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Autogenic succession, land-use change, and climatic influences on the Holocene development of a kettle-hole mire in Northern Poland

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Abstract

We reconstructed the Holocene developmental history of a kettle-hole peatland in the Tuchola Forest of Northern Poland, using pollen, testat amoebae and plant macrofossil indicators. Our aims were to determine the timing and pattern of autogenic succession and natural and anthropogenic influences on the peatland. Northern Poland is under mixed oceanic and continental climatic influences but has so far been less studied in a palaeoecological context than more oceanic regions of Europe. In the first terrestrial developmental phase of the mire, the testate amoebae-inferred depth to water table revealed two major dry shifts at ca. 9400 (end of lake phase) and ca. 7100 cal BP (a period of global cooling and dry shift in Western Europe). Conditions became wetter again in two steps at ca. 6700 and ca. 5800 BP after a dry event at ca. 6100 BP. The timing of the wet shift at 5800 BP corresponds to wet periods in Western Europe. Peat accumulation rates were low (0.1 mm yr^{-1}) between ca. 5600 and ca. 3000 BP when sedges dominated the peatland. In the last 2500 yrs surface moisture fluctuated with wet events at ca. 2750–2400, and 2000 BP, and dry events at ca. 2250–2100 and 1450 BP. After 1450 BP a trend towards wetter conditions culminated at ca. 500 cal BP, possibly caused by local deforestation. Over the mire history, pH (inferred from testate amoebae) was mostly low (around 5) with two short-lived shifts to alkaline conditions (7.5) at ca. 6100 and 1450 BP indicating a minerotrophic influence from surface run-off into the mire. Up to about 1000 BP the ecological shifts inferred from the three proxies agree with palaeoclimatic records from Poland and Western Europe. After this date, however correlation is less clear suggesting an increasing local anthropogenic impact on the mire. This study confirms that kettle-hole peatlands can yield useful palaeoenvironmental data as well as recording land-use change and calls for more comparable studies in regions are the interface between major climate influences.

Keywords: Holocene; palaeohydrology; human impact; testate amoebae; pollen; plant macrofossils; Poland; transfer function

1. Introduction

The abiotic and biotic characteristics of peatlands are determined by the geomorphological setting and the climate (Charman, 2002). As peatlands develop through time, autogenic processes, such as vegetation succession, play an increasingly important role, together with allogenic factors, such as climatic change or direct and indirect human influences (Campbell et al., 2000). Raised bogs, which depend primarily on precipitation for their water supply, are highly sensitive to climatic changes (Aaby, 1976; Dupont, 1986; Barber et al., 1998; Mauquoy and Barber, 2002; Barber et al., 2003) and are thus ideal for reconstructing the climatic history (Blackford, 2000; Chambers and Charman, 2004). Closed basin kettle-hole peatlands are similar to raised bogs in their ability to record the changes in climate, but these peatlands are also influenced by local hydrology. Kettle-hole peatlands therefore also integrate changes in the hydrology of the watershed area, which may be due either to natural causes or to human activities, such as logging (Warner et al., 1989; Campbell et al., 2000; Booth et al., 2004; Lamentowicz et al., 2007). The main challenge in palaeoecological investigation of peatlands in general and kettle-hole peatlands in particular is therefore to

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separate these different signals (Chambers, 1993). This is especially crucial for the Late Holocene because of the increasing human impact on the landscape.

From a climatic and palaeoclimatic perspective, Poland is an interesting region because it is under the influence of both oceanic (from the West and North-West) and continental (from the East) climates (Kożuchowski and Marciniak, 1991; Woś, 1999). Because of this climatic situation, Polish peatlands may be subject to a higher hydrological stress than more oceanic regions, especially during the summer months, and may thus be exceptionally sensitive to climatic change. More generally, palaeoenvironmental records derived from this region may not necessarily agree with those derived from regions under a more oceanic influence (e.g. in UK). However, less palaeoclimatic data is available from Northern Poland as compared to more oceanic regions of Europe. In order to assess to what extent the records from oceanic and more continental regions differ (Charman et al., 2004), more studies, and especially multiproxy studies, are needed in regions such as Poland.

This study addresses the possible use of non-ombrotrophic peatlands as palaeoclimatic archives. We reconstructed the Holocene developmental history of a kettle-hole peatland in the Tuchola Forest of Northern Poland with special focus on the terrestrialization sequence from lake to peatland. Our aims were: (1) to distinguish the relative importance of climate change, autogenic development and human influences on the different phases of development of the peatland, and, (2) to compare our results with palaeoecological data from other regions in Poland and beyond. We used three proxies: testate amoebae, pollen and spores, and macrofossils to cover a broad range of spatial scales from the very local (testate amoebae and macrofossils) to the regional (pollen and spores). Pollen and spores are further used for

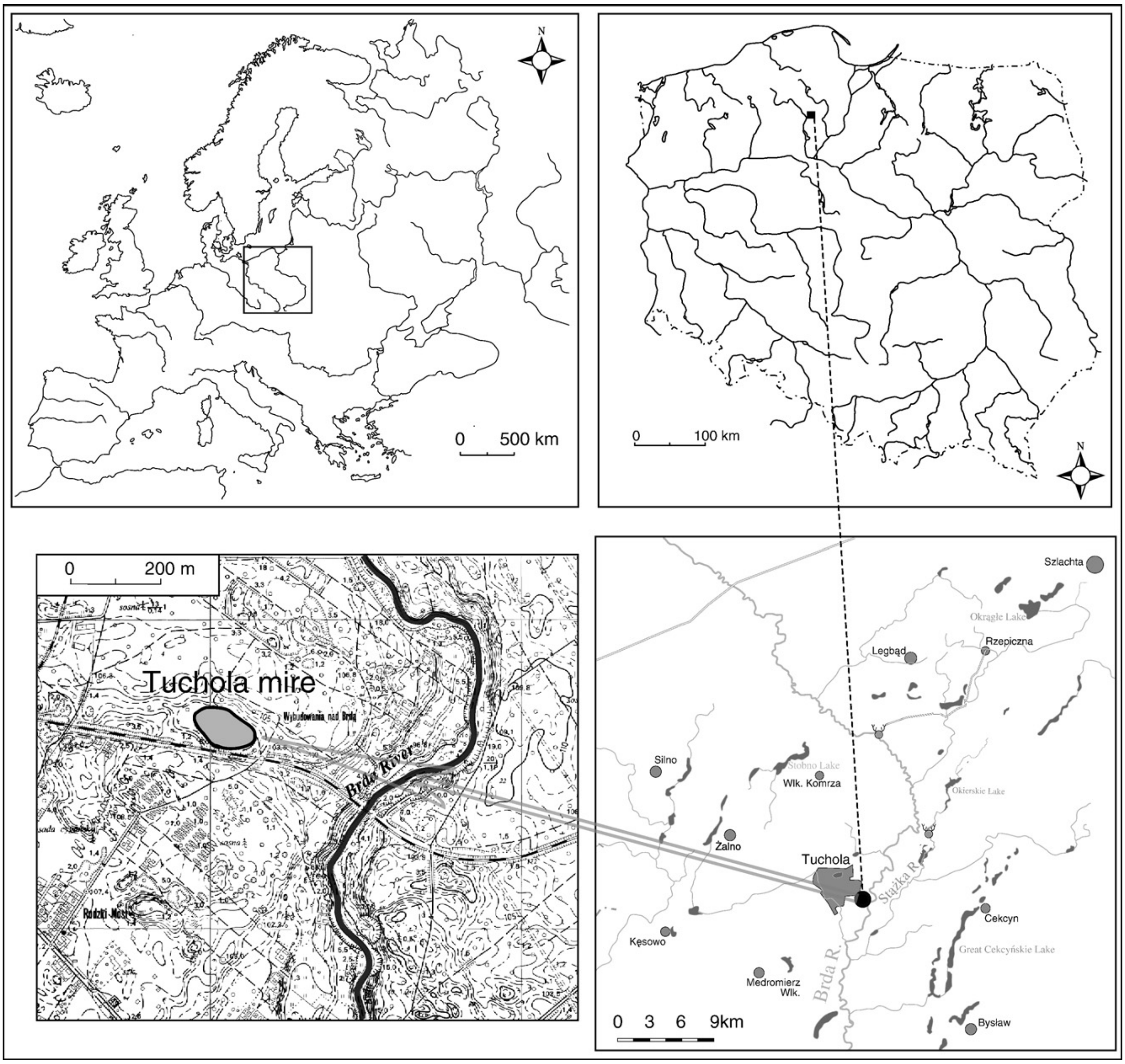


Fig. 1. Location of Tuchola Pinewoods and the study site in Poland.

