm^3 of sediments.

Kletno LMAZ II, *Chara-Potamogeton*, 295–285 cm

Chara proportion decreased (max. 187 oospors/50 cm^3) and *Potamogeton* remains increased; continued occurrence of *Nymphaea*; *Typha* has been found in all the samples. Among mosses *Drepanocladus* was identified. At the first time macrofossils of *Betula* (nutlets and fruit scales) and *Pinus* (bark and seed testae) were determined. Among the animal remains, Chironomidae (only big head capsules were calculated) and Oribatida had their maxima and Porifera gemmules were observed.

Kletno LMAZ III, *Potamogeton-Typha*, 285–235 cm

Seeds (mostly *Potamogeton rutilus*) and vegetative remains of *Potamogeton* sp. were dominant in the middle part of this LMAZ. Underlying layer contained a lot of *Ranunculus* sect. *Batrachium* and *Nymphaea* seeds. *Ceratophyllum* and *Nuphar* appeared as well. In the whole layer remains of rush components were found: *Phragmites* caryopses, fruits of *Typha*, *Schoenoplectus*, *Eleocharis* and *Sparganium*. Their proportion increased upwards. *Typha* had its maximum in the upper sample of this MAZ – 54 seeds/50 cm^3. *Carex pseudocyperus* increased upwards as well.

Among the Bryales, *Drepanocladus* was dominant. *Meesia longiseta* and *Sphagnum* were identified in low abundance. In the bottom sample of this layer stems with leaves were absent. Frequencies of *Betula* and *Pinus* remains increased upwards and in the uppermost sample they had their maxima. Bryozoa statoblasts, a few Cladocera ephippia and Chironomidae remains represented the animal fossils. Spongiae gemmulas quantity increased and reached 112 items per 50 cm^3 in the uppermost sample.

Kletno LMAZ IV, *Menyanthes-Vaccinium*, 235–200 cm

Rush plants and aquatics dissappeared almost completely. *Vaccinium oxycoccos*, *Rynchospora fusca*, *Carex limosa*, *C.* cf *rostrata* and *Menyanthes trifoliata* were recorded. The latter was the most abundant in the layer 220–215 cm, where 22 seeds/50 cm^3 were found. Variety of Bryales remains in the bottom part of this layer was as poor as in the upper part of the previous MAZ. *Meesia longiseta* was a dominant component in the layer at the depth of 230–225 cm, *Drepanocladus* was the most numerous in the overlying layer. Among tree remnants only pieces of wood occurred frequently. There were no remains of aquatic fauna.

DISCUSSION

History of Białowieża Forest in the light of palynological research of Dziedzinka and Kletno mires

The pollen diagrams (Figs 3, 4 and 7) show changes of the vegetation cover from the younger part of the late glacial until the present time (Noryśkiewicz, Milecka 2002; Noryś-

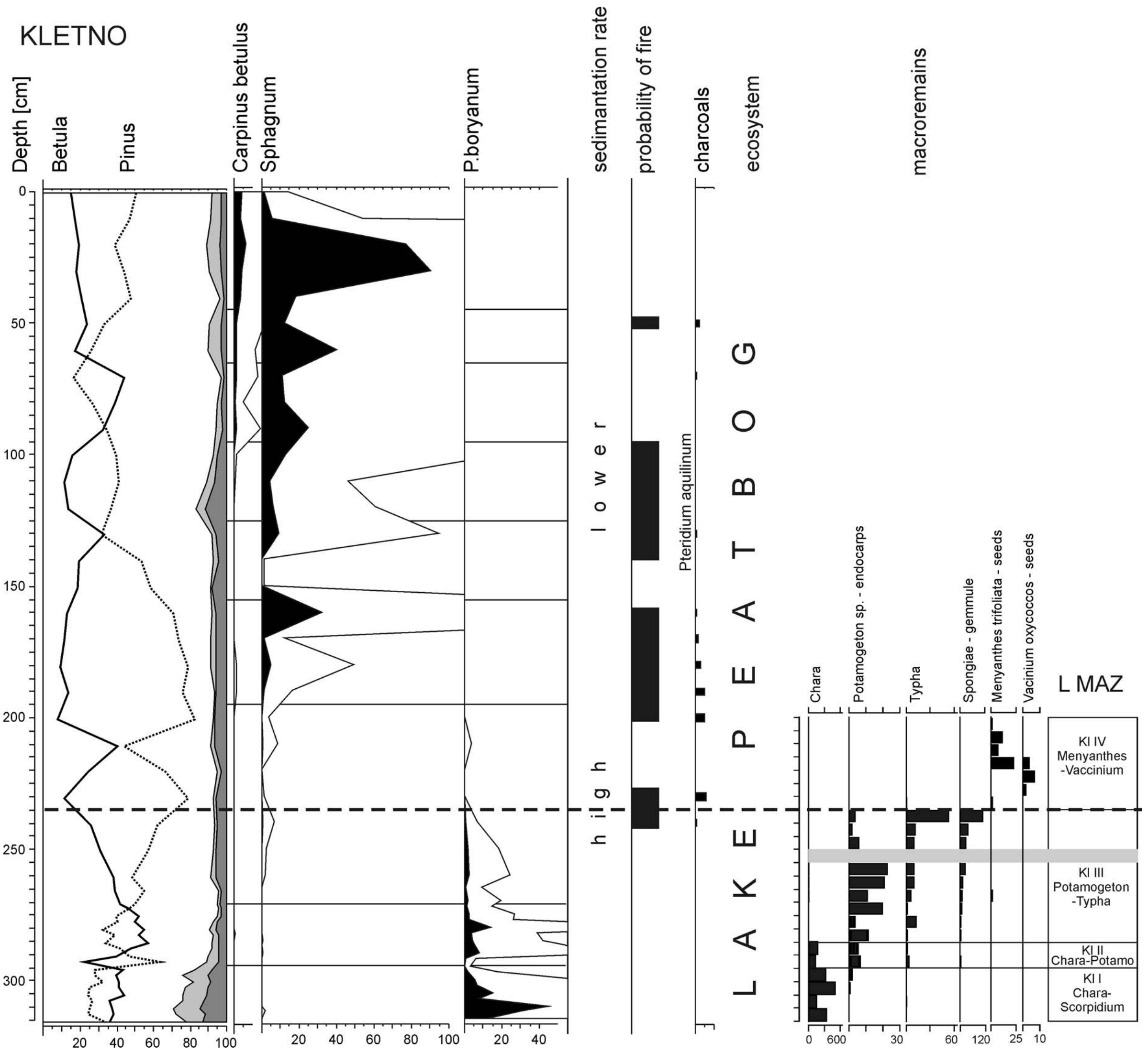

Fig. 7. Selected pollen curves, local pollen assemblage zones of the Kletno diagram, local macrofossil assemblage zones and stages of the basin development. The possibility of fires and the changes of accumulation rate are also marked.

kiewicz, Kowalewski 2002, 2003; Milecka, Noryśkiewicz 2003). It seemed that the Dziedzinka mire formed earlier, in the Alleröd period, but the interpretation of the bottom part of the diagram is ambiguous. An absolute chronology of the sediments was not established, the relative time scale is based on palynostratigraphy and comparison to the published studies made in adjacent regions (Kupryjanowicz 1991, 2000; Bałaga 1998, 2003; Ralska-Jasiewiczowa 1966).

