



Kettle-hole peatlands as carbon hot spots: Unveiling controls of carbon accumulation rates during the last two millennia

Monika Karpińska-Kołaczek^{a,*}, Piotr Kołaczek^a, Katarzyna Marcisz^a, Mariusz Gałka^b, Katarzyna Kajukało-Drygalska^a, Dmitri Mauquoy^c, Mariusz Lamentowicz^a

^a Climate Change Ecology Research Unit, Adam Mickiewicz University, Poznań, Bogumiła Krygowskiego 10, Poznań 61-680, Poland

^b University of Lodz, Faculty of Biology and Environmental Protection, Department of Biogeography, Palaeoecology and Nature Conservation, 1/3 Banacha Str., Łódź 90-237, Poland

^c School of Geosciences, University of Aberdeen, Aberdeen, United Kingdom

ARTICLE INFO

Keywords:

Carbon accumulation rate
Testate amoebae
Kettle-hole peatland
Climate changes

ABSTRACT

Understanding carbon sequestration patterns in time and space is crucial for models and future projections of carbon uptake. However, their past provides an insight to this understanding, and peatlands play an essential role in the carbon cycle. Hence, peat carbon accumulation rates (PCAR) were reconstructed for the last ± 1500 years in three Polish kettle-hole peatlands (Jaczno, Głęboczek and Pawski Ług bogs). Absolute chronologies, retrieved from the Bayesian age-depth models based on high-resolution ^{14}C AMS dating, provided good time control, whereas the selected time interval spanned a broad spectrum of environmental changes and human activity. An additional variable was connected to climate, as the chosen sites are situated along the west-east gradient of northern Poland.

The aim was to find factors responsible for changes in carbon accumulation, so the results of PCAR were combined with pollen, testate amoebae, plant macrofossil, and charcoal data. The research showed that the investigated peatlands varied regarding local environmental conditions (e.g. water level), peatland development, vegetation changes, and fire activity. Generally, the PCAR values were higher in the *Sphagnum*-dominated sections of the profiles with high shares of mixotrophic testate amoebae unless fire hampered the carbon sequestration. However, our research showed that the changes in carbon uptake resulted from various overlapping factors rather than just one. Nevertheless, high values of PCAR in Jaczno and Pawski Ług (mean 74.6 and 79.64 g C/m²/yr, respectively) point to kettle-hole peatlands being exceptionally efficient in carbon sequestration.

1. Introduction

Increases in the concentrations of greenhouse gases (GHG), among which carbon dioxide (CO₂) plays a key role, are unequivocally caused by human activities. GHG emissions triggered the increasing global warming, manifested by successively warmer decades since 1850 (IPCC, 2021). Any strategies for reducing CO₂ emissions, which is crucial for the long-term overcoming of the climate crisis, rely on knowledge about the conditions of natural carbon sinks and their response to ongoing global warming (cf. Gallego-Sala et al., 2018; Günther et al., 2020). Peatlands play an essential role in the carbon cycle thanks to their capacity to capture CO₂ and long-term storage of organic carbon (Baird et al., 2009; Yu et al., 2009; Charman et al., 2013). Carbon sequestration is possible due to the positive balance between photosynthesis (carbon

uptake) and respiration (carbon losses), as well as anoxic and acidic conditions during peat accumulation, which limits the decomposition of organic matter (Gorham, 1991; Rydin and Jeglum, 2013). Moreover, carbon accumulation is also controlled by plant production and organic matter decomposition related to the hydrology, vegetation, porosity, microbial activity, topography, regional climate, bedrock and potential biota (Yu et al., 2009). The increase in productivity and/or decrease in decomposition positively influence peat accumulation rates (Francez and Vasander, 1995; Kuhry and Vitt, 1996) and therefore CO₂ uptake. Wetlands, covering only 5–8 % of the land surface (Mitsch and Gosselink, 2007), hold between 20 and 30 % of the estimated global soil carbon (~3900 Pg) (Lal, 2008; Lal et al., 2018). In Europe, wetlands are ecosystems characterized by the highest carbon stock, even though nowadays they sequester carbon at a slower rate than forests (Hendriks

* Corresponding author.

E-mail address: monkar2@amu.edu.pl (M. Karpińska-Kołaczek).

<https://doi.org/10.1016/j.catena.2023.107764>

Received 3 August 2023; Received in revised form 12 December 2023; Accepted 17 December 2023

Available online 5 January 2024

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et al., 2020). Globally, peatlands (acidic wetlands) cover 3 % of the Earth's surface and store ca 600 Pg C (Yu et al., 2010) – twice as much carbon as the world's forests (Joosten et al., 2016; Beaulne et al., 2021; Loisel et al., 2021). Crooks et al. (2011) classified tropical and temperate boreal peatlands as ecosystems with the highest potential for long-term carbon stock among global wetlands.

Over extended periods of time and on regional scales, carbon sequestration efficiency depends mainly on climate and human activity (e.g. Charman et al., 2013; Loisel et al., 2014; Pontevedra-Pombal et al., 2019; Wilkinson et al., 2018). However, at local scales, other factors may affect it, thus changing its rate over time. Among them are i) geographical settings and hydrology (Kayranli et al., 2010; Bernal and Mitsch, 2012), ii) vegetation changes reflecting peatland succession (Loisel and Yu, 2013; Mathijssen et al., 2019; Gałka et al., 2022), and iii) fire activity (Turetsky et al., 2015). Together, these factors affect peat formation and thus regulate the peat and carbon accumulation rates, resulting in often locally and globally asynchronous PCAR patterns, as research on past carbon accumulation showed (Bacon et al., 2017; Baird et al., 2009). Nevertheless, disturbances in wetland habitats may convert them into greenhouse gas emitters, often reverting wetland ecosystems' role from carbon sinks into sources (Nahlik and Fennessy, 2016; Hemes et al., 2019; Harenda et al., 2018). To illustrate this process in Europe, wherever peat soils established on drained peatlands were converted into agricultural land, they produced more than 50 % of greenhouse gasses associated with agricultural land use, even though such areas cover ca. 3 % of agricultural land (Barthelmes et al., 2015).

A synthesis by Abdul Malak et al. (2021) revealed a higher mean carbon sequestration rate of mires, bogs and fens occurring in the Atlantic and temperate zone (57 ± 34 g C m²/yr) in comparison with the Boreal zone (34 ± 28 g C m²/yr). Hence, well-preserved peatlands from temperate areas that generally are highly transformed by humans, are (or might be) essential carbon sinks. One such area is Poland, a country located in the transitional zone, under the influence of Atlantic and continental (also boreal) air masses in central Europe (<https://www.weatheronline.co.uk/reports/climate/Poland.htm>). Overall, 5 % (1.6 mln ha) of the area of Poland is covered by peatlands (Kotowski et al., 2017). Based on peat type, 92.4 % of the peatland area consists of fens, and 3.3 % of transitional peatlands, whereas bogs make up 4.3 % of the area (Kotowski et al., 2017). Of the 2377 km² total area of peatlands protected by the Natura 2000 network in Poland, only 13.8 % are in a favourable state (FV; assessment of conservation status according to the Habitats Directive of EU, after Grzybowski and Glińska-Lewczuk, 2020). This seems to be reflected in high CO₂ emissions from drained and exploited peatlands, approximated at 34.6 Mt equiv. CO₂/yr (Kotowski, 2021), whereas the peat carbon stock in Poland was estimated at 2.1 Gt C (estimation based on Jabłońska et al., 2021).