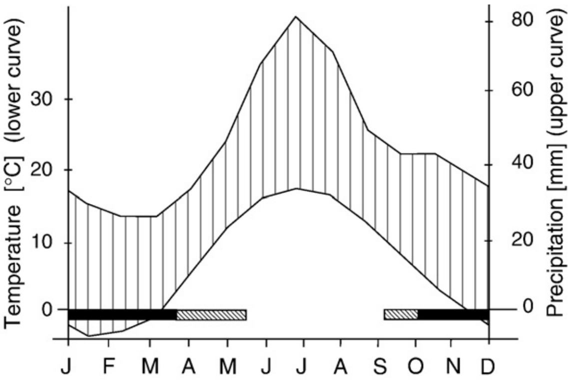


Fig. 2. Climatic diagram of Chojnice meteorological station (100 m a.s.l., 20 km NW from Tuchola) — average values for years 1951–1980. Figure description: black shaded area indicates months with frozen ground, grey-shaded area indicates months with night frost. 30-year annual averages: temperature: 6.8 °C; precipitation: 556 mm.

correlation with previous studies in the region. With respect to the developmental history of the mire, we hypothesized: (1) that in the early phases climate and autogenic development were the main factors influencing the system; (2) that human influences played an increasingly important role in the recent history of the site.

2. Study site

After the Pomeranian phase of the Vistulian (last ice age) glaciation, peatlands developed in river valleys, former lake basins, and kettle-holes (Liberacki, 1958; Tobolski, 2003). Tuchola peatland, a small (2 ha) basin filled with organic sediments, developed in one of these kettle-holes. It is situated in Northern Poland (Fig. 1), at the border between two geographical regions: the Brda Valley and Tuchola Pinewoods (Kondracki, 1998) (coordinates: 53°34′30"N; 17°54′05"W, 108 m a.s.l.), on the sandy outwash plain of the Brda river, approximately 2 km east of the edge of a morainic plateau and 400 m from the Brda riverbed.

The bog is situated in a depression without significant surface run-off and is surrounded by a *Pinus sylvestris*-dominated forest. Characteristic species of the peatland are *Betula pubescens* and *P. sylvestris* and *Lycopodium annotinum*, for vascular plants, and *Sphagnum recurvum*, *S. palustre*, *Polytrichum formosum*, *P. commune*, and *Pleurozium schreberi*, for bryophytes. In the western, southern, and eastern parts, peat was formerly extracted for domestic fuel, as attested by the presence of abandoned pits. Despite the extensive tree-cover, the peatland surface is flooded at least once a year, thus allowing species such as *Potentilla palustris* to grow. However, the water table fluctuates significantly over the course of the year and the site is also often non-flooded.

The climate of Poland is mainly influenced by the Iceland Low, and Azore high, pressure systems. During the year the pressure and associated climate shows a characteristic periodicity. The climate is influenced mostly by the Iceland Low in January and by the Azore high in summer. This high pressure system can influence Central and Eastern Europe as far as Ukraine. Its effect is to increase the flow of moist Atlantic air from the NW and W directions. Continental air from the East influences the region mainly during spring and autumn (Tomaszewska, 1964; Paszyński and Niedźwiedź, 1999).

The average annual rainfall in the Tuchola Forest area (for the period from 1981 to 1998) is 600 mm (Wójcik and Marciniak, 1993; Sadowski, 1994). July is the wettest month (approximately 200 mm) and August and September the driest ones. The average annual temperature is 7 °C (−3 °C in January and +17°C in July) (Churski, 1962; Kozłowska-Szczęsna, 1993). Fig. 2 presents the climatic diagram for Chojnice meteorological station (situated 20 km NW from Tuchola).

3. Methods

3.1. Coring and laboratory analyses

A total of six cores were taken using a Russian sampler (diameter: 50 mm, length: 50 cm) along a transect across the mire (Fig. 3). Following preliminary examination in the field, the central core (TU-4) was chosen for palaeoecological

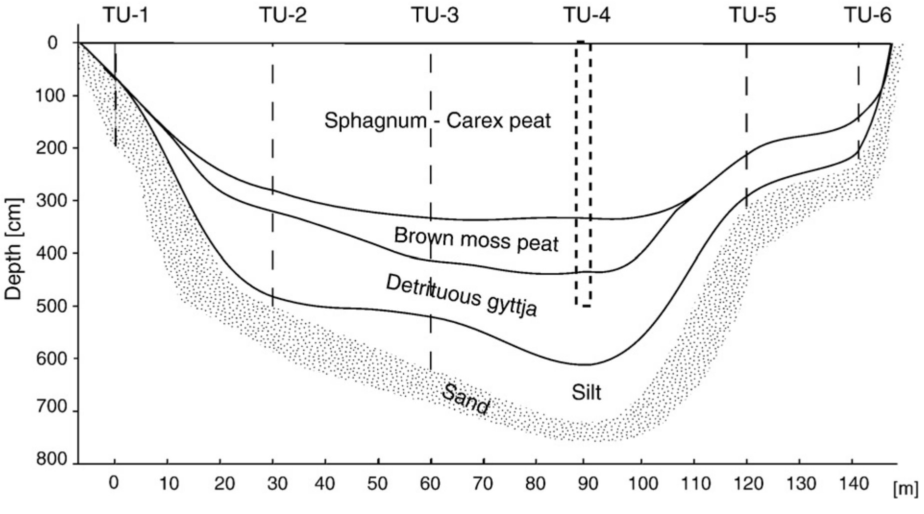


Fig. 3. Geological cross-section of the coring transect in Tuchola kettle-hole bog.

analyses. Each core section was preserved in PVC tubes and transported to the laboratory. The lithology was described using the Troels-Smith method (Troels-Smith, 1955).

Five pine bark macrofossils were dated by AMS radiocarbon analysis in Poznań Radiocarbon Laboratory (Table 1). The dates were calibrated using the OxCal 3.8 program (Bronk Ramsey, 1995, 2001). Additional dates were inferred from the regional pollen signals by comparison with a record from Lake Ostrowite, which is located approximately 25 km from the study site (Milecka and Szeroczyńska, 2005).

Samples for palynological analyses (1 cm^3) were taken every 5 cm, adding up to 101 samples in total. Sample preparation followed the standard laboratory protocol (Berglund and Ralska-Jasiewiczowa, 1986). Before acetolysis, the peat material was boiled for 10 min in 10% KOH. The residue was then sieved over a 200-µm mesh. Pollen of trees (AP) and shrubs were counted to a total of 500, under 400× magnification. Algal remains (e.g. *Pediastrum*) were recorded as well. Pollen of aquatic and telmatic plants was excluded from the percentage calculation. The identification of spores and algal remains was based on the available literature (Erdtman et al., 1961; Faegri and Iversen, 1978, 1989; Moore et al., 1991).

Samples for testate amoeba analysis were taken from the same depths as those for palynological analysis. A total of 90 samples were counted. The following procedure of sample preparation was used: 2 cm^3 of peat sediment was boiled in distilled water for 10 min. The material was then sieved over a 300-µm mesh. Testate amoebae were counted to a total of 200 individuals, at 200–400× magnification. The rotifer *Habrotrocha angusticollis*, commonly found in peat (Warner and Chengalath, 1988), was included in testate amoeba analyses.

Table 1
Radiocarbon dates obtained by radiocarbon (AMS) dating. Poz — dates for Tuchola mire (T4 core), OSTI — OST V — dates inferred from palynostratigraphic correlation with radiocarbon dated Ostrowite lake core (Milecka and Szeroczyńska, 2005)

N	Sample name	Depth (cm)	Material dated	Age ^{14}C BP–AMS	Calibrated age BP	Middle of 2σ range
1	TUCH I	65	Pine bark	1430±25	1σ 1333–1297 2σ 1355–1285	1320
2	TUCH II	210	Pine bark	4900±25	1σ 5649–5624 2σ 5660–5590	5575
3	TUCH III	360	Pine bark	4150±30	Date not used in interpretation because of inversion	–
4	TUCH IV	310	Pine bark	7530±30	1σ 8390–8330 2σ 8400–8290	8345
5	TUCH V	425	Pine bark	8250±40	1σ 9230 –9130 2σ 9430–9080	9255
6	OST I	172	Pine bark	2818±34	1σ 2960–2870 2σ 3040–2840	2940
7	OST II	190	Pine bark	4039±29	1σ 4490–4440 2σ 4580–4420	4500
8	OST III	197	Pine bark	4137±42	1σ 4710–4570 2σ 4830–4530	4680
9	OST IV	207	Pine bark	4860±50	1σ 5660–5580 2σ 5720–5570	5645
10	OST V	415	Pine bark	8110±50	1σ 9130–8990 2σ 9260–8970	9115

For plant macrofossils, the core was divided in 5 cm sections and 101 samples were analysed. The preparation methods were based on the accessible literature (Grosse-Brauckmann, 1986; Warner, 1990; Tobolski, 2000). The material was rinsed with water onto sieves with mesh sizes 0.25 and 0.5 mm. The residue was sorted under a stereoscopic microscope under 10–100× magnification. Two randomly chosen samples from each section were examined at 200–400× magnification to estimate the volume percentage of each plant taxon.

3.2. Diagrams preparation and numerical analyses

Percentage diagrams of plant macrofossils, pollen and testate amoebae were constructed with Tilia 2 and Tilia Graph (Grimm, 1992). The estimated percentage composition of particular macrofossils (e.g. *Sphagnum* and brown moss species) was presented using a five-degree scale. Countable remains (e.g. *Andromeda polifolia* seeds) were presented in absolute sums. Testate amoeba and pollen diagrams are based on percentage data.

For pollen and testate amoeba data we defined statistically significant biostratigraphic zones with use of ZONE version 1.2. (Juggins, 1991), by optimal sum-of-squares partitioning (Birks and Gordon, 1985; Birks, 1986). Their significance was tested with the broken-stick method (MacArthur, 1957), using the software BSTICK version 1.0 (Bennett, 1996). Were decided to determine macrofossil assemblage zones 'by eye' because of semi-quantitative character of the data.