Vegetation history

Late Glacial (Kl 1; Dzie 1, Dzie 2)

The bottommost part in the Dziedzinka profile (D1 L PAZ *Pinus-Betula*, four bottom samples 124–118 cm) shows the presence of forest in the region. *Pinus* was dominant and accompanied by a good amount of *Betula*. Pollen grains of *Juniperus* and *Hippophaë rhamnoides* indicate the development of juniper and sea-buckthorn bush in dry areas. Presence of heliophytes like *Artemisia* and Chenopodiaceae reveals not a very dense canopy and good light conditions at the ground. As shown by pollen analysis accumulation process started during the late Alleröd period, in agreement with the older estimate of Dąbrowski (1959). This is also confirmed by other sites (Kupryjanowicz 2003; Bałaga 1998, 2003).

Cooling of climate during the Younger Dryas caused changes in vegetation of the Białowieża region reflected both in the Dziedzinka and Kletno sediments: D2 L PAZ, *Salix-Juniperus*-NAP; Kl 1 L PAZ, *Salix-Juniperus* (Fig. 5). Pollen spectra indicate that the forest was more open and showed a mosaic pattern of park tundra, herb tundra with bush, steppe, and forest-tundra. Steppe communities with *Artemisia*, Chenopodiaceae, *Hippophaë rhamnoides* and *Juniperus* dominated at the poorest and driest areas. On better ones with more water, Poaceae and Cyperaceae were the most important. Higher proportion of *Salix* and *Betula nana* type show the development of patches with bush-tundra. The Kletno diagram shows higher proportion of NAP than that of Dziedzinka. Probably this is the result of more open character of the plant cover and local conditions reflected around the Kletno peatbog.

Early Holocene (Preboreal and Boreal Periods) (Kl 2, 3, 4; Dzie 3, 4, 5)

The beginning of the Holocene was marked with a lower proportion of open plant communities and a development of forest, which since then has been dominant in the Białowieża region up to the present. However at particular periods the main species and structure of the forest underwent distinct changes. *Betula-Pinus* forest was the main plant community at the beginning of the Holocene with a marked presence of Late Glacial elements like juniper, the latter being important at the beginning only (in Kl 1).

Then *Pinus* became the dominant species, but *Corylus avellana* and *Ulmus* were the next immigrating elements and they quickly grew in meaning. Then, one more mediocratic species – *Quercus* appeared. Much worse light conditions caused decreasing proportion of birch, continued since the beginning of the Holocene. There were only some open plant communities with heliophytes like *Artemisia* and Chenopodiaceae. *Juniperus* disappeared completely. Herbal elements occurred at wet places, as indicated by pollen grains of *Heracleum* type, *Potentilla* type and *Filipendula*. In the end of this period a quick expansion of *Alnus* took place dominating along the rivers and streams up to the present time.

Middle Holocene (Atlantic Period) (Kl 5, 6; Dzie 6)

Gradually the proportion of *Pinus* decreased in the forest. *Corylus avellana* and then *Ulmus*, *Quercus* and *Tilia* became the most important components of the more and more dense forest communities. *Betula* played a greater role, as it benefited probably locally better light conditions. A continued development of communities on wet areas took place and *Alnus glutinosa* was the most important element there.

The next stage shows full development of mixed, deciduous forest. *Quercus*, *Ulmus* and *Tilia* dominated the tree canopy and *Corylus avellana* the brushwood. *Pinus sylvestris* was still present probably on mesotrophic soils. The importance of deciduous tree species suggests dense canopy of the forest but the Kletno diagrams display higher NAP curves, because of more Poaceae which could exist in open communities and in some kinds of forests as well. *Pteridium aquilinum* in the understorey suggests fires (Behre 1981; Latałowa 1992). *Pteridium* likes a lot of mineral elements in the soil and often appears after fire. *Pteridium aquilinum* could also indicate clearing by fire (slash-and-burn) (Göransson 1986).

Late Holocene, older part (Subboreal Period) (Kl 7, 8; Dzie 7)

The mixed deciduous forest changed at the beginning of this period. All deciduous elements decreased, except *Corylus avellana*. This species grew in the brushwood or it produced more pollen grains due to less density of the forest. Better transport and spreading of pollen caused higher proportion of *Corylus avellana* in the pollen spectra. An increasing amount of *Betula* indicates better light conditions in the forest. NAP taxa are not numerous and they mostly occur in communities of the understorey: *Calluna vulgaris*, *Ledum palustre*, Ericaceae and *Pteridium aquilinum*. The latter species was still present at the beginning of this period but then it dissappeared.

Then *Quercus* forest developed with increasing proportion of *Pinus* and *Carpinus betulus*. Pollen grains of hornbeam occurred at the beginning of this period, but *Carpinus* trees were present already four thousand years ago (Ralska-Jasiewiczowa *et al.* 2004). The forest at the "*Quercus*" phase (Kl 8, Fig. 3) was gradually enriched with hornbeam. *Ulmus* and *Tilia* were still present, but *Fraxinus excelsior* decreased, probably replaced by *Alnus* on wet areas.

Rare pollen grains of *Fagus sylvatica* do not show the occurrence of this tree in the forest (see below).

Late Holocene, younger part (Subatlantic Period) (Kl 9; Dzie 8)

At the beginning of this period another change in species proportion in the forest communities occurred. *Quercus* and *Carpinus betulus* decreased clearly, and a second *Ulmus* fall appeared. *Tilia* was not very frequent but stable in amount. These elements were taken over by *Carpinus betulus* and *Picea abies*. A considerable variety of forest communities developed, that are still present in the Białowieża region depending on local soil and hydrological conditions. Proportion of herbs was low, dominated be Ericaceae dwarfshrubs.

In the youngest part of the diagram, human impact in the Białowieża forest is revealed. *Artemisia*, Chenopodiaceae, *Plantago lanceolata* and *Rumex* represent ruderal and pasture land. In the Białowieża National Park there was no cultivation. A few pollen grains of *Secale cereale* do not indicate cereal fields, but have been long distance transported. Pollen grains of other cultivated plants (except cereals) were not found.

Presence and proportion of some tree species

The proportion of *Carpinus betulus* is relatively low in the Białowieża Forest during the late Holocene; 5% in Kletno and 15% in Dziedzinka, are the maximum amounts reached only in the youngest phase of the forest development. Also other sites of NE Poland do not show a large abundance of hornbeam. Its proportion does not exceed 10% (Balwierz, Żurek 1987) or, as a rule, even 5% (Bałaga 1982; Kupryjanowicz 2000; Milecka, unpubl.). *Carpinus betulus* is a species well-growing under the influence of continental climate in middle east Europe, but pollen analyses of many sites show the development of forest with hornbeam also in Great-Poland and West Pomerania during the Subboreal Period (Ralska-Jasiewiczowa 1964, 1983; Tobolski 1987, 1991; Filbrandt-Czaja 1998, Milecka 1998; Makohonienko 2000). All these sites and isopollen maps for Poland (Ralska-Jasiewiczowa *et al.* 2004) show up to 30–50% of *Carpinus betulus* in the pollen sum. Hornbeam-oak forest was suggested to be unlike any kind of presently existing community (Tobolski 1991). In the eastern part of Poland such a community has never developed and isopollen maps show a lower proportion of *Carpinus betulus*. This indicates a balanced meaning of several deciduous forest components instead of a dominant role of *Carpinus betulus* as it was observed in Great-Poland.