The area of Poland still needs to be explored in terms of carbon accumulation in peatlands. Modern CO₂ emissions from peatlands were measured in manipulative and passive experiments on Linje (Lamentowicz et al., 2016; Samson et al., 2018), Rzecin (Chojnicki et al., 2007; Górecki et al., 2021), and Biebrza (Fortuniak et al., 2021; Jabłońska et al., 2021) peatlands. Long-term carbon accumulation rates have been reconstructed in a few palaeoecological studies in Poland (Fialkiewicz-Kozielec et al., 2014; Milecka et al., 2017); in some, however, the data have not yet been efficiently discussed (Lamentowicz et al., 2019a).

This study aimed to find the factors influencing carbon accumulation patterns in three peatlands: Jaczno, Głęboćzek and Pawski Ług, situated along the gradient of climatic continentality in Poland. All sites possess reliable absolute chronologies and were also previously explored in terms of ecosystem functioning. These datasets include the results of pollen, testate amoebae, plant macrofossil, micro-, and macrocharcoal analyses (Lamentowicz et al., 2019a; Lamentowicz et al., 2020b; Marcisz et al., 2020). Hence, they provide an excellent opportunity to decipher the impact of hydroclimate, plant communities or human impact factors responsible for long-term carbon accumulation. Moreover, different stages of peatland functioning recorded in peat deposits of these sites

may add another dimension to the discussion and answer the question whether the time passed from the onset of *Sphagnum* peat formation matters. To understand the differences in carbon sequestration at the three analyzed peatlands, we reconstructed carbon accumulation rates, in addition to those already published (Lamentowicz et al., 2019a), and compared them with the published results of other proxy analyses (Lamentowicz et al., 2019a; Lamentowicz et al., 2020b; Marcisz et al., 2020). When considering the human impact, an essential factor affecting carbon accumulation (Wilkinson et al., 2018), we selected a similar time interval (last ± 1500 years), as it represents a broad spectrum of human activity and includes population changes, from significant decline during the Migration Period until the demographic explosion after the Industrial Revolution.

2. Study sites

Three *Sphagnum*-dominated peatlands, located in Poland (Central Europe) in the gradient of decreasing continentality, were investigated in this study (Fig. 1). From east to west, the selected mires were Jaczno (Suwałki Lakeland, NE Poland), Głęboćzek (Tuchola Pinewoods, N Poland) and Pawski Ług (Łagów Lakeland, W Poland). They all share a relatively small size, from less than 1 ha (Głęboćzek) to 3.67 ha (Pawski Ług) and are surrounded by mixed forests with *Pinus sylvestris* and *Betula pubescens* (Lamentowicz et al., 2019a). In the east (Jaczno bog), an additional element is *Picea abies* (Marcisz et al., 2020), whereas in the west (Pawski Ług bog) the catchment is overgrown by *Quercus* spp. and *Fagus sylvatica* (Lamentowicz et al., 2020b). The vegetation of the Jaczno bog (easternmost site) is dominated by *Sphagnum angustifolium*. However, *S. medium/divinum* and plants typical of raised bogs (e.g., *Oxycoccus palustris*, *Andromeda polifolia*, *Eriophorum vaginatum*, and *Calluna vulgaris*) also occur (Marcisz et al., 2020). The Głęboćzek bog is a kettle hole covered by *Pinus sylvestris* and *Betula pubescens* forest with fallen trees. Its vegetation is dominated by *Sphagnum* spp., *Carex* spp. and shrubs (Lamentowicz et al., 2019a). The Pawski Ług bog (westernmost site) is an ombrotrophic peatland covered by *Sphagnum fallax*, *S. angustifolium* and other species typical of raised bogs: *Drosera rotundifolia*, *Oxycoccus palustris*, *Eriophorum vaginatum*, and *Ledum palustre*. The climate conditions reflect the continentality gradient, with the Jaczno site exposed to more severe conditions, caused by the influence of continental air masses. Pawski Ług is mostly affected by mild oceanic climate. Mean temperatures of the coldest (January) and warmest month (July) rise from east to west (Lorenc, 2005). Similarly, the length of the growing season increases westwards (Nieróbca et al., 2013) (Table 1).

3. Material and methods

3.1. A state of the art and data selection

Previous studies have focused upon the development of peatlands affected by climate, human and environmental changes but did not account for the influence of these factors on carbon sequestration (Lamentowicz et al., 2019a; Lamentowicz et al., 2020b; Marcisz et al., 2020). In this study, we adapted the previously published data on plant macrofossils and testate amoebae (TA) and used the already calculated age-depth models, peat accumulation rates (AR_{peat}) and TA-inferred depth to the water table (DWT) from Lamentowicz et al., (2019a), Lamentowicz et al. (2020b) and Marcisz et al. (2020) to decipher the drivers of carbon accumulation rates in these three peatlands. Among the TA species, we look specifically at mixotrophic testate amoebae (MTA), as a high abundance of species within this functional group is connected with acidic *Sphagnum*-dominated habitats (Marcisz et al., 2020) and is related to C sequestration in peatlands (Jassey et al., 2015). The CAR data for the Głęboćzek site are published (Lamentowicz et al., 2019a); however, these data have not been widely used for interpretation. The newly obtained data include the results of a new high-