We inferred the past depth to water table (DWT) and pH from the testate amoebae (percentage data) using transfer functions based on Polish surface samples (Lamentowicz and Mitchell, 2005). We (i.e. ML and EM) are currently expanding this data set to include more samples from a broader range of environmental conditions and optimizing the model's performance. A total of 123 modern samples were used to test and build the model used here. We tested the performance of five transfer function models: partial least squares (PLS), weighted averaging (WA), tolerance down-weighted averaging (WAtol), weighted averaging partial least squares (WA-PLS), Maximum Likelihood regression (ML) (Birks, 1995), using the software C2 (Juggins, 2003). Taxa that occurred in less than 4 samples were excluded from the data set as an initial filtering. In addition, we optimized the models by selectively removing species or samples that had residuals above a certain threshold, using an approach similar to that used by Payne et al. (2006). This approach is justified by the fact that if a species is too rare, there will not be enough information in the data set to model its response. Likewise, some samples may contain unusual combination of testate amoeba community and/or environmental characteristics and if the data set contains only few such samples these situations will be difficult to model. Also, some species may show a response that cannot be modeled accurately (e.g. bimodal distribution that could be due to the existence of two taxa with similar morphology but different ecological optima). For DWT we excluded samples with residuals higher than: 20 cm, 10 cm, 8 cm, 7 cm and 6 cm. For pH samples with residuals higher than 2, 1, 0.7, 0.5 and 0.3 units were removed from the training set. Finally, we compared the values obtained using the total testate amoeba community with values obtained using a model that excluded the idiosome shells produced by Euglyphida mainly. These shells are preferentially lost in most palaeoecological records and in some cases at least this could lead to errors in inferred water table and possibly pH (Mitchell et al., in press). Model performances were assessed using Root Mean Squared Error of Prediction (RMSEP) criterion (which assesses the random differences between observed and predicted values), maximum bias (which assesses the maximum error in any section of the environmental gradient) and the correlation between observed and predicted values. Using these criteria, we selected the weighted averaging model (WAtol) as the most appropriate for DWT reconstruction and the weighted averaging partial least squares (WA-PLS) model with log transformed species data for pH reconstruction.

As data on the environmental preferences of *Difflugia pulex* and *Difflugia urceolata* is currently lacking from our database, we interpreted the occurrence of these two species based on the available literature data (Laminger et al., 1979; Schönborn, 1981b; Ellison, 1995; Charman et al., 2000; Scott et al., 2001; Patterson and Kumar, 2002; Patterson et al., 2002) as well as personal observations.

4. Results and interpretation

4.1. Lithology and dating

Fig. 3 presents the geological profile of the bog. The total length of the analysed core (TU-4) was 700 cm. A stratum of beige-blue-grey silt is present in most of the basin, but reaches greatest thickness where core T4 was taken. This layer is overlain by detrituous–calcareous gyttja. A significant layer of well-preserved brown moss peat is present between 438 and 366 cm. The peat part of the core is mostly composed of sedge–bryophyte constituents in different stages of decomposition, the upper 20 cm being especially decomposed.

Ten dates obtained either by AMS radiocarbon dating or by correlating the regional pollen curve to a nearby study site are presented in Table 1. The calibration results are presented for each date with 1σ (=1SD or 68% of probability) and 2σ (= 2SD or 95% of probability). One date (TUCH IV) was clearly too young based on both the palynological data for that period and the other four dates. It was therefore not used. The lowest dated level (425 cm) yielded an age of 9430–9080 cal yr BP. Using this lowest dated level and the pollen spectrum, the estimated dates for the main lithological phases are ca. 11 000 cal yr BP for the beginning of gyttja sedimentation (625 cm), ca. 10 000 cal yr BP for the bottom of the studied part of core T4 (500 cm), ca. 9250 cal yr BP for the bottom of the brown moss peat (425 cm), ca. 7800 cal yr BP for the *Sphagnum* peat (325 cm), and ca. 3500 cal yr BP for the mixed cyperaceous–*Sphagnum* peat (210 cm). Below these levels, a preliminary pollen analysis revealed a complete Late Glacial history in a 1-meter thick layer of silt sediments, making it possibly the oldest known sedimentary record in the Tuchola Pinewoods area (Obremska, Tobolski, personal communication). Since our main focus was on the history of the terrestrialization of Tuchola mire and the Holocene history, only the top 500 cm of core T4 was used for this study. This represented the end of the lacustrine phase and the entire terrestrialization succession.

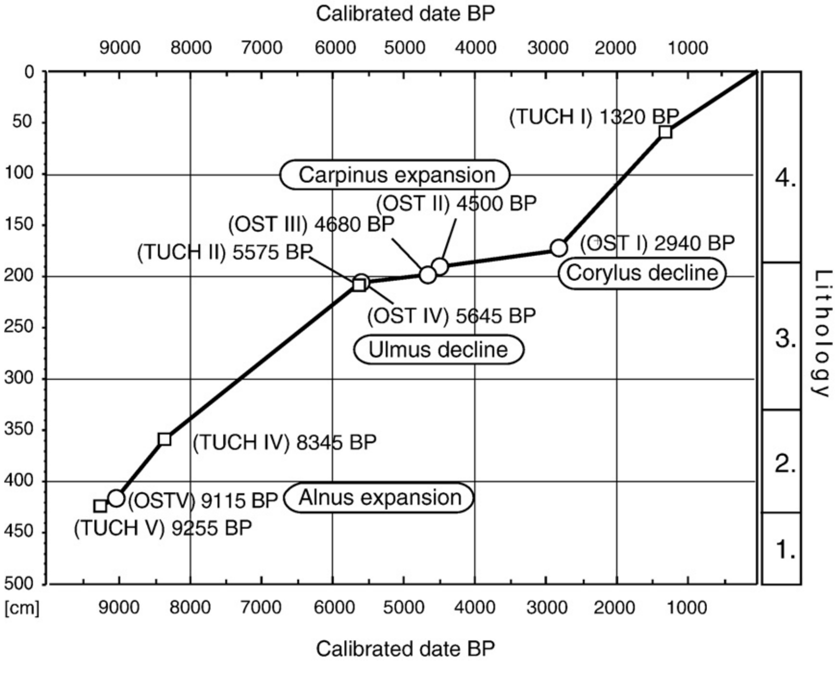


Fig. 4. Age-depth model of Tuchola mire. Squares: calibrated radiocarbon dates; circles: dates obtained by palynostratigraphic correlation between Tuchola mire (TUCH) and Lake Ostrowite (Tuchola Pinewoods) (Milecka and Szeroczyńska, 2005). The dates given in the figures correspond to radiocarbon dates. The scale corresponds to calibrated dates. Lithology: 1 — fine detrituous gittja; 2 — brown moss peat; 3 — *Sphagnum* peat; 4 — mixed cyperaceous–*Sphagnum* peat.

The peat accumulation rate, estimated by linear interpolation between the middle point of the 2σ range of calibrated dates (Fig. 4), was high, about 1.2 mm yr^{-1}, during the early stage from 9255 to 8345 cal yr BP (425 to 310 cm), and then decreased to 0.3 mm yr^{-1} during later stages from 8345 to 5575 cal yr BP (310 to 210 cm). Accumulation of peat declined considerably to an average of 0.1 mm yr^{-1} in the period between ca. 5575 and 2940 cal yr BP (210–172 cm) and increased to 0.6 mm yr^{-1} between ca. 2940 and 1320 cal yr BP. After ca.1320 cal yr BP (65 cm) the calculated rate declines again slightly to 0.4 mm yr^{-1}, but this value also takes into consideration the non-compacted acrotelm.

4.2. Testate amoeba-based transfer function for DWT and pH

Excluding the idiosome shell type did not change the inferred DWT or pH significantly (see further) and therefore we used the full model. For the DWT transfer function, the optimal model (WA tol) was obtained using the following option: species with less than 4 occurrences and samples with residuals higher than 7 were excluded from the training set. The maximum bias of the prediction was 8.9 cm and a root mean square error of prediction (RMSEPjack) was 4.3 cm. The value of RMSEP together with maximum bias shows the quality of the model and its usefulness for the reconstruction (Birks, 1995). The comparison of observed and predicted DWT values is presented in Fig. 5A. For the pH transfer function, the optimal model was obtained using the following option: species with less than 4 occurrences and samples with residuals higher than 0.7 pH units were excluded from the data set. The maximum bias of the prediction was 0.5 pH units and the RMSEP(jack) was 0.41 pH units. The comparison of observed and predicted pH values is presented in Fig. 5B. Both models perform significantly better than the previous one in which 36 samples were retained (Lamentowicz and Mitchell, 2005). The performance of the model used here is comparable with that of published transfer functions from other parts of the world (Booth, 2001; Payne et al., 2006; Booth, 2007; Charman and Blundell, 2007; Payne and Mitchell, 2007).