Single pollen grains of *Fagus sylvatica* were recorded during the Atlantic at Kletno and Dziedzinka as well. In the Subboreal the beech curves are continuous, but very low. A similar picture can be observed on the isopollen maps for north-eastern Poland. *Fagus* grains appeared 4000 BP (up to 0.5%), and according to the maps came from distant sites located probably on the south. The maps 3500–2000 BP show *ca.* 1–2% for NE Poland. Concurrently forests with high proportions of *Fagus* developed in NW and S Poland. It was the beginning of formation of the modern range of this species and its plant communities. The highest beech pollen content in the Białowieża region is found at 2000 BP, however it does not exceed 2% suggesting that *Fagus* has never reached the Białowieża Forest (Huntley, Birks 1983; Latałowa *et al.* 2004). The maps for the younger periods show lower percentages ranging between 1–2%. More studied sites are needed in the region to solve the problem of *Fagus* presence.

Is Białowieża different from other sites in NE Poland?

Pollen analyses reflect a succession of regional plant communities on mineral soils showing all successive stages in an adjacent area. However to compare the results of many sites in a reliable way, some points have to be kept in mind: a) only complete profiles are a good basis for palaeoecological research (*i.e.* with no hiatus); b) to get reliable results big and deep basins (lakes) should be analysed; c) in each site the basis for calculation of percentages (sum AP+NAP) should be the same; d) peat sediments give a lot of information concerning local environment *e.g.* hydrology and plant communities on wetlands but high proportions of local pollen types can distort the picture of regional changes; e) location of a site in a traditional settlement area, strongly influenced by human activity for thousands of years, gives results different from a site lying in areas forested up to the present time. We must say that the studies of the sites of NE Poland often do not fulfill these points. Some of them are incomplete, the time scales are not reliable, which make their comparison difficult. The Kletno and Dziedzinka cores have these disadvantages too, so very detailed descriptions and conclusions are not thought to be the final ones. Further research of the region is therefore needed.

There were some, climatically different stages during the Late Glacial with initial type of soils as well as a pioneer plant communities. Climate warming resulted in spreading of forest communities. Alternatively, cooling of climate caused recession of forest and development of steppe and tundra. At the beginning of sediment accumulation in the Kletno and Dziedzinka basins, (during the Alleröd period) Central Europe was covered with *Pinus* and *Betula* forest. Preserved trunks of *Pinus* from the area adjacent to Lake Kruklin (Stasiak 1964) are a direct proof of forest presence in NE Poland during Alleröd period. All the pollen diagrams from the eastern part of Poland show relatively high amounts of arboreal pollen, however stable presence of heliophytes indicates not very dense forests (Bałaga 1990; Kupryjanowicz 1991, 2000). Changing curves of *Pinus* and *Betula* recorded at many neighbouring sites (Moszne, Karaśne, Durne Bagno, Krowie Bagno, Bałaga 1990; Kupryjanowicz 1991) suggest a relation to local and soil rather than climatic conditions. During the Younger Dryas climatic cooling steppe and tundra plant communities developed. High values of *Juniperus* are a ”marker” for the Younger Dryas in North Poland, exceeding, e.g. at Stare Biele site 7% (Kupryjanowicz 2000) but proportion of *Juniperus* at Kletno and Dziedzinka sites (0.6%) is surprisingly low (Fig. 8). It seems that the differences are caused by a complicated soil–environment system. *Juniperus communis* is a heliophyte species of dry, sandy soils. Lack of appropriate local conditions could be the reason of its rare occurrence in the Białowieża Forest.

Attention has to be paid to the occurrence of *Quercus*, that seems to appear rather late in the early Holocene. The *Quercus* curve starts at Kl 4 and D 4 (Boreal) (Figs 3 and 4), but the content of oak pollen grains is very low, suggesting their transport from distant sites. The real, local presence of *Quercus* in the plant cover started in the middle Holocene. According to the isopollen maps (Milecka *et al.* 2004) late immigration of oak is characteristic for NE Poland. Many diagrams of this area (Balwierz, Żurek 1987; Kupryjanowicz 1991, 2000; Milecka, unpubl.) confirm that. During the late Holocene *Quercus* has a low proportion in the forest vegetation. Isopollen maps of *Quercus* sp. show percentages of 10–15% at almost all regions of Poland. NE Poland is an exception and *Quercus* values at all the sites mentioned above do not exceed 10%. Lower proportion of oak is a feature of this area up to the present time.

Fraxinus excelsior does not exceed 1%. The sediments of Stare Biele mire in Knyszyńska Forest (Kupryjanowicz 2000) and Machnacz peatbog near Białystok (Kupryjanowicz 1991) show similar values of *Fraxinus excelsior*. Ash appeared rather late and its local occurrence and development in plant communities should be connected with the climatic optimum and middle stage of the Atlantic period (cf. Tobolski 1995). Clearly higher values of *Fraxinus* are observed at Wizna site, Podlasie (Balwierz, Żurek 1987) and in the Miluki diagram at the site near Ełk (Milecka, unpubl.). It is hard to explain these differences and low proportion of ash in forest communities, especially in light of “multilateral specialisation” in life strategy of this species and its good ability to use many ways of reaching the reproductive success (Faliński, Pawlaczyk 1995). Local hydrographic conditions, that influence development of *Fraxinus excelsior* are the most probable reason of differences in its proportion. Activity of some animals (*e.g.* European bison, deer or beaver) can change the occurrence of ash in plant communities to some (low) degree (Faliński, Pawlaczyk 1995), but this phenomenon has not significant meaning. Frequency of *Fraxinus* at sites of the other regions in Poland is usually higher (more than 1%), but seldom exceeding 2% (Latałowa 1992; Noryśkiewicz 2002; Obremska, Lamentowicz 2002; Milecka, Szeroczyńska 2005).

After the climatic optimum *Ulmus* fall took place in Białowieża Forests. This phenomenon has been described at many sites of Central Europe (Troels-Smith 1953; Iversen 1973; Aaby 1986; Göransson 1986; Latałowa 1992; Miotk-Szpiganowicz 1992; Makohonienko 2000) and it is thought to be the final stage of the Atlantic Period and of the existence of mixed, deciduous forest. Usually however, in pollen diagrams *Ulmus* is the only declining species and the other mesophilous components stay at the stable level. In Kletno the difference is that *Tilia*, *Quercus* and *Fraxinus* fall concur-