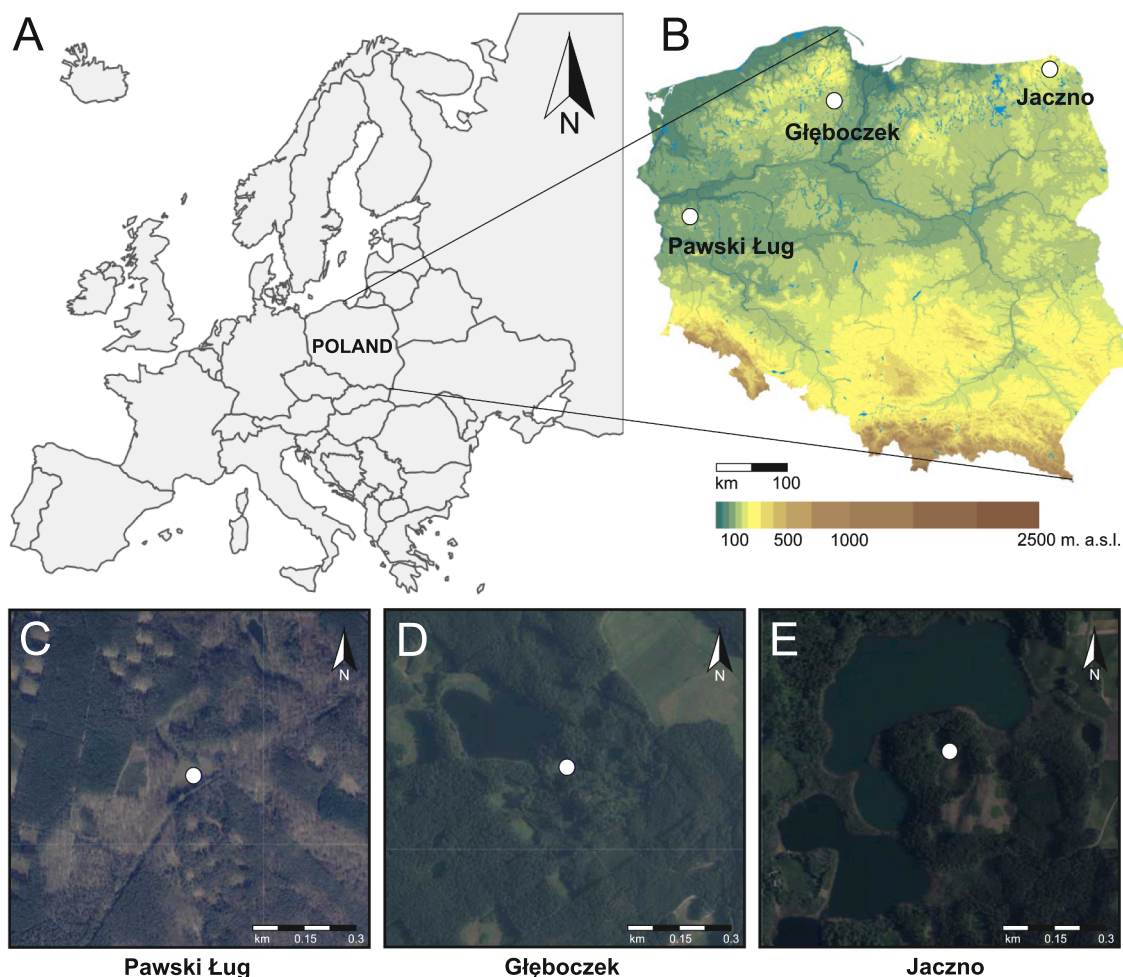


Fig. 1. The locality of the investigated peatlands. A – the map of Europe (source: <https://www.conceptdraw.com/How-To-Guide/picture/g...map-europe-germany/Geo-map-europe-contour-map.png>; access date: 12.06.2023); B – on the map of Poland (source: Wikipedia Commons, name: Physical map of Poland; access date: 11.06.23, author: Netzach); C – on the aerial photographs (white dots represent coring spots)(source: https://mapy.geoportal.gov.pl/imap/Imgp_2.html?gpmap=gp0, scale 1:5000).

resolution TA analysis from the Głęboćzek profile and calculations of CAR for the Pawski Ług and Jaczno profiles. Due to the various periods, as outlined by profiles, different time-resolution of samples and the presence of hiatuses, the following time intervals were selected: (i) 1890–40 cal. BP in Pawski Ług, (ii) 1720–660 cal. BP in Głęboćzek, and (iii) 1350–50 cal. BP in Jaczno. Moreover, the layers spanning the last 100 years (minimum), if present, were also excluded from the study as they are still affected by decomposition processes (comp. Young et al., 2019).

Each profile in this study was dated with the high-resolution ^{14}C Accelerator Mass Spectroscopy (AMS) dates. They were a basis for calculating the Bayesian age-depth models, from which absolute chronologies were derived. The models were taken from original publications (Lamentowicz et al., 2019a; Lamentowicz et al., 2020b; Marcisz et al., 2020) and were calculated by using the OxCal 4.3 software (Bronk Ramsey, 1995), applying the *P_Sequence* function (Bronk Ramsey, 2008; Bronk Ramsey and Lee, 2013) with IntCal13 (Reimer et al., 2013) and Bomb13NH1 (Hua et al., 2013) atmospheric curves used as the calibration datasets. Between the publication of papers by Lamentowicz et al., (2019a), Lamentowicz et al. (2020b) and Marcisz et al. (2020), and the preparation of our article, new ^{14}C calibration datasets were published (Reimer et al., 2020; Hua et al., 2022). So, we then recalculated the former age-depth models (Lamentowicz et al., 2019a; Lamentowicz et al., 2020b; Marcisz et al., 2020) using IntCal20 (Reimer et al., 2020) and Bomb21NH1 (Hua et al., 2022) atmospheric curves

(Supplementary Data 2 and 3). However, the results did not bring substantial changes to the age-depth models. All differences between calendar dates were within 1σ error, so we decided to calculate CAR based on the already published absolute chronologies to enable comparisons between data presented in this and former articles. This article presents the age as the mean (μ) value of modelled age (unit: cal. BP; BP – before present, i.e. 1950 CE), rounded to tens.

3.2. Palaeoecological analyses: New data

3.2.1. Peat carbon accumulation rate

Bulk density (BD) and loss-on-ignition (LOI₅₅₀) were carried out at contiguous 2 cm resolution in all profiles. Samples of known volume (up to 4 cm³) were weighed and dried at 105°C in the oven to calculate BD. Organic matter content was established using the loss-on-ignition method by incinerating samples at 550°C for 12 h and then weighing them again (Heiri et al., 2001).

For each sample, the peat accumulation rate was calculated based on the available absolute chronologies (Lamentowicz et al., 2019a; Lamentowicz et al., 2020b; Marcisz et al., 2020) and multiplied by the ash-free bulk density values and by 50% to obtain carbon accumulation rates (Loisel et al. 2014) at 2-cm contiguous resolution.

3.2.2. *Testate amoebae*

To obtain a reasonable number of samples for multivariate analysis,

Table 1
Site settings.

	Site		
	Pawski Ług	Głęboczek	Jaczo
Coring coordinates, altitude	52°19'33.1"N 15°16'20.4"E 116 m. a.s.l.	53°52'07.5"N 18°12'40.6"E 126 m. a.s.l.	54°16'37.0"N 22°52'34.7"E 178 m. a.s.l.
Area of peatland	3.67 ha	<1 ha	1.3 ha
Arboreal vegetation on peatland	The surface is covered mostly by <i>Sphagnum fallax</i> and <i>S. angustifolium</i> with <i>Drosera rotundifolia</i> , <i>Oxycoccus palustris</i> , <i>Eriophorum vaginatum</i> , and <i>Ledum palustre</i>	The peatland is overgrown by <i>Pinus sylvestris</i> and <i>Betula pubescens</i> forest with <i>Sphagnum</i> spp., <i>Carex</i> spp. and shrubs in the understorey	The vegetation is dominated by <i>Sphagnum angustifolium</i> with the addition of <i>S. medium/divinum</i> , <i>Oxycoccus palustris</i> , <i>Andromeda polifolia</i> , <i>Eriophorum vaginatum</i> , and <i>Calluna vulgaris</i>
The site from which meteorological data were retrieved (https://en.climate-data.org)	Łągów	Piece	Kleszczówek
Total annual precipitation	693 mm	690 mm	742 mm
Annual rainfall amplitude	44 mm	55 mm	55 mm
Mean July temperature	19.8 °C	18.4 °C	18.4 °C
Mean January temperature	-0.2 °C	-1.8 °C	-3.8 °C
Mean annual temperature	9.9 °C	8.4 °C	7.4 °C

the resolution of TA samples in the Głęboczek profile was increased compared with the previous study from 5 to 1 cm (Lamentowicz et al., 2019a). The samples from the top 100 cm, collected at 1-cm intervals (N = 100), were washed on 0.3-mm sieves, following the procedures described by Booth et al. (2010). They were analysed under a biological microscope ZEISS Axio Scope A1 (with Nomarski contrast) at ×400 magnification and counted to obtain a minimum of 150 tests per sample, if possible. Several keys and atlases (e.g., Meisterfeld, 2000a; Meisterfeld, 2000b; Clarke, 2003; Mazei and Tsyganov, 2006; Siemensma, 2019) were used to reach the lowest possible taxonomic level (species identification). Finally, 36 new TA samples and 4 from the previous study by Lamentowicz et al. (2019a); section 100–115 cm, ca. 1560–1720 cal. BP) were used for multivariate analyses.