4.3. Pollen, spores, plant macrofossils, testate amoebae and inferred DWT and pH

Pollen and spore types were separated into four categories: trees and shrubs, herbs, human impact indicators, and telmatophytes and aquatics (Fig. 6). We defined eight pollen zones (TU-po-1–TU-po-8) based on the dominant trees and the relative importance of non-arboreal pollen (NAP). The 61 recognized macrofossils types were separated into five categories: brown mosses, peat mosses, vascular plants, trees and shrubs, and aquatic organisms (Fig. 7). We divided the samples into six groups (TU-ma-1–TU-ma-6) representing the succession from aquatic plants to different types of *Sphagnum*-dominated vegetation.

A total of 45 testate amoeba taxa, plus the rotifer *Habrotrocha angusticollis*, were identified in the core. The most common species were *Amphitrema flavum*, *Assulina muscorum*, *Centropyxis aculeata* and *Hyalosphenia papilio*. Five testate amoeba zones were identified (TU-ta-1–TU-ta-5, Fig. 8). The changes in DWT and pH inferred from testate amoebae are presented in Fig. 8. During the history of this site the inferred DWT ranged between 6.8 and 18 cm (Mean = 11.8; Median = 11.8; SD = 2). After very wet conditions inferred for the lowermost sample of the peat core, the site remained quite wet for a long period of time. This stable period was followed by the first and most marked change in testate amoeba communities and the lowest inferred DWT close to 18 cm, corresponding to ca. 6700 cal yr BP (270 cm), inferred from a testate amoeba community dominated by *Assulina muscorum*, *A. seminulum*, *Heleopera petricola* and *Trigonopyxis arcula*. Following this

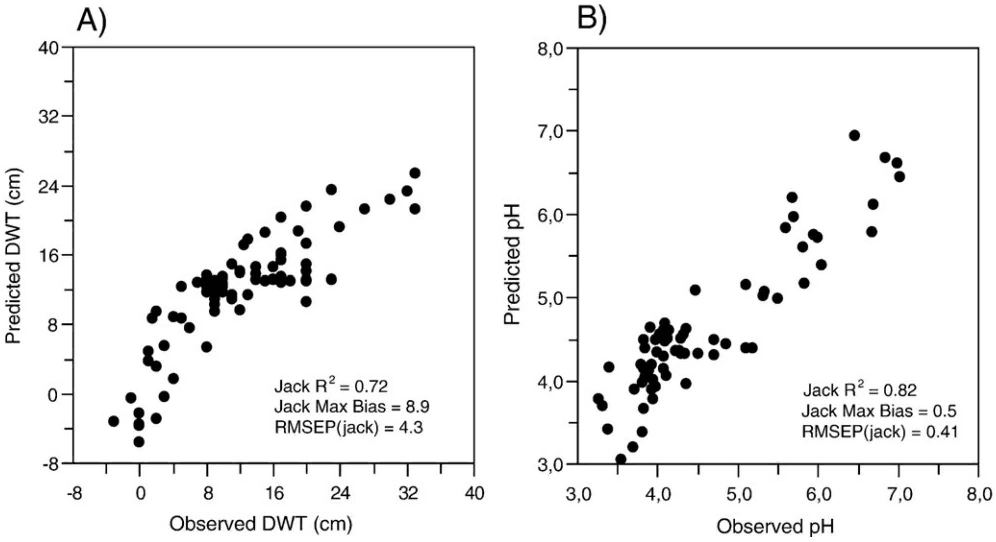


Fig. 5. Performance of (A) the depth to water table (DWT) jacknifed weighted averaging (WA tol) model and (B) the pH jackknifed weighted averaging partial least squares (WA-PLS) model based on an extended data set of respectively 123 (after data filtering) surface samples from Tuchola Forest.

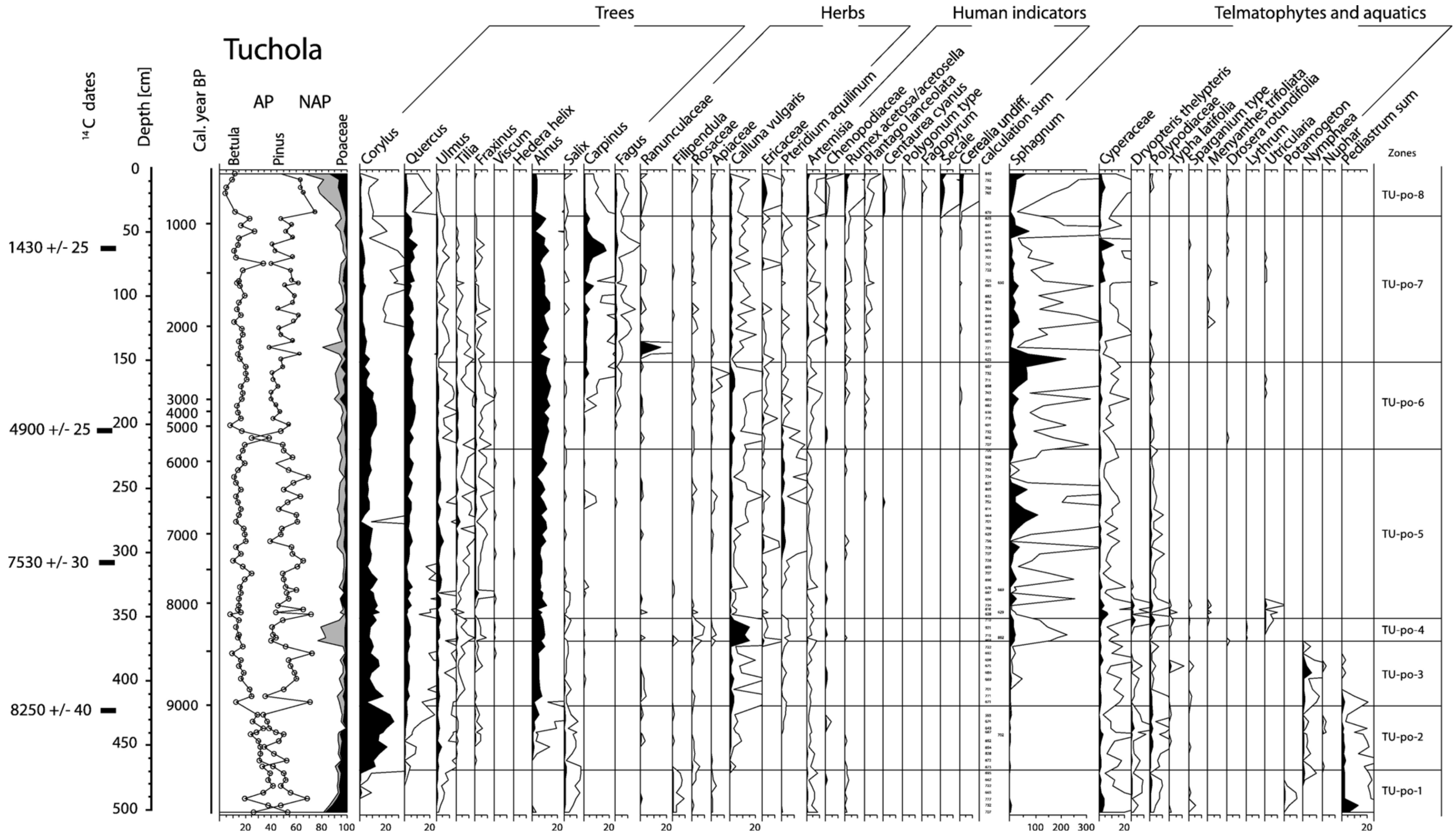


Fig. 6. Percentage pollen diagram from Tuchola mire. Lithology as in Fig. 4.

event the inferred DWT fluctuated mostly between 8 and 14 cm. The current trend is towards drier and more acidic conditions. The inferred pH of Tuchola mire fluctuated between 3.9 and 8.5 (Mean = 5.1; Median = 5; SD = 0.8) but during most of its history pH was around 5.0. The highest pH events occurred at approximately 9000 cal yr BP (438 cm, pH 8.5), later at ca. 6120 cal yr BP (219 cm, pH 7.4) and 1400 cal yr BP (70 cm, pH 7.4). The lowest pH value (3.9) inferred for the uppermost sample (1 cm) could be interpreted as reflecting the well-known vertical micro-distribution of testate amoebae in the acrotelm (Meisterfeld, 1977; Mitchell and Gilbert, 2004) and the preferential decomposition of idiosome-type shells (e.g. *Euglypha*) (Mitchell et al., in press) rather than a recent ecological shift. However, when we tested for this possible effect by using a transfer function excluding the Euglyphida with the exception of genus *Assulina* the inferred values were not significantly different (the value for the uppermost sample would be 4.0 instead of 3.9). We therefore consider this pH shift, which also agrees with a lowering of the water table, as real.