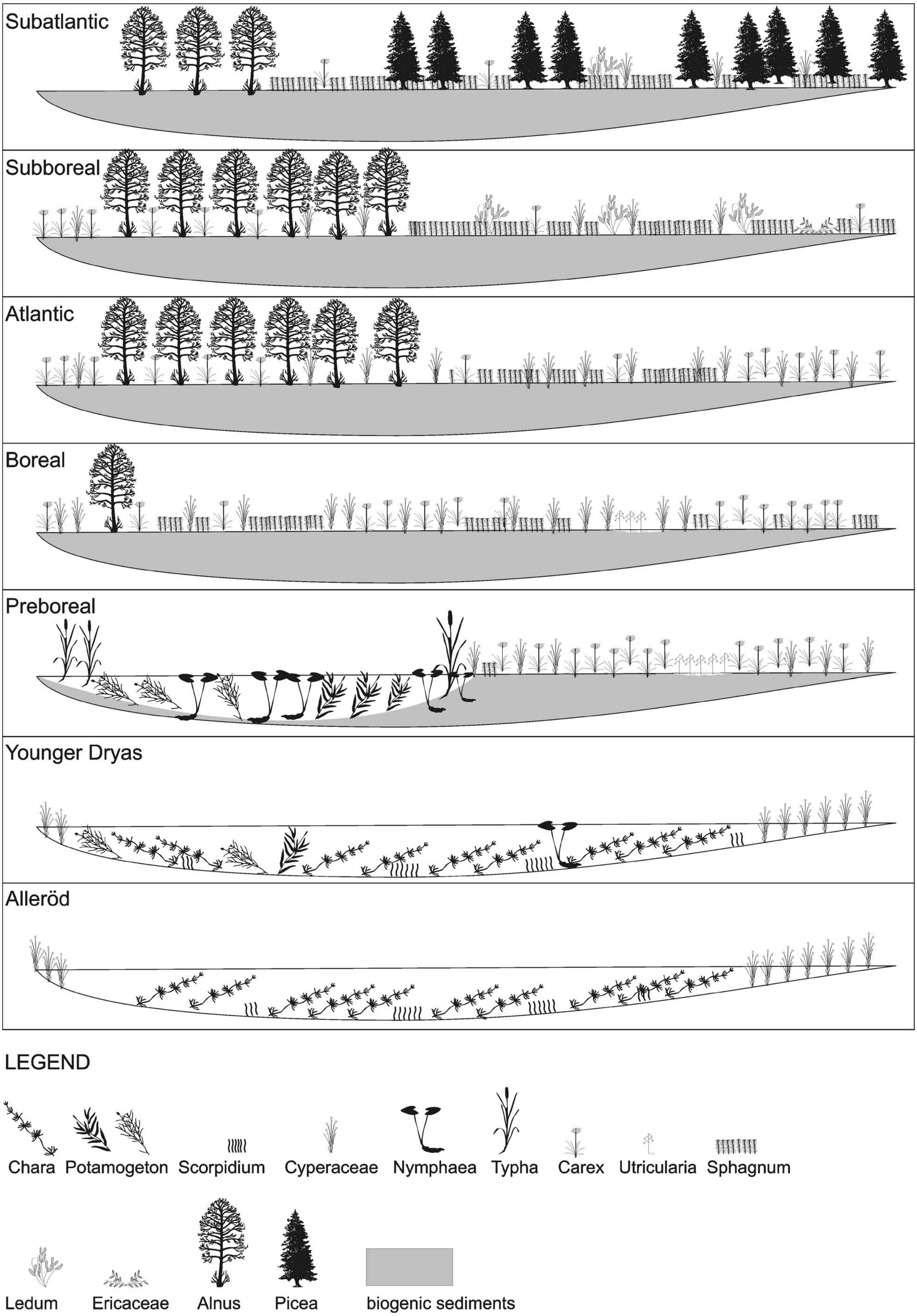

Fig. 8. Dominant components of the local plant communities in the accumulation basins in the different chronozones of the Late Glacial and the Holocene.

rently or almost concurrently with *Ulmus*. We can not say that definitely because of poor time resolution of the diagram. In Dziedzinka *Ulmus* and *Fraxinus* declines preceded the oak and *Tilia* falls. Then *Quercus* renewed to develop *Quercus*-*Corylus* forest, but *Ulmus* and *Fraxinus* stayed of no importance up to the present. Diminishing of *Tilia* and *Fraxinus* is seen at the sites in Knyszyńska Forest as well (Kupryjanowicz 2000). Proportion of *Fraxinus excelsior* in the surrounding of Lake Łukcze at Polesie has been low, but more or less stable in the Atlantic, Subboreal and Subatlantic Periods (Bałaga 1982, 1990). *Fraxinus*, just like *Tilia* belongs to the stable components of the forest at the area adjacent to Lake Łukcze. Their proportion was the highest during the climatic optimum and then they diminished until the present, but the lowering has been very slow and insignificant. It seems that the NE Polish sites give a different picture of the vegetation changes: increasing meaning of *Carpinus betulus* and then *Picea abies* caused lower proportions of mesophilous trees like *Ulmus*, *Tilia* and *Fraxinus*, but in the middle-east part of Poland, beyond the geographical range of *Picea*, proportions of trees were different.

During the youngest part of the Holocene the plant communities that exist in Białowieża Forest today, were developed. There are rich deciduous forests and mixed forests with high proportion of *Picea*. Pollen analyses in Knyszyńska Forest (Kupryjanowicz 2000) give a different picture. Proportions of deciduous trees are clearly lower. Curves of *Quercus*, *Corylus*, *Ulmus* and *Fraxinus* diminished and ceased, *Carpinus* presence has been slightly marked. It means that forest communities developing at that area were poorer in deciduous elements and conifers have been dominating. Next to *Picea*, high proportion of *Pinus* was remarkable too, probably as the result of pine plantations going on since the 19^{th} century. Similar results are obtained at Podlasie site (Balwierz, Żurek 1987). Absence of pollen grains of deciduous trees in the uppermost samples of the diagrams suggests lack of deciduous elements of the mixed forest, or that they have been rare and dominated by *Picea*. Miluki site near Ełk (Milecka, unpubl.) shows low amount of deciduous trees as well. However, human impact caused changes in vegetation there. Consequently, *Pinus*, herbs and human indicators have been dominating. The plant communities differ also south of the Białowieża Forest, in Łęczna-Włodawa Lake District, where absence of *Picea abies,* high proportion of *Quercus* and *Carpinus betulus*, and lower proportions of *Ulmus*, *Tilia* and *Fraxinus* are observed. This phenomenon is due to the natural geographical range of spruce and its limited occurrence south of Białowieża.

The special features of Białowieża Forest are conditioned by two main factors: a) continuous occurrence of forest throughout the Holocene and weak human impact; b) influences of continental climate and boreal zone which are stronger than in the other regions of Poland. These conditions resulted in low values of the *Fagus* curves in the Kletno and Dziedzinka diagrams. *Fagus sylvatica*, as subatlantic species was possibly absent in Białowieża. That's also why the proportion of mesophilous trees has decreased in the youngest part of the Holocene and *Picea abies*, an important component of boreal, coniferous forest has increased in significance and co-created many plant communities.

Mire development based on macrofossil and pollen analysis

Kletno

The development of a peatbog ecosystem was preceded by the existence of a shallow lake (Figs 6, 7 and 8). The same took place at Dziedzinka peatbog in the adjacent area. Pollen analysis unambiguously indicates the beginning of the accumulation process during the Late Glacial. Results of macrofossils analysis are less clear. The oldest stage of the sedimentation is documented only by remains of aquatic plants living in undisturbed, shallow lakes. Absence of tree macrofossils, *Pinus* and *Betula* in L MAZ Kl I provides an indirect proof of tundra existence during the Younger Dryas. The spectra of macro remains indicate the end of limnic accumulation at the same level as evidenced by the pollen diagram (disappearance of *Nymphaea* and *Pediastrum* curves, Fig. 6).

L MAZ Kl I is correlated with L PAZ Kl 1, represented by fine, detrituous gyttja with parts of rush roots, that are thought to be secondary in this layer. Since the beginning of the lake existence there have been communities of vascular macrophytes growing in shallow water together with some *Chara* species. *Scorpidium scorpioides* and *Chara* indicate the presence of calcium carbonate in the lake ecosystem. Surprisingly there was a small amount of identified plant remains, but a lot of animal remnants, especially undetermined chitinous parts of beetles. Oribatida disappeared together with *Chara* suggesting their relationship to Characeae. Continuous presence of *Nymphaea* indicates, that the lake depth has never exceeded 1.5–2 m (Podbielkowski, Tomaszewicz 1979).

Warming of climate at the beginning of the Holocene caused clear changes in the local plant communities. Abundance of *Chara* diminished and vascular plants played a more important role. *Scorpidium scorpioides* decreased as a result of declining calcium carbonate in the water. This rapid change is marked by development of *Pediastrum*, occuring at the turn of the late glacial to the Holocene. *Potamogeton rutilus* and *P. praelongus* as the main species among pondweeds suggest rather eutrophic environmental conditions. Appearance of *Typha* is an indicator of lake shallowing, as it grows at the shore and dissappears as late as after the lake extinction.