The quantitative reconstruction of DWT, based on testate amoebae, was conducted with C2 software (Juggins, 2003), using the training set (more than 200 samples) developed for northern Poland by Lamentowicz and Mitchell (2005) and Lamentowicz et al. (2020a). The results of the analyses were used to obtain a quantitative depth-to-water table (DWT) reconstruction for which the WA.inv.tol model was applied (comp. Amesbury et al., 2016).

3.2.3. Data integration and statistical analysis

Relationships between peat carbon accumulation rate (PCAR), the concentration of macrocharcoal (CHAC_{macro}; size fraction 100–500 μm), depth to the water table (DWT) inferred from the testate amoebae, botanical composition of peat (only taxa with calculated percentages) and mixotrophic testate amoebae were explored using Non-metric Multidimensional Scaling (NMDS). CAR, CHAC_{macro} and DWT were treated as environmental variables and drawn as vectors, whereas plants (botanical components of peat) and testate amoebae were added to the

biplots. Bray-Curtis dissimilarity was applied, and the appropriate solution was identified by comparing the final low-stress quantities. Statistically significant ($p < 0.05$) environmental variables were fitted using the *envfit* procedure with 999 permutations. Analyses were performed using a *vegan* package (Oksanen et al., 2017) for R software (R Development Core Team, 2014). The number of samples taken to NMDS varied from 182 (Jaczo), through 47 (Pawski Ług), to 40 (Głęboczek).

To explore the strength of individual correlations between CAR, environmental components (CHAC_{macro} and DWT) and mixotrophic testate amoebae, a Pearson correlation coefficient was applied using PAST software (Hammer et al., 2001). The results of testate amoebae, plant macrofossils, DWT, CAR and CHAR_{macro} were drawn as diagrams using the TILIA Graph program (Grimm, 1991).

4. Results

4.1. Peat accumulation rate

The accumulation rate of peat (AR_{peat}) varied between the sites, with the highest values of AR_{peat} (max. 0.645 cm/yr) and the highest amplitudes recorded in the Pawski Ług profile. The lowest values (min. 0.003 cm/yr, near hiatus zone) were characteristic of the Głęboczek profile, which simultaneously was the most stable in terms of AR_{peat} changes (Fig. 2). The mean AR_{peat} values point to the fastest growth of the Pawski Ług peatland (mean = 0.3162 cm/yr), a bit slower at the Jaczo peatland (mean = 0.2996 cm/yr) and the slowest at the Głęboczek site (mean = 0.0871 cm/yr) (Fig. 2).

4.2. Macrocharcoal

Macrocharcoal records point to low fire activity at the Jaczo and Pawski Ług peatlands. However, the latter was even less prone to fires after reaching the peatland state (ca. 640 cal. BP). The Głęboczek site endured several significant fire episodes (at ca. 1650, 1300, 1060, and 900 cal. BP) (Fig. 3; for more details see Lamentowicz et al., 2019a).

4.3. Peat carbon accumulation rate

The highest peat carbon accumulation rate (PCAR) was recorded for the Pawski Ług profile (maximum = 271.3 g C/m²/yr and mean = 79.64 g C/m²/yr). In contrast, another extreme was revealed by the Głęboczek profile with a minimum equal to 2.63 g C/m²/yr and a mean of 37.29 g C/m²/yr (Fig. 3). Jaczo peatland accumulated carbon with a mean value of 74.6 g C/m²/yr, a maximum reaching 114.58 g C/m²/yr and a minimum of 18.22 g C/m²/yr. These values were similar to Pawski Ług peatland (Figs. 2 and 3).

The long-term changes in carbon accumulation display different patterns. At Pawski Ług bog, the period of the quite stable CAR lasted from ca. 1900 to 640 cal. BP (mean 18.9 g C/m²/yr). Then, together with the change in the plant composition, reflecting the rich fen – bog transition (Fig. 3), the values of CAR visibly rose and recorded a mean of 101.7 g C/m²/yr. A change from rich fen to bog occurred in the Głęboczek profile, but it failed to affect CAR in the same way (Fig. 3). Its mean value for the period before vegetation change (ca. 1700–1500 cal. BP) was 42.5 g C/m²/yr, whereas for the younger section (ca. 1500–660 cal. BP) a mean value of 36.77 g C/m²/yr was recorded. The record from the Jaczo peatland, within the whole analysed time frame (ca. 1350–50 cal. BP), revealed no such significant changes in plant composition (Fig. 3). However, carbon accumulation varied there in time. At the beginning (ca. 1350–1170 cal. BP), the values were low (mean 20.8 g C/m²/yr), then rose slightly to the mean of 45.5 g C/m²/yr, to finally achieve the highest mean of 123.3 g C/m²/yr during the period between ca. 1050–930 cal. BP. Afterwards, the CAR curve decreased but fluctuated until ca. 750 cal. BP when it started to rise again. The period of more effective carbon accumulation (mean 83.6 g C/m²/yr) lasted until ca. 520 cal. BP and was followed by a sharp fall in