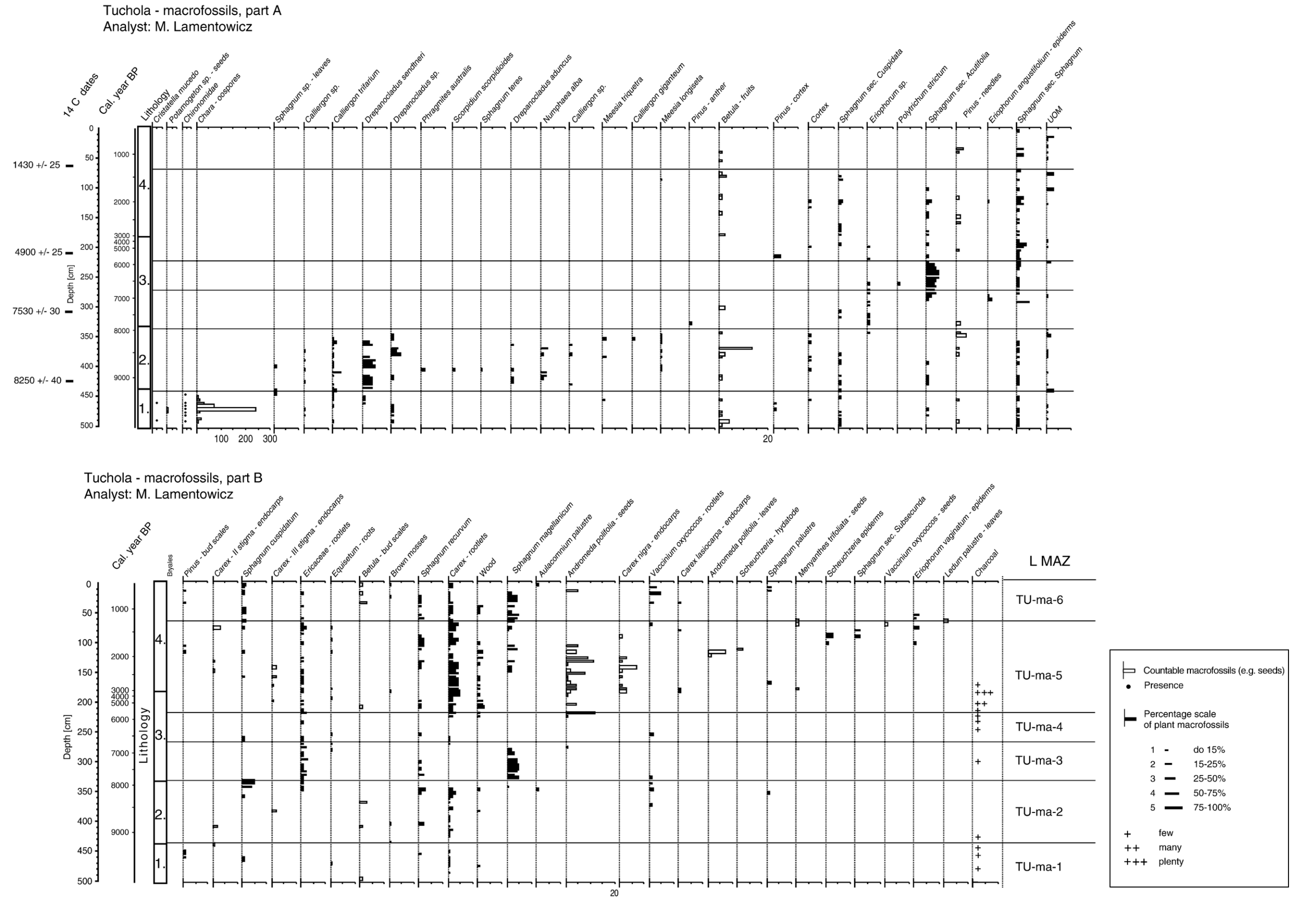
4.4. Developmental history of Tuchola mire

The developmental history of Tuchola mire inferred from pollen and plant macrofossil diagrams and testate amoebae is synthesized hereafter. Biostratigraphic zones for pollen, macrofossils and testate amoebae and key events are summarized in Fig. 9.

Limnic stage: Ca. 10,000 to ca. 9300 cal yr BP (500–425 cm) (zones: TU-po-1, TU-po-2, TU-ma-1, TU-ma-2, TU-ta-1) — By analogy to the proposed origin of many kettle-holes in general and those of the Brda outwash plain in particular (Galon, 1953, 1958), this small basin probably originated from dead ice remaining from the Vistulian glacier. During the Preboreal, the study site was a lake surrounded by a forest with *Betula*, *Pinus* and *Ulmus* and some *Salix* trees or shrubs. *Corylus* and, later, *Quercus* appear towards the end of the first pollen zone (P1), which corresponds approximately to the limit between the Preboreal and the Boreal, while *Alnus* remained almost entirely absent. In addition, local fires probably connected with drought phases took place, as attested by charcoal (Fig. 7). From the beginning of the Holocene to ca. 9430–9080 cal yr BP, pollen, spores and macrofossils indicate a shallow lake environment with Cyperaceae dominating the lakeshore vegetation with *Sphagnum* and brown mosses. Only few testate amoebae were recovered from this level and only one genus: *Centropyxis* (*C. aculeata*, *C. discoides*, and *C.* sp.). These species might have lived in the lake sediments or in very wet mosses growing on the lakeshore.

Telmatic stage: Ca. 9300 to 7800 cal yr BP (425–325 cm) (zones: TU-po-2, TU-po-3, TU-po-4, TU-ma-2, TU-ta-1, TU-ta-2) — The transition from lake to telmatic vegetation took place in the early part of the Boreal and is reflected by a clear trend towards drier conditions and lower pH around 9400 cal yr BP. Peat began to accumulate at ca. 9430–9080 cal yr BP. This phase includes zones TU-po-2 and TU-po-3 (*Corylus*, *Ulmus* — up to the *Pinus* decline). Zone TU-ma-2 represents the telmatic phase that lasted from ca. 9300 to 7800 cal yr BP. *Pinus* and *Betula* forests with *Corylus* were growing around the Tuchola basin. *Corylus* started to decline and the forest, dominated by deciduous trees started to resemble the modern one, with the notable absence of *Carpinus*. Around the mire, heathlands developed at the expense of the pine forest. Along with the forest decline and the increasing dominance of *Calluna vulgaris* (TU-po-4), the rest of the vegetation was also changing. Among marsh and aquatic plants in shallow water habitats *Utricularia* spp. occurred, together with *Dryopteris thelypteris* and *Pseudocalliergon trifarium* and *Meesia triquetra* as well as Cyperaceae (TU-ma-2). As a result of hydroseral succession, sedge and brown moss communities took over the area and the rate of peat accumulation was high. *Nymphaea* sp. and *Nuphar* sp. were growing in small, shrinking pools or during phases of high water levels, but no open water remained as attested by the absence of the alga *Pediastrum*. The dominant brown mosses were *Drepanocladus sendtneri* and *Pseudocalliergon trifarium* — both of which are peat-forming plants also known from other sites in Northern Poland (Jasnowski, 1957a,b; 1959). These mosses indicate alkaline conditions (Glime et al., 1982; Tallis, 1983). The good preservation of brown mosses attests of very wet conditions. The terrestrialization gradually proceeded and the transition to a *Sphagnum*-dominated mire lasted approximately 500 ^{14}C years. The number of recoverable testate amoeba shells was too low to reach statistically relevant numbers in about half of the samples. Although this pattern of samples with high and low recoverable numbers of testate amoebae might suggest frequent environmental changes (e.g. in fluctuating hydrological conditions), when only the usable samples are considered the inferred DWT appears very stable (TU-ta-1 and TU-ta-2). The presence of *Amphitrema flavum* and *Hyalosphenia papilio* indicates a poor fen or bog hollow with wet *Sphagnum* mosses, in agreement with the macrofossil data.

First terrestrial phase: Ca. 7800 to 5600 cal yr BP (325–210 cm) (zones: TU-po-5, TU-po-6, TU-ma-2, TU-ma-3, TU-ma-4, TU-ma-5, TU-ta-2, TU-ta-3) — Most of the Holocene developmental history of Tuchola mire consisted in a long-lasting terrestrial phase. This phase corresponds to two pollen assemblage zones: part of *Ulmus* forest (TU-po-5), mixed deciduous forest (TU-po-6), three macrofossil assemblage zones (TU-ma-2 to TU-ma-5), and two testate amoeba assemblage zones (TU-ta-2 and TU-ta-3). As for the previous phase, at the beginning of the terrestrial phase, plant and testate amoeba communities were unstable, probably because of the dynamic hydrosere development and the rapid transformation from lake to mire. Peat moss communities were initially dominated by *Sphagnum cuspidatum*, growing in an acid and wet habitat. *S. cuspidatum* marks the transition between the telmatic and terrestrial phases and characterizes beginning of macrofossil zone TU-ma-3. This bog hollow species expanded into moist habitats at the expense of brown mosses. The dominant testate amoeba species, *Amphitrema flavum* and *Hyalosphenia papilio*, are in agreement with the macrofossil data. As for the previous phase, we tentatively interpret the lack, or low numbers, of testate amoebae in several samples as caused by abrupt, possibly seasonal, water level changes. However,



Tuchola - macrofossils, part A
Analyst: M. Lamentowicz

Tuchola - macrofossils, part B
Analyst: M. Lamentowicz

Fig. 7. Plant macrofossils diagram from Tuchola mire. Taxa were sorted by weighted average. Lithology as in Fig. 4.