At the beginning of the Holocene (L MAZ III) proportion of pondweeds increased but Characeae disappeared completely. Increasing trophy of the basin could be one reason of these phenomena. It is also confirmed by a big amount of *Nymphaea* seed testae and continuous presence of seeds of *Ranunculus* sect. *Batrachium*. *Typha* increased a little next to *Phragmites* rushes. These events reflect the continuous process of lake shallowing and getting the bottom more boggy. Such conditions made a suitable ground for *Carex pseudocyperus* and *Eleocharis palustris*, eutrophic species entering the rushes at boggy, not stable bottom (Podbielkowski, Tomaszewicz 1979). The last stage of shallowing of the lake was dominated by *Typha* rushes. Disappearance of water invertebrates was a consequence of decreasing open water area and volume of water. There was the only dynamic increase of Porifera quantity in the upper part of the sediments and it confirms quick decrease of the water volume. Continuous presence and high proportion of *Drepanocladus* indicates meso-and/or eutrophic water conditions. *Drepanocladus* grew together with *Meesia longiseta*. The remains of this species (leafless stems) were hardly found at this level (L MAZ III/IV turn) but they were identified more often in the lower and upper layers of the sediments. During the last stage of the lake existence, some water level changes could take place, which probably caused good conditions for higher microorganisms activity.

The rushes were overtaken by terrestrial species. Occurrences of *Vaccinium oxycoccos*, *Menyanthes trifoliata*, *Carex limosa* and *Carex rostrata* are especially important because they indicate development of plant communities in mesotrophic, peatland conditions, the first stage of peat-forming terrestrial communities. They have developed a dense vegetation cover as a basis for trees and shrubs growth. Existence of local trees is documented by an increasing amount of remains of bark, branches and pieces of wood. Presence of *Menyanthes trifoliata* pollen grains correlates well with its seeds in the sediments. Clear decrease in *Menyanthes* remains is concurrent to dynamic increasing abundance of *Sphagnum* spores, which suggests intensive development of *Sphagnum* peat during the early Holocene (probably Boreal period) (Figs 7 and 8). At the same time some charcoals were found. They probably document fires in the Białowieża Forest.

Dziedzinka

The Dziedzinka basin was not deep enough to develop a typical lacustrine sedimentation leading to gyttja. During the initial stage (in the Late Glacial) *Chara* communities did not develop, either. At the beginning the basin looked like a telmatic zone and existed as an extent boggy area overgrown with shallow lake and rush plants (*Potamogeton*, *Carex* spp., *Sparganium* spp.). The layer of biogenic sediments containing remains of aquatic organisms is not thicker than 30 cm. Appearance of *Menyanthes* fruits marks the level of shallowing of the basin (95–100 cm) which is confirmed by clear decrease in planktonic organisms as *Pediastrum*. According to pollen analysis, terrestrialization of the area took place at the beginning of the Holocene, earlier than at the Kletno site. The next stage of sediment accumulation took place in stable hydrological conditions of high groundwater level. Cyperaceae were the main element of the peat-forming community and sedentation process of organic material was dominant. Charcoals appeared for the first time.

In the middle of the early Holocene a peat layer (80–60 cm) was formed. Differentiated degree of decomposition indicates water level changes. Such unstable conditions probably prevailed through several thousands of years, up to the end of the climatic optimum.

There is a high proportion of *Eriophorum* remains with charcoals above 60 cm. There are also traces of *Sphagnum* and *Pinus* remains. That kind of sedentation process is dated by pollen analysis to the late Holocene (probably the Subboreal period). Presence of *Eriophorum* and *Sphagnum* peat suggest oligotrophic conditions in the basin.

Eriophorum was the main component of the sediment up to 32 cm and then *Sphagnum* was dominating. However, *Sphagnum* spores were present since the Preboreal, so it appeared earlier in Dziedzinka than at the Kletno site. Probably *Sphagnum* appeared at the margins of the basin at first and then it spread into the center (to the location of S-20 core) following oligotrophication. An intensive terrestric accumulation was possible as late as in the Subboreal when the climate was wetter. This fact confirms the conclusion of Żurek (1993) about the time of development of bogs and transitional peatbogs in the accumulation basins without run-off at the beginning of the Subboreal.

Water level changes and sediments accumulation rate

Clear discrepancy was revealed between the accumulation rates of the older and younger sections of the sediment (Fig. 7). The thickest section accumulated at the beginning of the Holocene despite limnic character of the environment. The thinnest layer of sediment represents the climatic optimum. This layer was accumulated after the shallowing of the lake, in rather terrestrial environment. We did not found indicators of hiatus in the sequence of sediments, however we cannot exclude that some layers of sediments could be destroyed *e.g.* by the forest fires. A significant lowering of water level at the mire was the other reason for a break in the accumulation process. So we can suppose, that the thin layer of peat of the middle Holocene was the result of an extremely low accumulation rate, but loss of sediment layers was possible as well. Kupryjanowicz (2003) draw similar conclusions concerning the sites in Knyszyńska Forest (Machnacz and Stare Biele) and Biebrza Valley (Żurawisko). Deep layers of sediments (gyttja) accumulated during the oldest part of the Holocene were found at Maliszewo peatbog in Biebrza Valley (Balwierz, Żurek 1987). According to these authors during the Boreal period the rate of accumulation was 1.13 mm/year. All these data may suggest that the phenomenon found at some sites had a regional meaning and was a result of hydrological changes in NE Poland. However it was connected with mires as ecosystems sensitive to water level changes and limnic sediments directly underlying the peat *i.e.* accumulated in shallow lake in the final stage of its overgrowing. Accumulation rate found in the lakes existing up to the present is not so differentiated and does not show clear changes (cf. Bałaga 1990; Milecka, unpubl.).

Indication of fires in the Białowieża Forest

Content of charcoals identified during the pollen analysis is an indicator of fires in plant communities. Some greater charcoal particles have been found in macrofossil analysis as well. However, the research has not shown the levels with clear content of charred parts of organic origin. In the pollen diagram of Kletno a small proportion of charcoals was observed at the depths of 230, 200–170 and 50 cm, and macrofossil analysis noted presence of charcoals in 205–200 cm (the younger layers were not analysed). The highest probability of fires can be determined for the younger phase of the Preboreal and during the Boreal. Indirectly, probability of fires (Fig. 7) is also indicated by *Pteridium aquilinum* spores in the pollen diagram. Continuous curve of *Pteridium* during the Atlantic Period suggests possibility of natural or anthropogenic fires caused by Neolithic man.

GENERAL CONCLUSIONS

Palaeoecological analyses revealed some trends in the development of the Białowieża region ecosystems. Possible hiatus in the investigated sections causes some doubts, whether our results are complete or not. For that point more research is needed. On the basis of the results available, it can be concluded that:

1. Process of organic sediment accumulation started during the Late Glacial in the Alleröd period (Dziedzinka) or in the Younger Dryas (Kletno). It was the initiation of shallowing of the lakes. Then the hydroserial succession ceased limnic sedimentation and open water table disappeared at the beginning of the Holocene during the Preboreal.

2. Both limnic sediments and overlying peat allowed the description of regional and local plant communities succession by the content of identified sporomorphs and macro remains. During the Late Glacial two stages of the succession were revealed, steppe and open forest during the Alleröd period and tundra-like vegetation during the Younger Dryas.