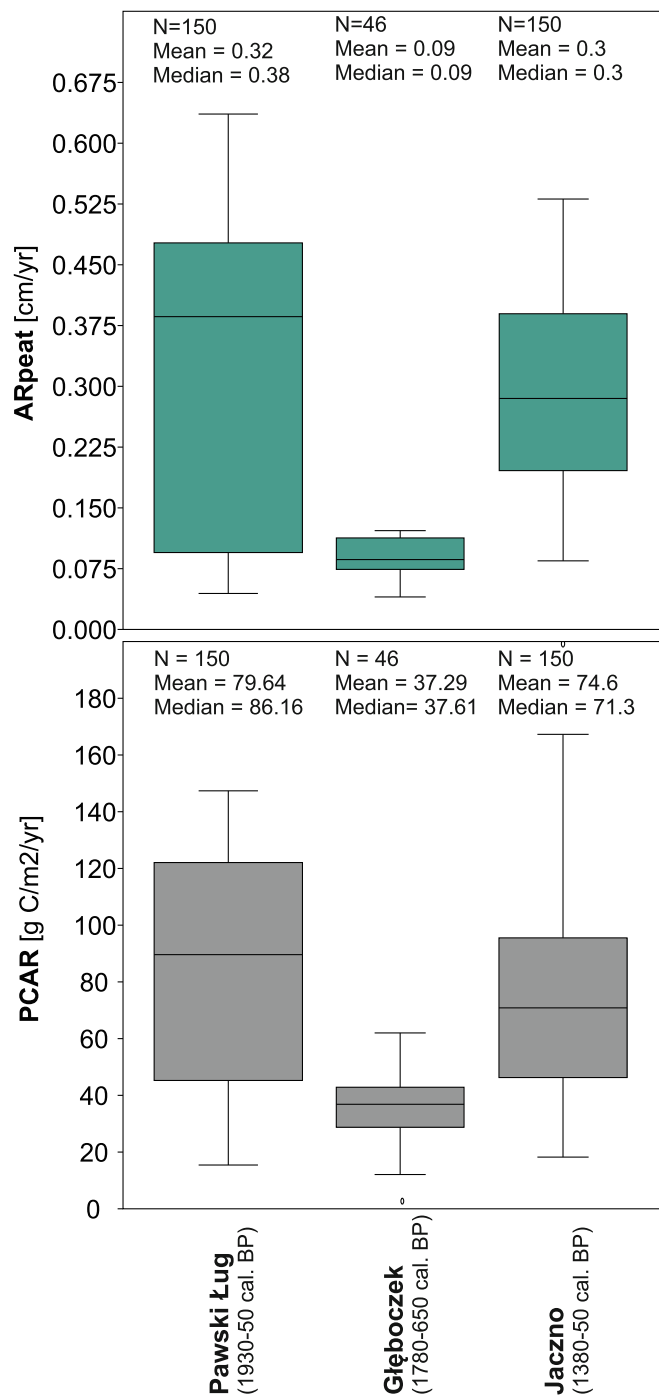


Fig. 2. Boxplots showing peat accumulation rates (AR_{peat}) and peat carbon accumulation rate (PCAR) in three studied sites.

CAR to the level of 33 g C/m²/yr. Up to the surface (ca. 50 cal. BP), an increase in CAR values is observed (the maximum 114.58 g C/m²/yr).

4.4. *Testate amoebae*

New data from the Głębozec profile revealed a low frequency of tests in most samples. In 32 out of 100 samples, their abundance failed to reach even 100 tests. In contrast to previous TA analysis from the Głębozec profile, many more small taxa were detected in the topmost 100 cm layer, probably an effect of a better-quality microscope (Nomarski contrast) (cf. Lamentowicz et al., 2019a, Supplementary data). The most frequent taxa were *Cryptodiffugia oviformis* (0–96 %), *Galeripora*

discoides (0–24.3 %), *Galeripora catinus* (0–21.9 %), *Assulina muscorum* (0–43.6 %), *Centropyxis aculeata* (0–66.7 %), *Phryganella acropodia* (0–38.9 %), and *Trigonopyxis arcuata* (0–53 %) (Supplementary Data 1). In general, *C. oviformis* dominated in layers younger than ca. 1130 cal. BP. MTA, such as *Archerella flavum*, *Hyalosphenia papilio* and *Heleopera sphagni*, were not numerous and occurred in layers older than 1030 cal. BP.

The Głębozec site revealed the driest conditions among the three analysed sites. DWT ranged between 5.8 and 34.6 cm (mean 22.6 cm), with an uncertainty of 7.8–8.9 cm. DWT values distinctly increased from ca. 1340 cal. BP and almost did not fall below 20 cm from ca. 1130 cal. BP. This probably was a bias related to the high abundance of *C. oviformis*.

All profiles revealed different patterns of forest and peatland changes, which were shaped by different climatic conditions and patterns of human impact (Fig. 3). In the Jaczno profile, except for several episodes during which *Eriophorum vaginatum* became the dominant component of peat (at ca. 1000 and 1050 cal. BP) and the water level was higher (low DWT; ca. 500–250 cal. BP), both vegetation and water level records were relatively stable (Fig. 3). This stability is also visible in the record of MTA (Fig. 3: *A. flavum*, *H. papilio* and *H. sphagni*; after Marcisz et al., 2020), whose total shares are similar in time but different for particular taxa. In the case of the Pawski Ług profile, the shares of MTA were similar before and after the vegetation shift (herbs into *Sphagnum* mosses; ca. 640 cal. BP), but they were more fluctuating in the *Sphagnum* zone (Fig. 3). In the Głębozec profile, the presence of MTA was very limited but the optimum of their occurrence took place during the period after the peatland vegetation shift when monocots were replaced by *Sphagnum* mosses (ca. 1500–1150 cal. BP; Fig. 3). The Jaczno site was moderately wet (mean DWT = 11.3 cm with generally stable values). Distinct DWT fluctuations occurred after ca. 430 cal. BP. The Pawski Ług bog was wet (mean DWT was ca. 2.1 cm) ca. 1890–640 cal. BP and moderately wet ca. 640–40 cal. BP (mean DWT was ca. 10.7 cm; Fig. 3).

4.5. Statistical analyses

Non-metric Multidimensional Scaling (NMDS) revealed the lack of common patterns in all profiles (Fig. 4) and the highest significance levels of PCAR in the Pawski Ług and Jaczno profiles ($p = 0.001$). All environmental variables in the Pawski Ług profile recorded significant values ($p \leq 0.002$). On the other hand, the Głębozec profile displayed a low significance level, with the most significant values for DWT ($p = 0.003$), but for PCAR and CHAC_{macro} they were not significant. High significance levels were also identified in the Jaczno profile, in which PCAR and DWT had $p < 0.05$. Generally, CHAC_{macro} had the weakest significance, except for the Pawski Ług profile ($p < 0.01$). NMDS showed a correlation between PCAR and DWT in the Pawski Ług profile, whereas, in other profiles, PCAR seems to have no significant relationship with other environmental variables. Fig. 5.

The Pawski Ług profile revealed a distinct division of Pearson's correlation coefficient values. Positive statistically significant correlations of PCAR ($p < 0.05$) were identified to DWT ($r = 0.61$), *Heleopera petricola* ($r = 0.43$), *Sphagnum angustifolium* ($r = 0.41$), *S. medium/divinum* (previously *S. magellanicum* s.l.) ($r = 0.46$), Ericaceae ($r = 0.65$), whereas negative ones for *Sphagnum palustre* ($r = -0.51$), *Sphagnum* Sect. *Acutifolia* ($r = -0.51$), unidentified herbs ($r = -0.75$), *Nymphaea alba* ($r = -0.76$) and CHAC_{macro} ($r = -0.33$). The NMDS biplot confirmed this result, showing the communities characteristic of the terrestrialising lake and/or early stage of *Sphagnum* peatland development.