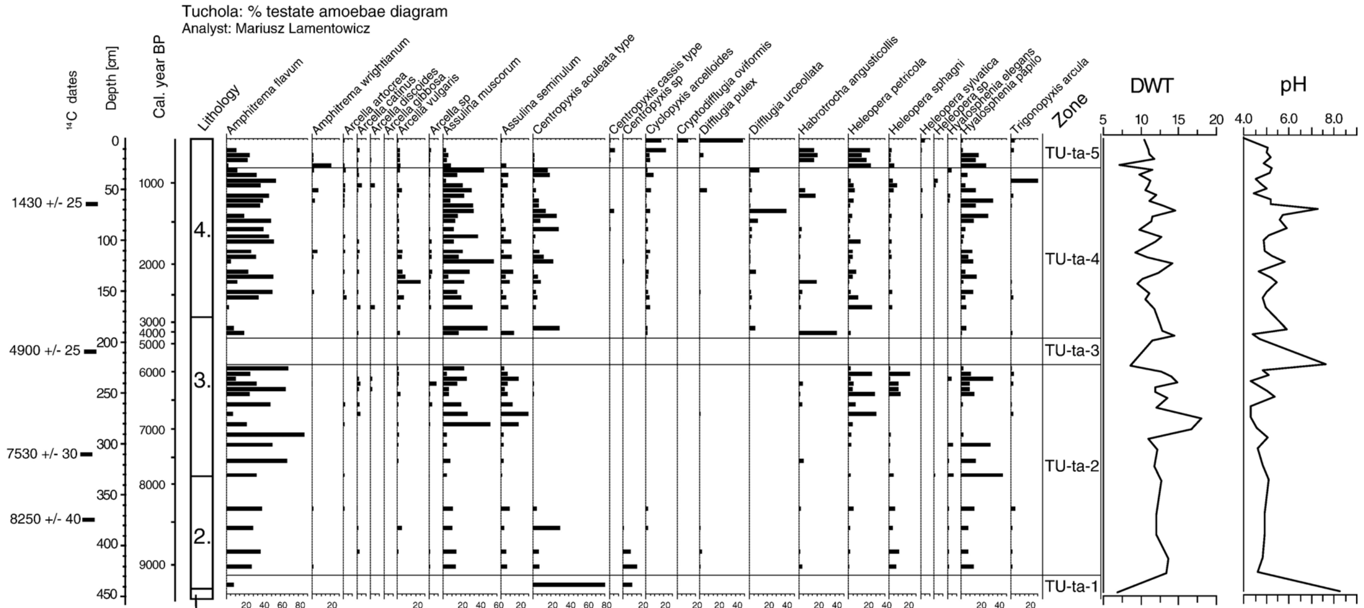


Fig. 8. Percentage diagram of testate amoebae and inferred depth to water table (DWT) in Tuchola kettle-hole mire during the Holocene. Reconstruction for depth to the water table (DWT) was based on WA(tol) model and pH was reconstructed based on WA-PLS model (Fig. 5). Lithology as for Fig. 4.

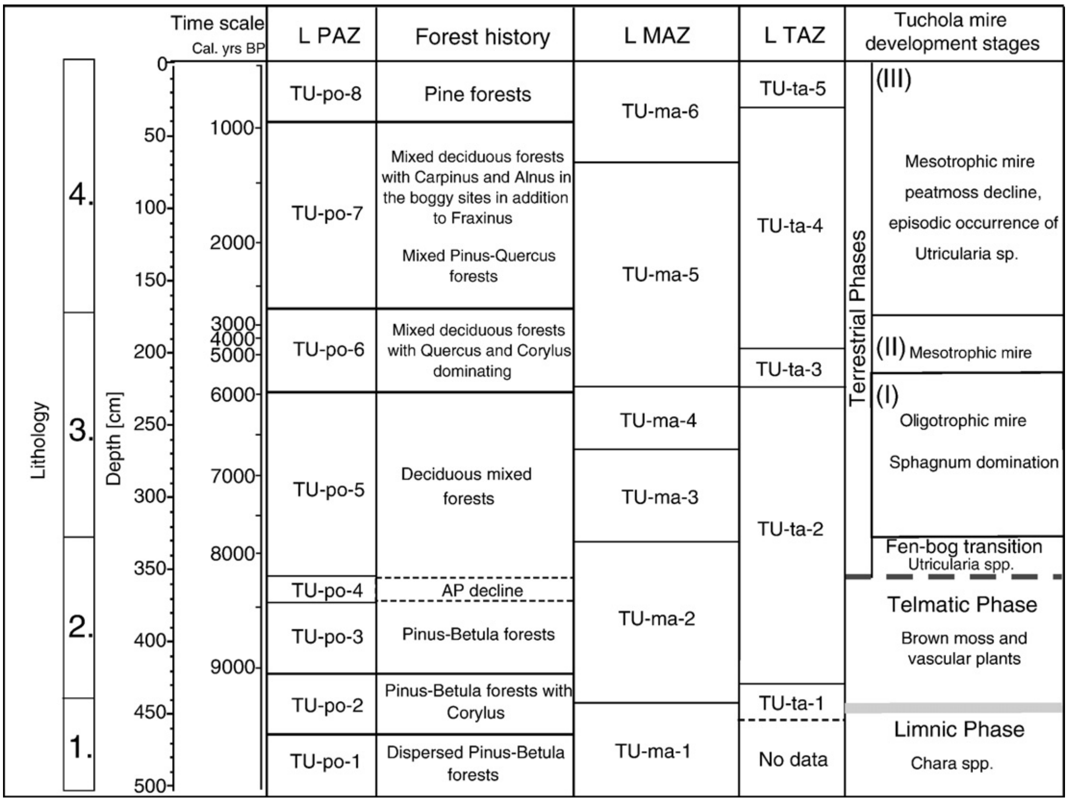


Fig. 9. Developmental stages of Tuchola mire: comparison of pollen, plant macrofossils and testate amoeba data. Lithology as in Fig. 4.

such changes are not obvious from the macrofossils and pollen data. Similar fluctuations occur in the *Sphagnum* curve, but patterns of spore production are not necessarily connected to specific environmental conditions. Once the lake was filled with organic sediments and completely overgrown, the bog surface shifted to a *Sphagnum magellanicum* and Ericaceae (TU-ma-3) — dominated community more characteristic of ombrotrophic conditions (approx. 7800 cal yr BP–330 cm depth).

At ca. 7150 cal yr BP (285 cm depth), testate amoebae indicate a dramatic shift towards drier conditions (top of zone TU-ta-2). The wet indicator *Amphitrema flavum* disappears and species characteristic for drier micro-sites (e.g. *Assulina muscorum* and *Assulina seminulum*) (Tolonen, 1986) become dominant. Accordingly, the inferred water level decreased sharply to close to − 18 cm, its lowest level in the entire history of the mire.

Following this dry event, testate amoebae indicate a sharp transition towards (comparatively) wetter conditions at ca. 6750 cal yr BP (265 cm depth) when *Amphitrema flavum* dominates again. The inferred water table then fluctuates around an intermediate level (slightly below the overall average for the site), before rising between ca. 6120 cal yr and ca. 5800 cal yr BP to reach the second highest level in the terrestrial phase of the mire history. In the same period the dominance of peat mosses from the Acutifolia section (TU-ma-2) (up to ca. 6000 cal yr BP) indicates relatively dry and oligotrophic conditions, followed by a shift to wetter conditions with the rise of *Sphagnum* sect. *Sphagnum*.

There is a distinctive limit at ca. 5800 cal yr BP (220 cm depth) (lower boundary TU-po-6, lower boundary of TU-ma-5, TU-ta-3), between oligotrophic *Sphagnum* peatland and mesotrophic peatmoss-sedge mire, indicating a higher trophic status. The high degree of peat decomposition does not allow the precise identification of peatmosses. Gradually, *Sphagnum* communities were replaced by *Carex* spp. species and *Sphagnum* of the Cuspidata section (e.g. *Sphagnum recurvum*) indicating more mesotrophic conditions. At the same level, testate amoebae also indicate a shift towards drier conditions, and even more markedly towards slightly alkaline conditions (shift from pH <5 to 7.5).

Second terrestrial phase: Ca. 5600 to 2900 cal yr BP (210–170 cm) — The termination of the Atlantic period was a time of considerable changes for the bog as well as for the surrounding vegetation. Tree taxa such as *Carpinus betulus* and *Fagus* appeared in the area, whereas *Ulmus* and *Pinus* declined. This phase corresponds to one pollen assemblage zone: *Quercus–Corylus* forest (TU-po-7); two macrofossil assemblage zones (TU-ma-5 and TU-ma-6) and two testate amoeba assemblage zones (TU-ta-3 and TU-ta-4). Macroscopic charcoal indicates increasingly abundant local fires throughout this phase and peak at ca. 4700 cal yr BP (200 cm depth), suggesting a possible early anthropogenic influence on the landscape.