3. The Holocene history contains five stages of plant cover development: *Betula-Pinus* forest at the beginning, *Pinus-Betula* forest with increasing proportion of *Corylus avellana* in the Boreal, mixed deciduous forest in climatic optimum, *Quercus-Carpinus* forest in the Subboreal and at last, development of various types of plant communities which are existing in the Białowieża Forest up to the present.

4. There was a relatively low content of *Carpinus betulus* during the Subboreal and Subatlantic periods. Pollen analysis and isopollen maps for Poland show the main centres of hornbeam forest development to have been in Great Poland and Pomerania, whereas the NE part of Poland shows rather constant frequency of *Carpinus* pollen.

5. A low content of pollen grains of *Fagus sylvatica* indicates, that the Białowieża Forest has possibly never been inhabited by this species.

6. There are only weak indications of fires in the Białowieża Forest. Presence of charcoals in pollen and macrofossil samples and occurrence of *Pteridium aquilinum* spores show the probability of fires during a short period of the Preboreal and in the Boreal and Atlantic Periods. Also some charcoals were recorded in the youngest phase of the Subboreal Period.

REFERENCES

Aaby B. 1986. Trees as anthropogenic indicators in regional pollen diagrams from Eastern Danmark. In Behre K.E. (ed.) *Anthropogenic indicators in pollen diagrams*, 73–94. Balkema, Rotterdam, Berlin.

Aalto M. 1970. Potamogetonaceae fruits. I. Recent and subfossil endocarps of the Fennoscandian species. *Acta Botanica Fennica* 88, 1–85.

Balwierz Z., Żurek S. 1987. The Late Glacial and Holocene vegetational history and paleohydrological changes at the Wizna site (Podlasie Lowland). *Acta Palaeobotanica* 27, 121–136.

Bałaga K. 1982. Vegetational history of the Lake Łukcze environment (Lublin Polesie, E. Poland) during the Late-Glacial and Holocene. *Acta Palaeobotanica* 22, 7–22.

Bałaga K. 1990. The development of Lake Łukcze and changes in the plant cover of the south-western part of the Łęczna- Włodawa Lake District in the last 13 000 years. *Acta Palaeobotanica* 30, 77–146.

Bałaga K. 1998. Post-glacial vegetational changes in the middle Roztocze (E Poland). *Acta Palaeobotanica* 38, 175–192.

Bałaga K. 2003. Hydrological changes in the Lublin Polesie during the late glacial and Holocene as reflected in the sequences of lacustrine and mire sediments. *Studia Quaternaria* 19, 37–53.

Behre K.E. 1981. The interpretation of anthropogenic indicators in pollen diagrams. *Pollen et Spores* 23, 225–245.

Berglund B.E. Ralska-Jasiewiczowa M. 1986. Pollen analysis. In Berglund. B.E. (ed.) *Handbook of Holocene Palaeoecology and Palaeohydrology*, 455–484, John Wiley & Sons, Chichester – New York – Brisbane – Toronto – Singapore.

Bertsch K.H. 1941. Früchte und Samen. Ein Bestimmungsbuch zur Pflanzenkunde der vorgeschichtlichen Zeit, 1–247. Stuttgart.

Borowik-Dąbrowska M., Dąbrowski M.J. 1972. Natural and anthropogenic vegetation changes in Białowieża National Park (original: Naturalne i antropogeniczne zmiany roślinności Białowieskiego Parku Narodowego). *Archeologia Polska* XVIII, 181–200 (in Polish).

Dąbrowski M.J. 1959. Late Glacial and Holocene vegetation history of Białowieża Primeval Forest (original: Późnoglacjalna i holoceńska historia lasów Puszczy Białowieskiej). *Acta Societatis Botanicorum Poloniae* 28, 197–248 (in Polish).

Faliński J.B. 1986. Vegetation dynamics in temperature lowland primeval forests. Dr W. Junk Publishers, Dordrecht-Boston-Lancaster.

Faliński J.B., Pawlaczyk P. 1995. An outline of ecology (original: Zarys ekologii). In Bugała W. (ed.) *European Ash Fraxinus excelsior L. Our forest trees.* (orginal: *Jesion wyniosły Fraxinus excelsior L. Nasze drzewa leśne*) 17, 217–305. Sorus, Poznań – Kórnik (in Polish).

Filbrandt-Czaja A. 1998. Vegetation history of the northern part of Lednicki Landscape Park highlighting of anthropogenic factor (original: Historia roślinności północnej części Lednickiego Parku Krajobrazowego ze szczególnym uwzględnieniem czynnika antropogenicznego). *Biblioteka Studiów Lednickich* III, 9–41 (in Polish).

Göransson H. 1986. Man and the Forest of Nemoral Broad – Leafed Trees During the Stone Age. In Königsson L.K. (ed.) *Nordic Late Quaternary, Biology and Ecology*. *Striae* 24, 143–152.

Grimm E. C. 1987. CONISS: A fortran 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers & Geosciences* 13, 13–35.

Grimm E.C. 1990. Tilia and Tilia_graph: PC spreadsheet and graphics software for pollen data. *INQUA Working Group on Data-Handling Methods*, Newsletter 4.

Grosse-Brauckmann G. 1972. Über pflanzliche Makrofossilien mitteleuropäischer Torfe. I. Gewebereste krautiger Pflanzen und ihre Merkmale. *Telma* 2, 19–55.

Grosse-Brauckmann G. 1974. Über pflanzliche Makrofossilien mitteleuropäischer Torfe. II. Weitere Reste (Früchte und Samen, Moose u. a.) und ihre Bestimmungsmöglichkeiten. *Telma* 4, 51–117.

Grosse-Brauckmann G. 1992. Über pflanzliche Makrofossilien mitteleuropäischer Torfe. III. Früchte, Samen und einige Gewebe (Fotos von fossilen Pflanzenresten). *Telma* 22, 53–102.

Huntley B., Birks H.J.B. 1983. An atlas of past and present pollen maps for Europe: 0–13000 years ago. Cambridge University Press.

Iversen J. 1973. The Development of Danmark's Nature since the Last Glacial. *Geology of Denmark Survey Bulletin* V, 7-C, 1–126.

Juggins S. 2003. C2 User guide. Software for ecological and palaeoecological data analysis and visualisation. Newcastle upon Tyne, UK, University of Newcastle.

Katz N.J., Katz S.W., Kipiani M.G. 1965. Atlas and keys of fruits and seeds occurring in the Quaternary deposits of the USSR (original: Atlas i opredelitel płodow i semian wstreczajuszczychsia w czetwerticznych otłożeniach SSSR). Izdatielstwo Nauka, Moskwa (in Russian).

Katz N.J., Katz S.W., Skobiejewa E.I. 1977. Atlas of plant fossils in peat (original: Atlas rastitielnych ostatkow w torfach). Izdatielstwo Nauka, Moskwa (in Russian).

Kupryjanowicz M. 1991. Eemian, Early and Late Vistulian, and Holocene vegetation in the region of Machnacz peat-bog near Białystok (NE Poland) – preliminary results. *Acta Palaeobotanica* 31, 215–225.

Kupryjanowicz M. 2000. Habitat and vegetation changes of Stare Biele mire in Knyszyńska Forest (original: Przemiany siedlisk i roślinności torfowisk uroczyska Stare Biele w Puszczy Knyszyńskiej). Politechnika Białostocka, *Rozprawy naukowe* 70, 78–97 (in Polish).

Kupryjanowicz M. 2003. Palynological investigation in northern Podlasie Region. History, present state and main problems (original: Badania palinologiczne na północnym Podlasiu, historia, stan obecny, główne problemy). *I Polska Konferencja Paleobotaniki Czwartorzędu, conference abstract.* Białowieża 22-24 V 2003, 15–18.