In the Jaczno profile, PCAR was positively correlated with significance $p < 0.05$ only for *Sphagnum angustifolium* ($r = 0.62$). *A. flavum*, *H. papilio*, DWT, *S. medium/divinum* and *Sphagnum fuscum* revealed negative correlations (with $p < 0.05$) to PCAR. On the contrary, NMDS showed the opposite pattern of relations between *S. angustifolium* and PCAR, whereas, among other peat-forming taxa, the response of

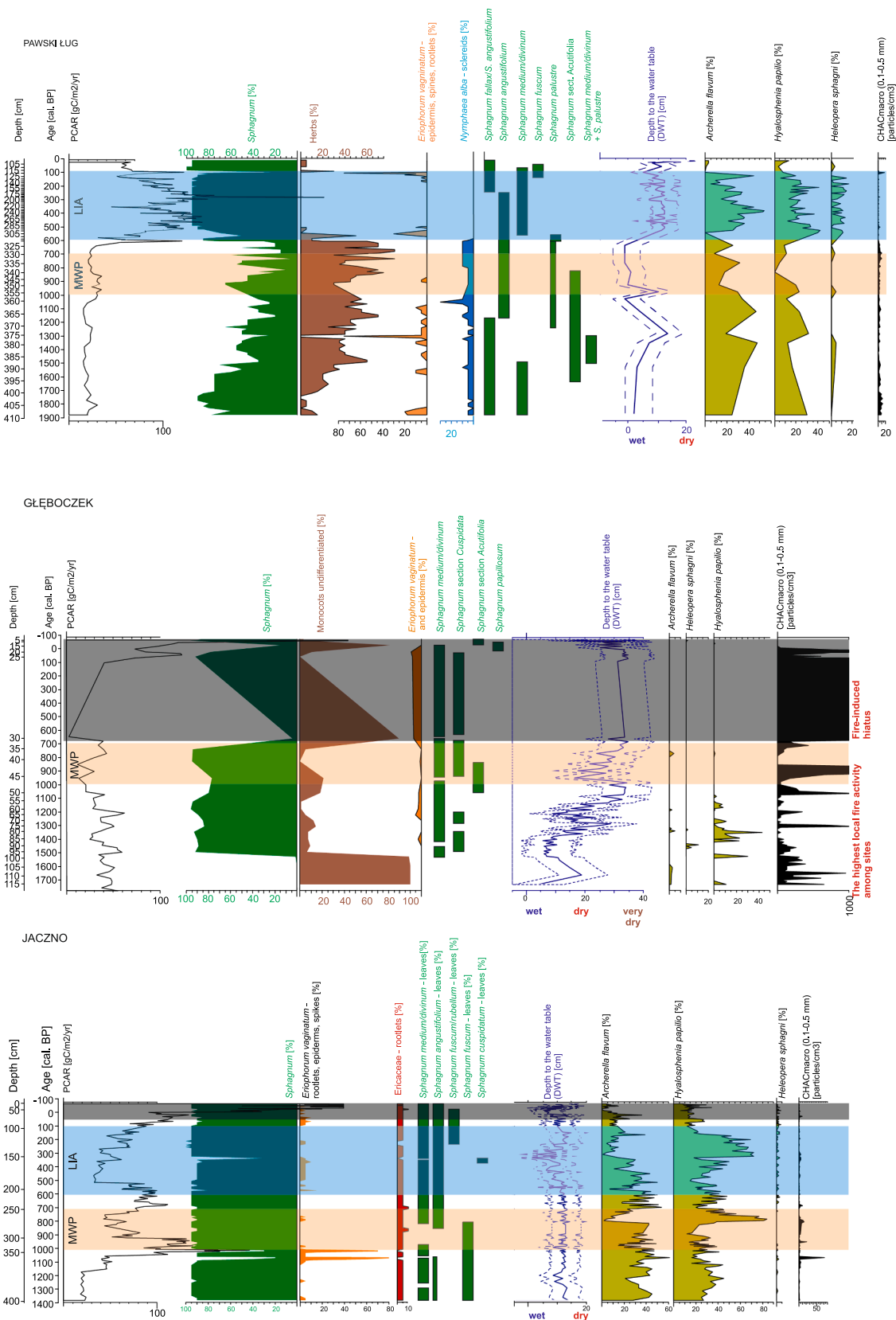


Fig. 3. Peat carbon accumulation rates (PCAR) against peatlands' development, water level changes, fire activity and presence of mixotrophic testate amoebae (Lamentowicz et al., 2019a; Lamentowicz et al., 2020b; Marcisz et al., 2020). The light orange belt reflects the Medieval Warm Period, whereas the light blue one is the Little Ice Age. The grey area represents part of the diagram excluded from the interpretation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

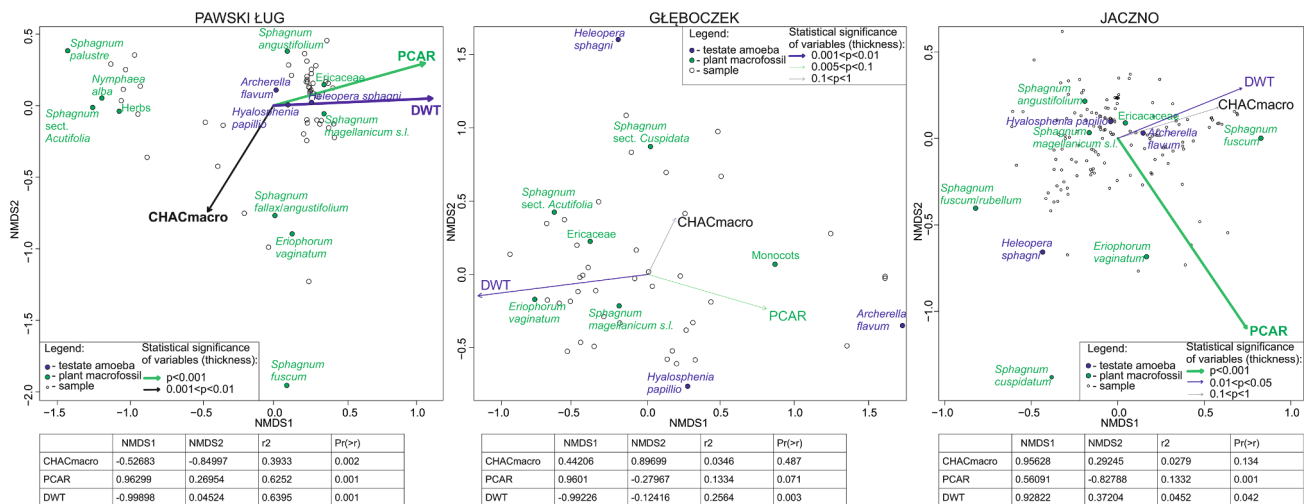


Fig. 4. NMDS scatter plots showing the correspondence between peat-forming taxa (reconstructed from plant macrofossils) and TA (Lamentowicz et al., 2019a; Lamentowicz et al., 2020b; Marcisz et al., 2020). Note that the thickness of lines expressing vectors reflects the p-values. Abbreviations: PCAR – peat carbon accumulation rate, CHACmacro – macrocharcoal accumulation rate, DWT – depth to the water table.

E. vaginatum is consistent with PCAR.

The Głęboczek profile displayed a negative correlation ($p < 0.05$) between PCAR and DWT ($r = -0.43$), as well as Ericaceae ($r = -0.41$), which is an opposite pattern in comparison with the Pawski Ług profile. Similarly, to this profile, PCAR revealed a negative correlation to *Sphagnum Sect. Acutifolia* ($r = -0.5$). NMDS from the Głęboczek, despite its low consistency, rather confirmed these negative correlations.