Possibly in part due to the *Pinus* decrease, *Quercus*, *Corylus*, and *Tilia* increase in relative abundance to reach their Late Holocene maximum between ca. 5600 and 4400 cal yr BP (210 and 180 cm). These events are synchronous with changes in the hydrology, trophy and vegetation of Tuchola bog. Fluctuating water table and a higher trophic status would also account for the very low peat accumulation rates (0.1 mm yr^{-1}) recorded between 5600 and 2940 cal yr BP (Fig. 4). This period is also reflected in the macrofossils and testate amoeba data. The disappearance of testate amoebae at ca. 5600 cal yr BP (210 cm depth) might be due to water and trophy level fluctuations. This interpretation is supported by the simultaneous occurrence in one sample just above this level of three species commonly found in dry micro-sites: *Cryptodifflugia oviformis*, *Difflugia pulex* and *Assulina muscorum* together with a wet indicator *Centropyxis aculeata*. Another minor shift to low and then high pH and a dry period of unknown duration (because of the low temporal resolution in that part of the core) were recorded at ca. 4400 cal yr BP (190 cm). Testate amoeba species characteristic for eutrophic conditions such as *Difflugia urceolata* and *Cyclopyxis arcelloides* appeared above the 5800 cal yr BP limit and were subsequently present in many levels. *Difflugia urceloata* was not included in our transfer function model, but it was described as an indicator of relatively alkaline conditions (pH >6.2) (Ellison, 1995) and eutrophic conditions associated with increasing anthropogenic influences (Schönborn, 1981a), thus providing an independent confirmation to our inferred pH. In a palaeolimnological context, this taxon has been interpreted as an indicator of human impact in the form of eutrophication (Schönborn, 1981a; Scott et al., 2001; Patterson and Kumar, 2002; Patterson et al., 2002). In our case the presence of *D. urceolata* may indicate flooding (possibly seasonal) of the mire surface by mineral-rich water.

Third terrestrial phase: Ca. 2900 cal yr BP to present (170–0 cm) — In this period, peat accumulation increased again, testate amoebae indicating gradually wetter conditions between ca. 2750 and 2400 cal yr BP followed by a short-lived dry event at ca. 2250–2100 cal yr BP. This phase corresponds to two pollen assemblage zones (TU-po-7–TU-po-8), two plant macrofossil assemblage zones (TU-ma-5 and TU-ma-6) and two testate amoeba assemblage zones (TU-ta-4 and TU-ta-5). Distinctive human impact is inferred from the presence of anthropogenic pollen indicators such as *Plantago lanceolata* and *Rumex acetosa*/*acetosella*, although, the abundance of macroscopic charcoal decreases during this period. Conditions then fluctuated with a series of wet (ca. 2000, 1700, 1100, 750, and most clearly at ca. 500 cal yr BP) and dry (the clearest one at ca. 1450 cal yr BP) events. Following a deforestation event inferred from the pine and alder decline at ca. 1800 cal yr BP (90 cm depth), hornbeam (*Carpinus betulus*), which had appeared early in the Subboreal, gradually increased in abundance to culminate at ca. 1300 cal yr BP. At the same time *Ulmus* was gradually decreasing. The local wetland vegetation was composed of sedges (*C. nigra* and *C. lasiocarpa*) and peat mosses (*Sphagnum recurvum*, *Sphagnum cuspidatum*).

The last dry event inferred from testate amoebae took place at ca. 1450 cal yr BP (75 cm). Interestingly, the decrease of pine corresponds to a very sharp increase in pH, *Difflugia urceolata* and *Betula* pollen. The *Carpinus betulus* pollen curve was also rising and reached its absolute maximum shortly after this dry event. *Difflugia urceolata* reached its maximum when pine decreased and pH was high. Following the palaeoecological interpretation of this taxon used for the previous phase, we interpret the presence of *D. urceolata* as an indication of local human impact before the *Carpinus* peak. The timing of this event corresponds to the Wielbark culture in Pomerania (Grzelakowska, 1989a,b; Miotk-Szpiganowicz, 1992; Noryśkiewicz, 2006).

After the dry event at ca. 1450 cal yr BP, the relative abundance of *Amphitrema flavum* and *Assulina muscorum* was more constant than in the past, thus suggesting more stable hydrological conditions. From ca. 1250 cal yr BP (65 cm; ca. 750 AD) onwards, the pollen record indicates a gradual deforestation and increased dominance of herbaceous species. The peatland vegetation was dominated by *Carex* sp. and *Sphagnum magellanicum*, and *Betula* appeared at the coring site. The inferred surface moisture fluctuated but with a clear trend towards wetter conditions that culminated with a marked wet event at ca. 500 cal yr BP (ca. 1350 AD). Further evidence for wetter condition is found in the plant macrofossils with the presence of indicators of shallow water habitats such as *Utricularia* spp. The last stage, described as TU-po-8 in the pollen diagram and TU-ta-5 in the testate amoeba diagram is the terminal phase of the kettle-hole bog development, ending with the surface being overgrown by birch (*Betula pubescens*) and pine (*Pinus sylvestris*), along with the decreasing water table level.

5. Discussion

The position of the water table in peatlands may be governed by different climatic factors in different regions. For example, precipitation is the most important factor in England but temperature becomes more important in Estonia and Sweden (Schoning et al., 2005), however, recently Charman (2007) noticed that summer temperature plays a greater but still subsidiary role in higher latitude, continental settings. Also humification data from the Swiss Jura Mountains (Roos-Barraclough et al., 2004) show that temperature can be a more important factor for peatland development than precipitation in colder areas. At present, it is difficult to determine which of temperature or rainfall is the most important factor governing the hydrology of Tuchola mire. The comparison of palaeohydrological signals from Tuchola with those from other Polish sites can nevertheless provide some clues (Fig. 10). Although the Polish climate differs from that of more oceanic regions of Western Europe, the similarity between the palaeoclimatic record from British raised bogs or Swiss lakes and peatlands and lakes from Northern Poland (Pomerania, including this study) suggests a dominant influence of the North Atlantic circulation. The relative influences of autogenic and allogenic factors during some of the different developmental phases of the mire are discussed hereafter.

5.1. 9300–7150 cal yr BP (425–285 cm)

At the onset of peat accumulation, the conditions were wet, corresponding to the end of the lake phase. This period

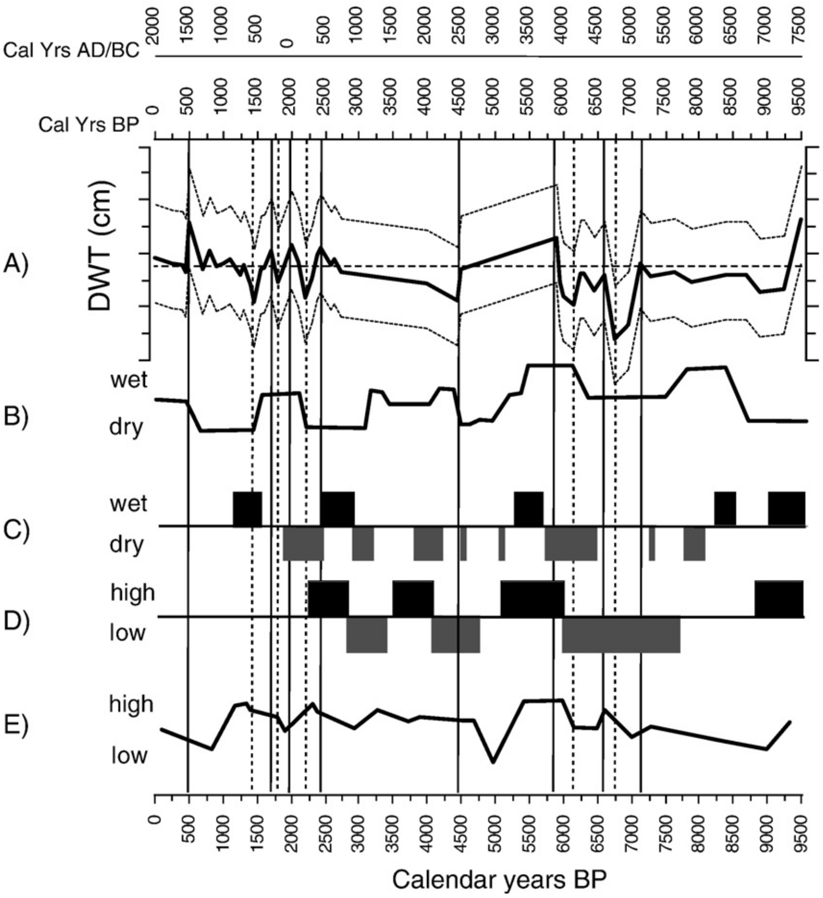


Fig. 10. Comparison of the palaeohydrological record in Tuchola mire with palaeoenvironmental changes recorded in mires and lakes of Poland and Europe and global signals. A) — Water table changes in Tuchola kettle-hole mire inferred from testate amoebae; B) — Water level changes in lakes of Tuchola Pinewoods based on macrofossils and diatoms analyses (Tobolski, 1990); C) — Wet and dry phases recorded in peatlands of Eastern Poland based on peat humification analysis (Żurek and Pazdur, 1999); D) — Water level in lakes of Northern Poland based on pollen and plant macrofossils analysis (Ralska-Jasiewiczowa, 1989); E) — Relative water level changes in Gosciaz lake (Central Poland) based on carbon isotope analysis (Pazdur et al., 1995).

corresponds to the end of a wet phase in lakes and peatlands of Northern, Central and Eastern Poland (Fig. 10) (Ralska-Jasiewiczowa, 1989; Pazdur et al., 1995; Żurek and Pazdur, 2000; Żurek et al., 2002). Low lake levels were recorded during this period in the vicinity of Tuchola (Tobolski, 1990). However, if such conditions also occurred in Tuchola, these may not have been recorded because the mire surface was a floating bog and the position of the water table relative to the surface would have been almost constant. Thus, up to about 7800 cal yr BP, the development of Tuchola was dominated by the autogenous hydroseral succession from lake to bog and climatic signals were not likely to be recorded at the coring site.