Latałowa M. 1992. Man and vegetation in the pollen diagrams from Wolin Island (NW Poland). *Acta Palaeobotanica* 32, 123–149.

Latałowa M., Ralska-Jasiewiczowa M., Miotk-Szpiganowicz G., Zachowicz J., Nalepka D. 2004. Fagus sylvatica L. – Beech. In Ralska-Jasiewiczowa M., Latałowa M., Wasylikowa K., Tobolski K., Madeyska E., Wright H.E. Jr. & Turner Ch. (eds) *Late Glacial and Holocene history of vegetation in Poland based on isopollen maps*, 95–105. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.

Makohonienko M. 2000. Natural history of Gniezno (original: Przyrodnicza historia Gniezna). Homini, Bydgoszcz-Poznań (in Polish).

Milecka K. 1998. History of human activity in Giecz and Wagowo areas based on pollen analysis (original: Historia działalności człowieka w okolicach Giecza i Wagowa w świetle analizy pyłkowej). *Biblioteka Studiów Lednickich* III, 43–95 (in Polish with English summary).

Milecka K. The results of pollen analysis of Miłuki site (original: Wyniki analizy pyłkowej na stanowisku Miłuki) (in Polish, unpubl).

Milecka K., Noryśkiewicz A.M. 2003. The development of Kletno mire based on pollen analysis from Białowieża Primeval Forest (original: Rozwój torfowiska Kletno w świetle analiz paleoekologicznych na terenie Puszczy Białowieskiej). *I Polska Konferencja Paleobotaniki Czwartorzędu, conference abstract* Białowieża 22-24 V 2003, 29–30 (in Polish).

Milecka K., Szeroczyńska K. 2005. Changes in macrophytic flora and planktonic organisms in Lake Ostrowite, Poland as a response of climatic and trophy fluctuations. *The Holocene* 15, 74–84.

Milecka K., Kupryjanowicz M., Makohonienko M., Okuniewska-Nowaczyk I., Nalepka D. 2004. *Quercus* L. – Oak. In Ralska-Jasiewiczowa M., Latałowa M., Wasylikowa K., Tobolski K., Madeyska E., Wright H.E. Jr., Turner Ch. (eds) *Late Glacial and Holocene history of vegetation in Poland based on isopollen maps*, W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, 189–199.

Miotk-Szpiganowicz G. 1992. The history of the vegetation of Bory Tucholskie and the role of man in the light of palynological investigations. *Acta Palaeobotanica* 32, 39–122.

Noryśkiewicz A. M. 2002. The Holocene history of the forest near Wierzchlas on the basis of palynological investigation from Lake Mukrz (original: Holoceńska historia lasów okolic Wierzchlasu na podstawie analizy pyłkowej osadów z jeziora Mukrz). In Banaszak J., Tobolski K. (eds) *Bory Tucholskie National Park on the background of the projected Biosphere Reserve* (original: *Park Narodowy Bory Tucholskie na tle projektowanego rezerwatu biosfery*), 195–204. Homini, Bydgoszcz-Charzykowy (in Polish).

Noryśkiewicz A.M., Kowalewski G. 2002. Development of the Dziedzinka raised bog (the Białowieski National Park) on the basis of palynological and plant macrofossils analysis. *Acta Agrophysica* 67, 197–206.

Noryśkiewicz A.M., Kowalewski G. 2003. Postglacial history of Dziedzinka mire (original: Postglacjalna historia roślinności torfowiska Dziedzinka). *I Polska Konferencja Paleobotaniki Czwartorzędu, conference abstract* Białowieża 22-24 V 2003, 32–34 (in Polish).

Noryśkiewicz A.M., Milecka K. 2002. Development of the Kletno peat-bog and postglacial and Holocene transformation of the Białowieża primeval forest vegetation in the light of pollen analysis. *Acta Agrophysica* 67, 207–216.

Obremska M., Lamentowicz M. 2002. Geology and history of kettle-hole bog on Brda Outwash plain on the base of pallen and testate amoebae (Protozoa) analyses (original: Geologia i historia torfowiska kotłowego na sandrze Brdy koło Tucholi na podstawie analizy palinologicznej i korzenionóżek *Testacea*). In Banaszak J., Tobolski K. (eds) *Bory Tucholskie National Park on the background of the projected Biosphere Reserve* (original: *Park Narodowy Bory Tucholskie na tle projektowanego rezerwatu biosfery*), 205–218. Homini, Bydgoszcz-Charzykowy (in Polish).

Paszewski A., Poznański F. 1936. Contribution to the history of the Białowieża Primeval Forests I (original: Materiały do historji lasów Puszczy Białowieskiej). *Roczniki Naukowe Rolnictwa i Leśnictwa* 36, 58–67 (in Polish).

Paszewski A. 1937. Contribution to the history of the Białowieża Primeval Forests II (original: Dalsze badania nad historią lasów Puszczy Białowieskiej na podstawie analizy pyłkowej torfowisk. *Roczniki Naukowe Rolnictwa i Leśnictwa* 36, 183–187 (in Polish).

Podbielkowski Z., Tomaszewicz H. 1979. An outline of hydro- botany (original: Zarys hydrobotaniki). Warszawa, PWN (in Polish).

Ralska-Jasiewiczowa M. 1964. Correlation between the Holocene history of the *Carpinus betulus* and prehistoric settlement in North Poland. *Acta Societatis Botanicorum Poloniae* 33, 463–468.

Ralska-Jasiewiczowa M. 1966. Bottom deposits of Lake Mikołajskie (Masurian Lakeland) in the light of paleobotanical investigation (original: Osady denne Jeziora Mikołajskiego na Pojezierzu Mazurskim w świetle badań paleobotanicznych). *Acta Palaeobotanica* 7, 1–118 (in Polish).

Ralska-Jasiewiczowa M. 1983. Isopollen maps for Poland: 0–11000 years B.P. *New Phytologist* 94, 133–175.

Ralska-Jasiewiczowa M., Miotk-Szpiganowicz G., Zachowicz J., Latałowa M., Nalepka D. 2004. *Carpinus betulus* L. – hornbeam. In Ralska-Jasiewiczowa M., Latałowa M., Wasylikowa K., Tobolski K., Madeyska E., Wright H.E. Jr., Turner Ch. (eds) *Late Glacial and Holocene history of vegetation in Poland based on isopollen maps*, W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, 69–79.

Stasiak J. 1964. History of Kruklin Lake as revealed by the deposits of its littoral zone (original: Historia Jeziora Kruklin w świetle osadów strefy litoralnej). *Prace Geograficzne IG PAN* 42, 1–94. Warszawa.

Tobolski K. 1987. Holocene vegetational development based on the Kluki reference site in the Gardno-Łeba plain. *Acta Palaeobotanica* 22, 179–222.

Tobolski K. 1991. Gegenwärtiger Stand der paleobotanischen und biostratigraphischen Forschungen in Lednicer Landschaftspark (original: Dotychczasowy stan badań paleobotanicznych i biostratygraficznych Lednickiego Parku Krajobrazowego). In Tobolski K. (ed.) *Introduction to paleoecology of Lednicki National Park* (orignal: *Wstęp do Paleoekologii Lednickiego Parku Krajobrazowego*), 11–34. Wydawnictwo Naukowe UAM. Poznań (in Polish).