5. Discussion

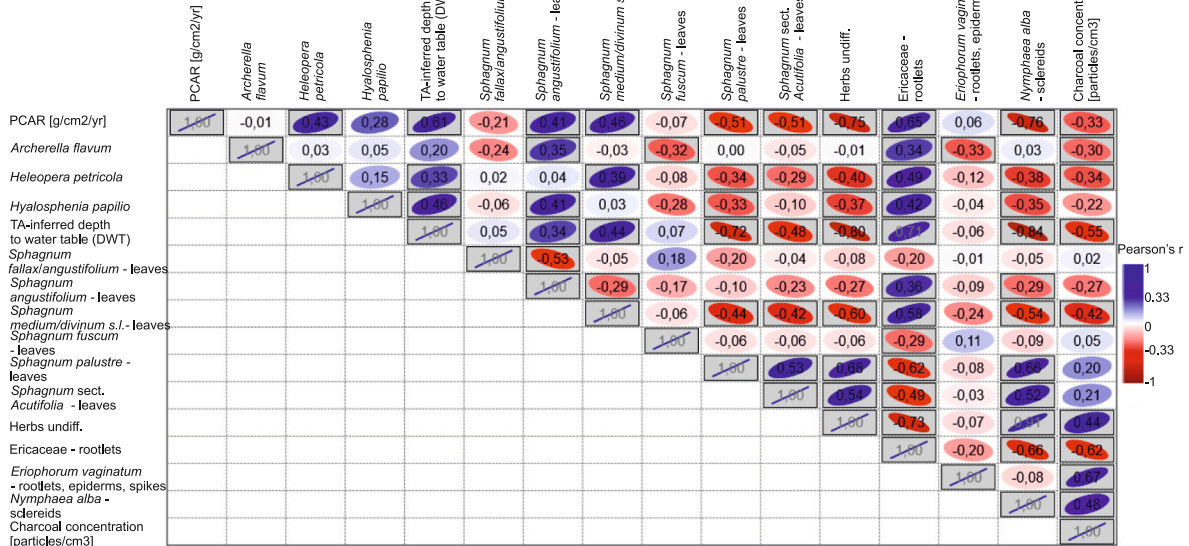
The investigated peatlands, in the selected time frames, vary regarding local environmental conditions, climate, patterns of peatland development, vegetation changes and fire activity. Together, they represent the whole spectrum of scenarios leading to the observed differences in the carbon accumulation rates.

The Głęboczek peatland is an example of a mire with highly unstable environmental conditions, affected by frequent fires. After a periodically inundated fen stage covered with vascular vegetation, *Sphagnum* encroached and simultaneously the water level dropped (Fig. 3; Lamentowicz et al., 2019a). The vegetation change did not influence the PCAR significantly, as it still oscillated around a value of $40 \text{ g C m}^{-2}\text{yr}$, which is close to the mean value for boreal peatlands (Abdul Malak et al., 2021) and even higher than the value proposed by Loisel et al. (2014) for typical lowland peatlands ($22.9 \pm 2.0 \text{ g C m}^{-2}\text{yr}$) or Vasander and Kettunen (2006; $17\text{--}24 \text{ g C m}^{-2}\text{yr}$ throughout the Holocene). However, Polish peatlands are characterized by relatively high carbon accumulation rates, e.g., Rzecin peatland sequestered carbon with a mean of 171 and 191 $\text{g C m}^{-2}\text{yr}$ (R1 and R2 core, respectively; Milecka et al., 2017) and so this value is below the ability of local peatlands. This is probably connected to the frequent fires that hampered peat growth. Nevertheless, a more distinct decrease in PCAR occurred later, ca. 1400 cal. BP, simultaneously with the significant drop in the water level (Fig. 3), a probable result of local forest regeneration that took place from 1500 to 1000 cal. BP (Lamentowicz et al. 2019a). Generally, the afforestation leads to higher evapotranspiration values that result in a drop of the groundwater table (Andréassian, 2004), and the prolonged drought enhances decomposition processes (Stirling et al., 2020) and results in low PCAR, as observed in the Głęboczek profile. With another lowering of the water table at ca. 1150 cal. BP, PCAR decreased further, which coincided with the decrease of mixotrophic testate amoebae that are important for carbon fixation (Jassey et al., 2015). Their absence results from unfavourable water and light conditions, as these species are typical of wetter habitats (Lamentowicz and Mitchell, 2005), and

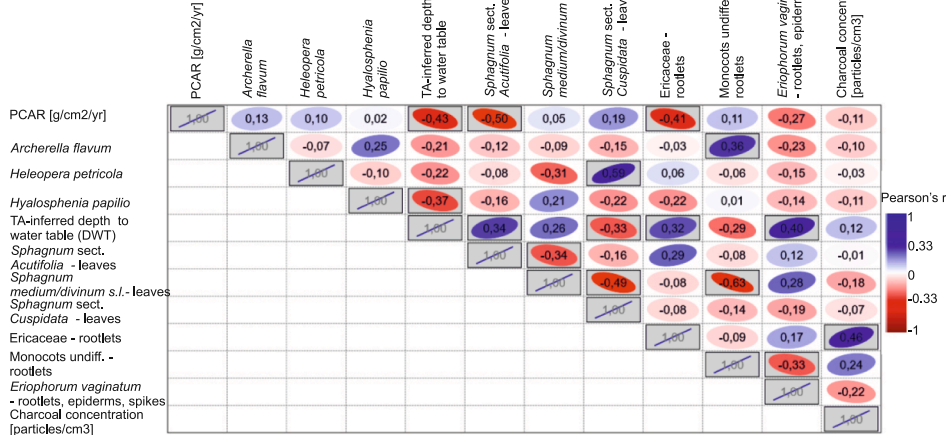
probably the encroachment of trees/shrubs on the dry peatland surface (comp. Lamentowicz et al., 2019a) hampered the photosynthesis processes. At the time of the Medieval Warm Period (MWA), the PCAR oscillated around a value of $20 \text{ g C m}^{-2}\text{yr}$, which is still higher than that recorded in the drained Bagno Bruch fen ($<10 \text{ g C m}^{-2}\text{yr}$; Fiałkiewicz-Kozieł et al., 2014). However, all these changes points to the water table and fires as important determinants controlling PCAR in this period. However, the higher than nowadays temperatures in the second part of the MWP (Przybylak et al., 2020) seem to overcome the negative impact of the low water table and to a small extent facilitated peat growth and carbon accumulation (Fig. 3). The lowest PCAR value ($12 \text{ g C m}^{-2}\text{yr}$) was recorded at ca. 850 cal. BP, after the severe fire on the dehydrated peatland (Fig. 3). Unfortunately, without multiple cores, we cannot compare a spatial aspect of carbon accumulation, which might have varied between different parts of the Głęboczek peatland (comp. Korhola et al., 1995; van Bellen et al., 2011). However, due to the small size of the site (ca. 1 ha), we assume that the core is representative and responded to local environmental changes.