5.2. 7150–6800 cal yr BP (285–265 cm)

The driest period in the history of Tuchola mire corresponds to a period of relatively low water table in lakes of Tuchola Pinewoods (Tobolski, 1990), low water table levels in lakes of Northern Poland (Ralska-Jasiewiczowa, 1989), and a period of fluctuating water level in Gościąż lake (Central Poland) (Pazdur et al., 1995). By contrast this event was apparently not recorded in peatlands of Eastern Poland (Żurek and Pazdur, 2000; Żurek et al., 2002). In a broader context, this period corresponds to a period of rapid cooling from the GRIP record (Johnsen et al., 1992), a deeper Iceland Low, weaker Siberian High, a short-lived cold period in Scandinavia recorded as lower tree limit (Karlén and Kuylenstierna, 1996), an extended period of low lake levels in the Jura Mountains (Magny, 2004), and a major shift from wet to dry conditions in bogs of North-West England (Barber et al., 2004).

5.3. 6200–5800 cal yr BP (240–220 cm)

This wet phase corresponds to high water table were recorded in lakes of Northern Poland between 6000 and 5000 cal yr BP (Ralska-Jasiewiczowa, 1989), in Gościąż lake between 6000 and 5200 cal yr BP (Central Poland) (Pazdur et al., 1995). Beyond Poland, the strong wet shift at ca. 5800 cal yr BP matches well with a short wet phase recorded in bogs of Northern England (Barber et al., 2003), and corresponds approximately to a wet shift in mires from Germany and Netherlands recorded at ca. 5450 cal BP (Van Geel, 1978) and to high lake levels in the Jura Mountains between ca. 5650 and 5200 cal yr BP (Magny, 2004).

5.4. Ca. 5600 BP — possible early human impact

According to Ralska-Jasiewiczowa et al. (2003), humans started to have an impact on forests in Poland as early as ca. 6500 BP. This date coincides with the level at which macroscopic charcoal begin to be observed regularly in Tuchola. If we exclude the records from >9000 BP, which most likely indicate natural fires (Fig. 7). Around ca. 5600 cal yr BP, *Carpinus* and *Fagus* appeared, *Ulmus* declined, *Pinus* reached its lowest percentage, and macroscopic charcoal increased in abundance. In addition to this, the first appearance of the grazing indicator *Plantago lanceolata* in the pollen record provides further evidence for human activity. *Pteridium aquilinum* could also be interpreted as indicative of human impact on the forest (Göransson, 1986). A similar situation had previously been recorded for Tuchola Forest area by Miotk-Szpiganowicz (1992 & personal communication). The timing of these changes corresponds approximately to the development of Neolithic settlements, which had started in Northern Central Europe around 6500 BP, and accelerated through the decreasing density of woodlands brought about by a large reduction in elm trees (Ralska-Jasiewiczowa et al., 2003). In agreement with this idea, the oldest, Mesolithic Komorniki culture and Neolithic human activities were described in the river valleys of Tuchola Forest (Grzelakowska, 1989a,b). This early evidence of human impact also agrees with data from the Świętokrzyskie Mountains (380 km south from Tuchola), where charcoal was found together with anthropogenic indicators at ca. 5000 yrs BP (Szczepanek, 1961). Taken together, the three lines of evidence suggest that humans have started to influence the mire hydrology as early as ca. 6000 cal yr BP. However, as this wet period also corresponds to records of wet periods from other sites in Poland and Europe, a more global climatic control (at least in part) is also likely.

5.5. 3000 cal yr BP–present (180–0 cm)

After the hiatus or low accumulation period (ca. 5500–3000 cal yr BP), considerable fluctuations of water table depth and pH were inferred from testate amoebae (Figs. 8 and 10): A dry shift at ca. 2250–2100 BP (130–120 cm), wet shifts at ca. 2750–2400 BP (135–150 cm) and 2000 BP (125 cm) partly coincide with record from Gościąż Lake and lakes and mires of Eastern Poland. The wet phase culminating at ca. 2750–2400 BP corresponds to a wet phase in the Jura lakes (at 2750 BP) (Magny, 2004), in raised bogs in Britain and Ireland at ca. 2750–2350 cal yr BP (Barber et al., 2003) and climatic deterioration in the Netherlands (Van Geel et al., 1996). It may also correspond to wet shifts recorded in mires from Germany and Netherlands at ca. 2850 cal BP (Van Geel, 1978), and in raised bogs of Northern England at 2760 BP (Charman and Hendon, 2000). The short-lived dry event at ca. 2000 cal yr BP corresponds to a period of warmer temperatures in the GRIP oxygen isotope data and a higher Iceland Low (Johnsen et al., 1992; Mayewski et al., 2004) thus suggesting that this event was probably caused by a major climate change. However these fluctuations were less dramatic than the ones inferred for the earlier part of the record and most of these events were recorded in only one sample. Their magnitude and timing therefore needs to be confirmed by further studies.

Two clearer events took place at 1450 cal yr BP (70 cm) (dry and high pH shift) and 500 cal yr BP (22 cm) (wet and low pH shift). The wet–dry shift and pH increase at ca. 1450 cal yr BP, took place at a time when *Carpinus* was increasing sharply shortly before it reached its highest percentage in the pollen record. *Carpinus* grows mainly on fertile brown soils (Faliński and Pawlaczyk, 1993) and was very abundant during the Late Holocene in the morainic areas of the Wielkopolska region (Makohonienko, 2000b). It was therefore not a very significant tree species in the Tuchola outwash-plain area and is not represented in high percentage in the Tuchola pollen record and also in other records from this area (Miotk-Szpiganowicz, 1992, 1993; Noryśkiewicz, 1999; Milecka, 2005). The abundance of *Carpinus* pollen only increased when the *Pinus* curve declined. Given the regional context, we interpret the *Pinus* decline as a probable sign of human activity and then the *Carpinus* peak indicates forest regeneration during the Migration Period, named also Völkerwanderung or Barbarian Invasions, a human migration (Kaczanowski and Kozłowski, 1998; Kokowski, 2005) which took place AD 300–700 in Europe, and that marks the transition from Late Antiquity to the Early Medieval Period. The inferred change in chemistry and hydrology on the mire could have been caused by a change in land use as suggested by very low grazing indicators in the pollen record. The total of arboreal pollen was very high during this period but major changes took place with a sharp increase in *Betula* and a decrease of *Pinus* pollen. The increase of *Betula* parallels the testate amoeba-inferred decreasing water table a possible indication that these trees were spreading over the mire. This event predates the Migration Period and a decline in *Carpinus* can be attributed to anthropogenic causes. An analogous situation was noted in Northern Poland (Milecka, 2005) and Wielkopolska (Western Poland) (Makohonienko, 2000a) between 3000 and 1300 BP. A similar pattern of changes in the surrounding vegetation was also recorded by Obremska (2006) in a kettle-hole mire located on Brda outwash plain 25 km away from our site.

The last major wet shift took place in Tuchola mire at ca. 500 cal yr BP and agrees with wet shifts in mires of North-Western Europe (Mauquoy and Barber, 1999; Mauquoy et al., 2002; Barber et al., 2003), Northern and Western England (Charman and Hendon, 2000), Denmark (Aaby, 1976), and Norway (Nilssen and Vorren, 1991). This period also corresponds to climate cooling of the Little Ice Age reflected as a strong shift to deeper Iceland Low and stronger Siberian High and glacier advances in Sweden (Mayewski et al., 2004). This climatic deterioration might have been reinforced by human impact and forest opening (Bertrand et al., 2002). However, by contrast to these similar patterns, from 1000 yrs BP onwards, the palaeohydrological signal recorded in Tuchola mire was only partially correlated with that of other Polish sites: The level of lakes in Tuchola Pinewoods was low until about 500 cal yr BP and then rose but unlike our record they did not decline after 500 cal yr BP (Tobolski, 1990). No major shifts were recorded in peatlands of Eastern Poland and lakes of Northern Poland (Ralska-Jasiewiczowa, 1989; Żurek and Pazdur, 1999).

6. Conclusions

We analysed the Holocene developmental history of a kettle-hole mire located in Northern Poland using pollen, testate amoebae and plant macrofossils in order to assess the relative influence of autogenic succession, and natural and anthropogenic allogenic influences. Testate amoeba analysis allowed the inference of hydrological and pH changes, some of which neither appeared in the plant macrofossils nor in the pollen record. Comparing our palaeohydrological and pH signals to results from other studies in Poland and beyond, we draw the following general conclusions:

(1) Tuchola mire followed the classical hydrosere development of kettle-hole bogs.
(2) Although kettle-hole bogs are usually not considered as optimal for palaeoclimatic studies, our record provides evidence that such peatlands can indeed be used to reconstruct past climate as well as human activities.
(3) The pattern of water table fluctuation in Tuchola mire over the Holocene is comparable to many other records from Poland and elsewhere in Europe up to ca. 1000 BP. Such correlations generally suggest a common response to the general climate rather than to direct local human influence.
(4) Although possible human impact on Tuchola Pinewoods is suggested as early as 6000 cal yr BP, it became more important only in historical times. Tuchola mire is therefore a good site from which to derive reliable climatic record from peat sediments.

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