Tobolski K. 1995. Ash in past landscapes (original: Jesion w minionych krajobrazach). In Bugała W. (ed.) *European Ash Fraxinus excelsior L. Our forest trees.* (orginal: *Jesion wyniosły, Fraxinus excelsior L. Nasze drzewa leśne*), 17, 7–17. Sorus. Poznań – Kórnik (in Polish).

Tobolski K. 2000. Guidebook to identification of peat and lake sediments (original: Przewodnik do oznaczania torfów i osadów jeziornych). PWN, Warszawa.

Troels-Smith J. 1953. Ertebølle Culture – Farmer Culture. Results of the post ten years excavations in Aamosen Bod, West Zealand (original: Ertebøllekultur – Bodenkultur. Resultater af de sidste 10 Aars Undersogelser i Aamosen, Vestsjaelland). *Aarbøger for nordisk Oldkyndighed og Historie* 1953, 5–62 (in Danish).

Troels-Smith J. 1955. Characterization of unconsolidated sediments (original: Karakterisering af lose jordarter). *Danmarks Geologiske Undersogelse* IV,3,10, 1–73 (in Danish).

Żurek S. 1993. Paleohydrological changes in wetlands (original: Zmiany paleohydrologiczne w mokradłach). *Przegląd Geograficzny* 64, 75–95 (in Polish).

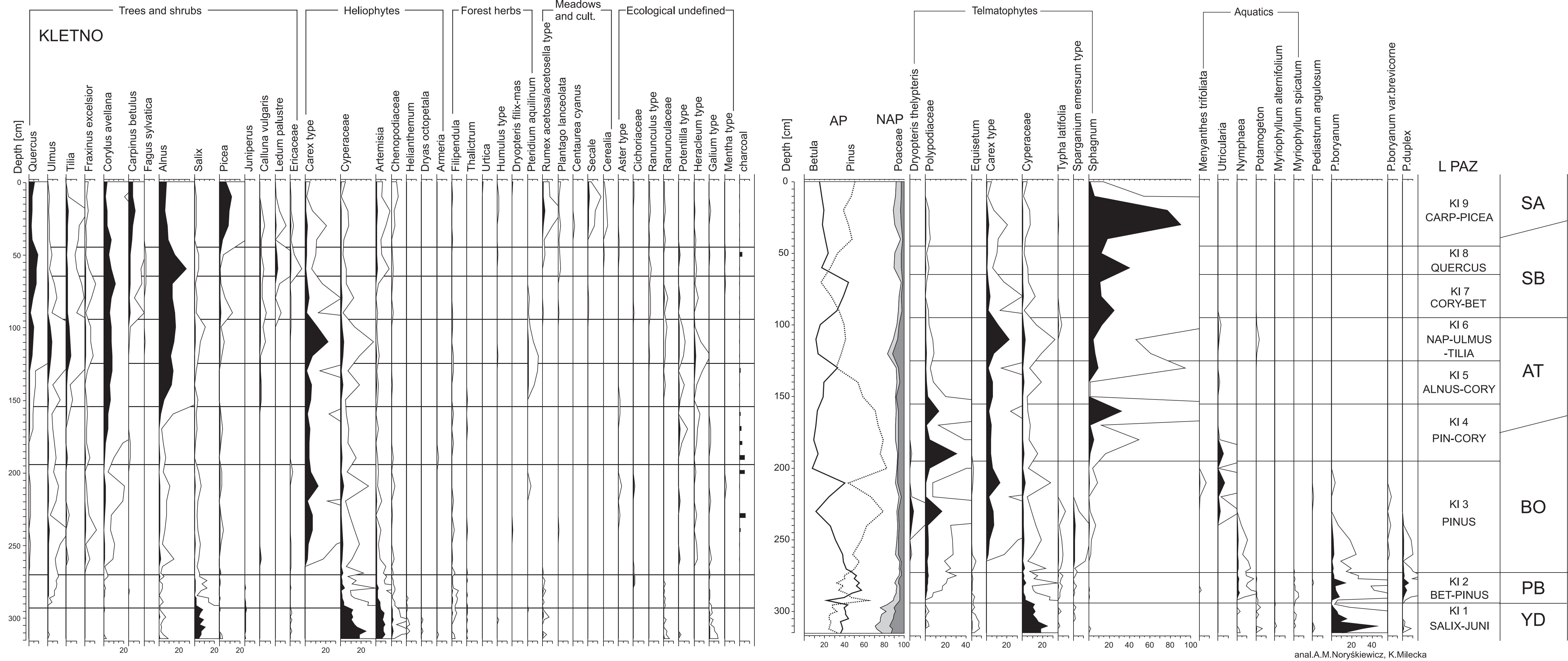

Fig. 3. Percentage pollen diagram of Kletno

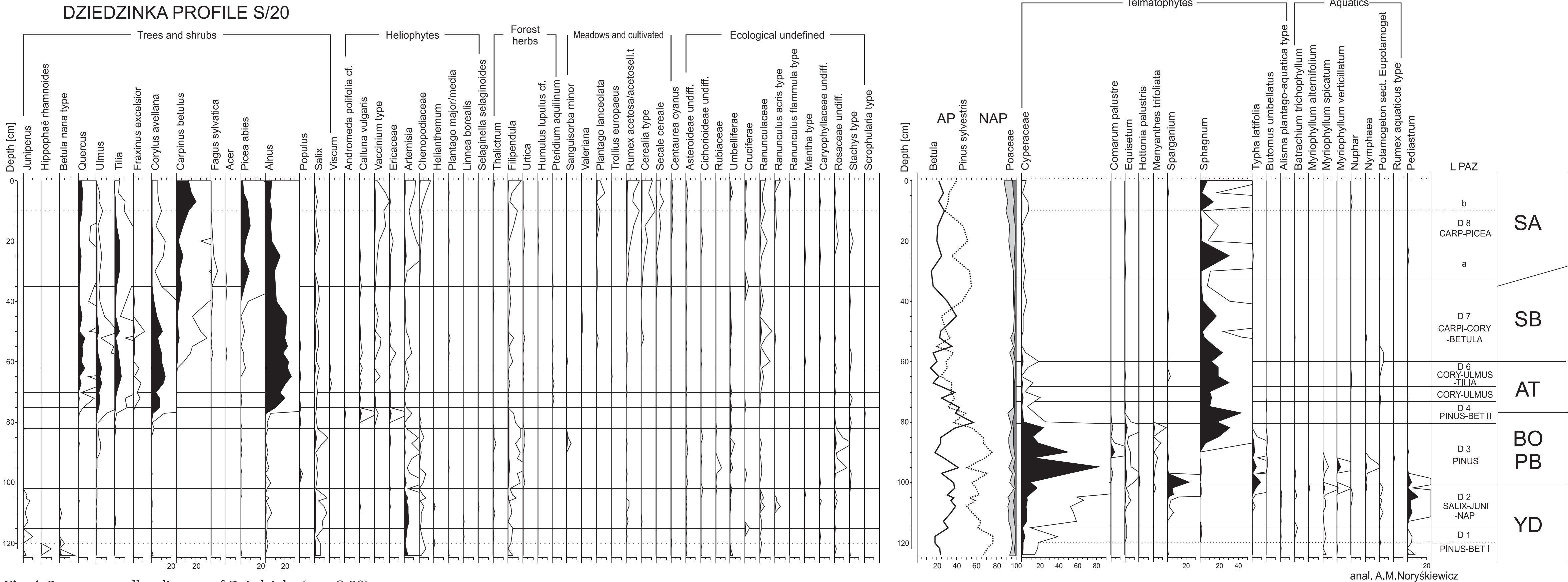

Fig. 4. Percentage pollen diagram of Dziedzinka (core S-20)