On the opposite side is the Jaczno peatland with stable hydrological conditions for almost 900 years (from 1400 to 500 cal. BP, Fig. 3) and generally high water levels. The lack of trees on most of the peatland surface (comp. Marcisz et al., 2020), provided good light availability (Payne et al., 2016; Creevy et al., 2018), reflected in the high percentage of MTA. This should have contributed to high PCAR values because of their importance for carbon fixation (Jassey et al., 2015), but this was not a decisive factor. Initially, the DWT oscillated around 12.5 cm (mean 11.9 cm), which is close to the value of 11.7 cm, established as a threshold for vegetation turnover (Lamentowicz et al., 2019b). However, no major changes in the vegetation were observed until ca. 800 cal. BP when *Sphagnum medium/divinum* became the dominant peat-forming taxa (Fig. 3; Marcisz et al., 2020). Despite good hydrological conditions and high shares of MTA, the PCAR values were low and characteristic of drier peatlands (mean $20 \text{ g C m}^{-2}\text{yr}$) from 1400 to 1150 cal. BP. Then they abruptly rose to almost $50 \text{ g C m}^{-2}\text{yr}$, and it seems that the fire episode ca. 1050 cal. BP triggered peat growth and, consequently, another sudden increase in the CAR (up to the maximum value in the profile). Even though the thermal conditions were good until 700 cal. BP (MWP), which should stimulate carbon sequestration (comp. Gallego-Sala et al., 2018), the CAR values decreased at ca. 900 cal. BP. This change was not connected to the water level, human impact (Marcisz et al., 2020) or major vegetation shift, which took place later (800 cal. BP). Only a change of dominating *Sphagnum* taxa happened then (Fig. 3) but it should not have affected carbon accumulation potential as

PAWSKI ŁUG



GŁĘBOCZEK



JACZNO

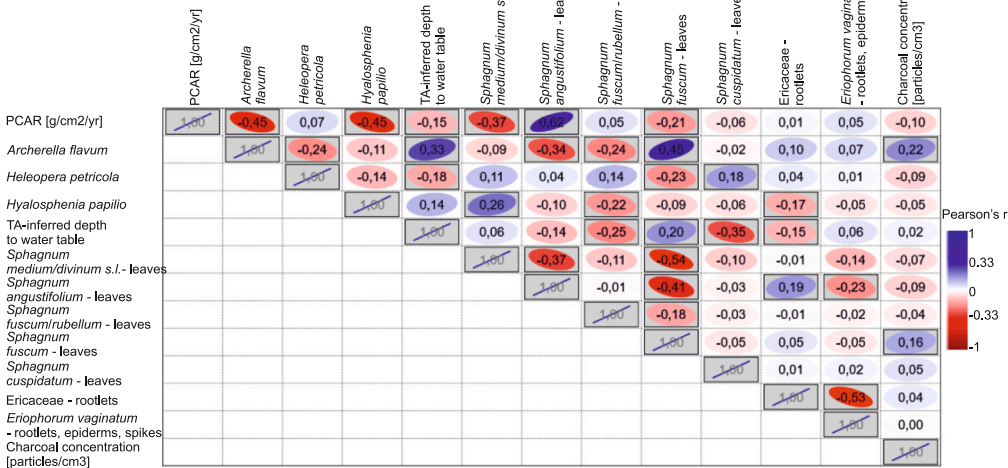


Fig. 5. Pearson's correlation plots showing the correspondence between peat carbon accumulation rate (PCAR), mixotrophic testate amoebae and peat-forming species (Lamentowicz et al., 2019a; Lamentowicz et al., 2020b; Marcisz et al., 2020).

Broek et al. (2017) claim. However, there is research suggesting that warming could lead to weaker C accumulation due to enhanced aerobic decay (Qiu et al., 2020), and this seems a plausible explanation here. From ca. 500 cal. BP fluctuations in the water level possibly affected the PCAR by slowing peat growth. Its values decreased to a minimum of 35 g C m²/yr then, but, together with the stabilisation of DWT at ca. 220 cal. BP, the PCAR values increased again, even though it was the Little Ice Age (LIA) period. In the period of water level fluctuations, when the water table was higher, no significant changes in the vegetation were observed (Marcisz et al., 2020).

The Pawski Ług bog, being the westernmost site influenced by Atlantic air masses, should be the most productive peatland (comp. Abdul Malak et al., 2021). Indeed, this site recorded the maximum values of carbon accumulated in time – 271.3 g C/m²/yr (ca. 300 cal. BP). However, its mean value (79.64 g C/m²/yr) is similar to that recorded in the Jaczno peatland (NE Poland). This is connected to the history of the peatland, which at the beginning was a slowly growing fen/floating mat sequestering carbon with a mean of 18.9 g C/m²/yr. The macrocharcoal record points to small local fires, which, together with the insignificant human impact until 600 cal. BP, fail to be held responsible for such slow growth. The reason might be the presence of a shallow water body with nymphaeids and green algae that indicate eutrophic conditions (Fig. 3, Lamentowicz et al. 2020b). Probable high levels of P and N in the water might have negatively affected the growth of peat mat/fen (Harpenslager et al., 2015; Koks et al., 2019), and thus its potential for carbon accumulation. From ca. 1000 cal BP, the increasing temperature connected to the MWP caused possibly an increase in the PCAR but then carbon accumulation slowed down. A similar pattern was recorded in the Jaczno profile and might be connected with peat desiccation due to rising temperatures and droughts (Qiu et al., 2020). The peat accumulation accelerated with the change into ombrotrophy, a possible effect of human-induced deforestation (Lamentowicz et al., 2020b). During the LIA, i.e. the time of probably colder conditions, the mean values (2.6 mm/yr) were among the highest observed in Poland (comp. Dury Lakes, Pawlyta and Lamentowicz, 2010; Mukrza, Lamentowicz and Obremaska, 2010; Mechacz Wielki, Gałka et al., 2017). This might be connected with the early stage of peatland development that can support faster C accumulation (Charman et al., 2015).

6. Conclusions

Our data provide a new look at the diversity of carbon accumulation patterns in three peatlands located along a W-E gradient. We incorporated many proxies to unveil the drivers of change in carbon accumulation, and we found very complex patterns related to the local vegetation, local environment and fires. However, we did not find clear significant correlations with environmental variables that were assumed to be essential for the peat accumulation rates in all sites. Nevertheless, the PCAR values were generally higher in *Sphagnum* peats with high relative abundance of mixotrophic testate amoebae, not affected by fire. This situation is unsurprising, considering carbon fixation's multivariate context in peatlands, which consequently leads to often globally and locally asynchronous PCAR patterns. Considering the mean Holocene value of 22.9±2.0 g C/m²/yr (Loisel et al., 2014), our data shows nearly three times a higher PCAR value (ca 64C/m²/yr) in the Jaczno and Pawski Ług profiles. It can be explained by the exceptional local conditions of these kettle-hole peatlands, possessing generally stable and high water tables during the last 1500 years. This also shows the great potential of small peatlands (<10 ha) as carbon accumulation hot spots, which have, so far, been overlooked. Such kettle hole peatlands, being still in good condition, possess thick peat deposits (Jasnowska and Jasnowski, 1981; Succow and Joosten, 2001; Succow and Jeschke, 1990) dispersed across the European landscape and might be important carbon hot spots and carbon sinks that need further (monitoring and experimental) studies.

CRedit authorship contribution statement

Monika Karpińska-Kołaczek: Writing - original draft, Writing - review and editing, Visualization. **Piotr Kołaczek:** Visualization, Writing – original draft, Writing – review & editing. **Katarzyna Marcisz:** Data curation, Writing – review & editing, Fieldwork. **Mariusz Gałka:** Resources, Writing – review & editing. **Katarzyna Kajukalo-Drygalska:** Data curation. **Dmitri Mauquoy:** Data curation, Writing – review & editing. **Mariusz Lamentowicz:** Study design, Fieldwork, Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We would like to thank the anonymous reviewers for their comments that helped us to improve the manuscript. The research was funded by the National Science Centre (Poland), grant 2015/17/B/ST10/01656.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.catena.2023.107764>.

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