Drivers of peat accumulation rate in a raised bog: impact of drainage, climate, and local vegetation composition

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SUMMARY

We used variation partitioning to assess the relative importance of drainage, climate and local vegetation composition for the development of a raised bog. As a case study we selected Teiči (Teici) Bog in Latvia (north-east Europe). Explanatory variables together explained 74 % of the variation in peat accumulation and only the residue of 26 % remained unexplained. Our study showed that the local vegetation composition and dominant *Sphagnum* species significantly influence peat accumulation rates. The results of linear models revealed that, under natural conditions, minor drainage and even strong drainage of the peat is associated with a positive growth balance of the system. However, drainage systems can have a measurable impact on peatland ecosystems situated farther away. Our study demonstrates that the average peat accumulation rate in Teici Bog over the last 150 years was 3.5 mm *per* year. Although the peat accumulation rate has been affected by drainage over the last half-century, it is still 2.8 mm *per* year. There was no strong correlation with the historical climate record, suggesting that the bog area has buffered the influence of climate change over the last 150 years.

KEY WORDS: chronology, macrofossils, testate amoebae, variation partitioning, water level reconstruction

INTRODUCTION

Ombrotrophic bogs are unique ecosystems with specific flora and fauna, whose biodiversity should be preserved for future generations. Conservation and restoration management of ombrotrophic bogs has been proven to be important for maintaining ecosystem services at local and global scales (CBD 2010, IPCC 2014, Hudson *et al*. 2015). Peatlands also provide important raw material—peat is the main constituent of horticultural growing media or substrates in the EU. The lives of most cultivated vegetables, fruits, herbs, flowers and trees begin in peat.

In comparison with ecological studies that usually focus on timescales extending from weeks to decades, palaeoecological records provide long-term assessments of peatland succession and past biodiversity (Willis & Birks 2006, Reitalu *et al.* 2014). The dynamics of palaeoecological proxies in response to complex environmental changes can give insights into ecosystem processes and services over time and provide background information for conservation and management activities (Jeffers *et al*. 2015, Perring *et al*. 2015).

The development of ombrotrophic peat bogs is influenced by many factors such as local vegetation (van Breemen 1995, Karofeld 1998, Laine *et al*. 2015), oxygen exposure time of the surface peat layer (acrotelm) (Philben *et al*. 2014), hydrology (Lamentowicz *et al*. 2015), climate, and human impact (Lamentowicz *et al*. 2008, Feurdean *et al*. 2015). These factors influence peat and carbon accumulation rates, which are keystone issues for the ongoing climate change in the Northern Hemisphere (Korhola *et al*. 2010, Charman *et al*. 2013, Loisel & Yu 2013, van der Linden *et al*. 2014, Charman *et al*. 2015, Ineson *et al*. 2015, Lamentowicz *et al*. 2016).

In a longer time perspective, it has been demonstrated that territories located in the transitional area between the oceanic and continental climate regions of the temperate zone have been sensitive to climatic variability throughout the last postglacial period (Sillasoo *et al*. 2007, Heikkilä & Seppä 2010, Muschitiello *et al*. 2013). Climate-driven changes underlie the establishment of peat bogs and control the speed of peat growth in both vertical and lateral directions (Ilomets *et al*. 1984, Korhola *et al*. 2010, Kalnina *et al*. 2015).

Sphagnum mosses are amongst the principal formers of ombrotrophic peat (Clymo 1970). *Sphagnum*-dominated ombrotrophic bogs of the temperate zone are usually preceded by minerotrophic fens that host mainly vascular plants and brown mosses (Gałka *et al*. 2013, 2015). The vegetation becomes isolated from any supply of groundwater and is fed exclusively by precipitation (Hughes 2000, Malmer 2014). Therefore, any artificial drainage in or around a bog reduces *Sphagnum* peat biomass accumulation and leads to the loss of many of the ecosystem services that ombrotrophic bogs provide, such as climate regulation, carbon sequestration and storage, water regulation, habitats for wildlife, and recreation for people (Bonn *et al*. 2014).

The majority of bogs in Europe were partially or completely drained for agriculture, forestry and fuel throughout the 19^{th} and early 20^{th} centuries and even earlier (de Zeeuw 1978, Kearns 1978). The development of peat extraction technologies included the installation of massive drainage networks in the vicinities of bogs. In the Baltic countries, the drainage of peatlands was relatively extensive from the 1950s to the 1980s (Lode *et al*. 2010, Paal *et al*. 2016). Consequently, almost all raised bogs in Estonia, Latvia and Lithuania have been influenced by drainage works to a lesser or greater degree and, today, it is unlikely that a truly pristine bog can be found. However, according to Latvian Ministry of Agriculture data, drainage systems in Latvia are in bad condition nowadays because of poor management; e.g. the drainage systems in half of the country's forest land (peatlands in Latvia are classified as forest land) do not function at all.

Although Teiči (referred to hereafter as Teici)—the biggest peat bog complex in Latvia—was subject to minor drainage during the 1920s–1930s and to major drainage in the 1960s–1980s, it became a nature reserve in 1982 and thus escaped the planned peat extraction (Namatēva 2012). The first dams, intended to restore the original water level, had already been installed in 1999 (Bergmanis *et al*. 2002, Namatēva 2011). Thus, Teici Bog serves as a valuable study site where the nature of peat accumulation under natural and anthropic disturbances can be evaluated.

The aim of this paper is to use Teici Bog as a case study to determine the peat accumulation rate of an ombrotrophic bog in the temperate zone under natural conditions and human influence; and to assess the relative importance of drainage, climate, peat characteristics and local vegetation composition. Because it is challenging to disentangle the separate and combined effects of multiple causal factors (Tuittila *et al*. 2007, Seddon *et al*. 2014), we use variation partitioning to allow an assessment of the relative importance of influencing factors independently as well as their joint effect on peat accumulation.

METHODS

Study area

The study area lies within the Teici peat bog complex (14,400 ha) in eastern Latvia (Figure 1). It comprises 15 bog domes at altitudes ranging from 108 to 114 m a.s.l. Teici has been a Nature Reserve since 1982. The most common micro-landscape consists of hummocks and hollows formed by *Sphagnum* species (*S. balticum*, *S. capillifolium*, *S. magellanicum*, *S. majus*), *Calluna*-*Eriophorum*, *Eriophorum*-*Andromeda*, *Rhododendron*-*Chamaedaphne* and *Rhynchospora*-*Andromeda* (Namatēva 2012).

Shrubs and trees are scarce in Teici Bog and consist of *Betula nana*, *Betula pubescens* and *Pinus sylvestris*. The surroundings of Teici present a predominantly agricultural landscape with forested patches consisting of *Betula pendula*, *Betula pubescens*, *Picea abies* and *Pinus sylvestris* with scattered stands of *Ulmus laevis*, *Ulmus glabra*, *Tilia cordata*, *Alnus incana*, *Alnus glutinosa* and *Quercus robur*.

The first drainage in the vicinity and in the bog was introduced at the end of the 1920s and in the early 1930s. However, at that time the ditches were excavated manually and the drainage did not have a visually significant impact on the hydrological regime. From the 1960s to the 1980s, a second phase of drainage took place, and this time it involved massive works using specialised auto-motorised equipment, which is likely to have impacted the bog's hydrology (Bergmanis 2004). Later, in 1999, the first set of dams was constructed in order to restore the hydrology of the bog to its natural pre-drainage state (Bergmanis *et al*. 2002).

The climate of this area is influenced by both the continental climate of Eurasia and the maritime system of the North Atlantic Ocean, and the annual frequency of arctic and sub-polar air masses is fairly

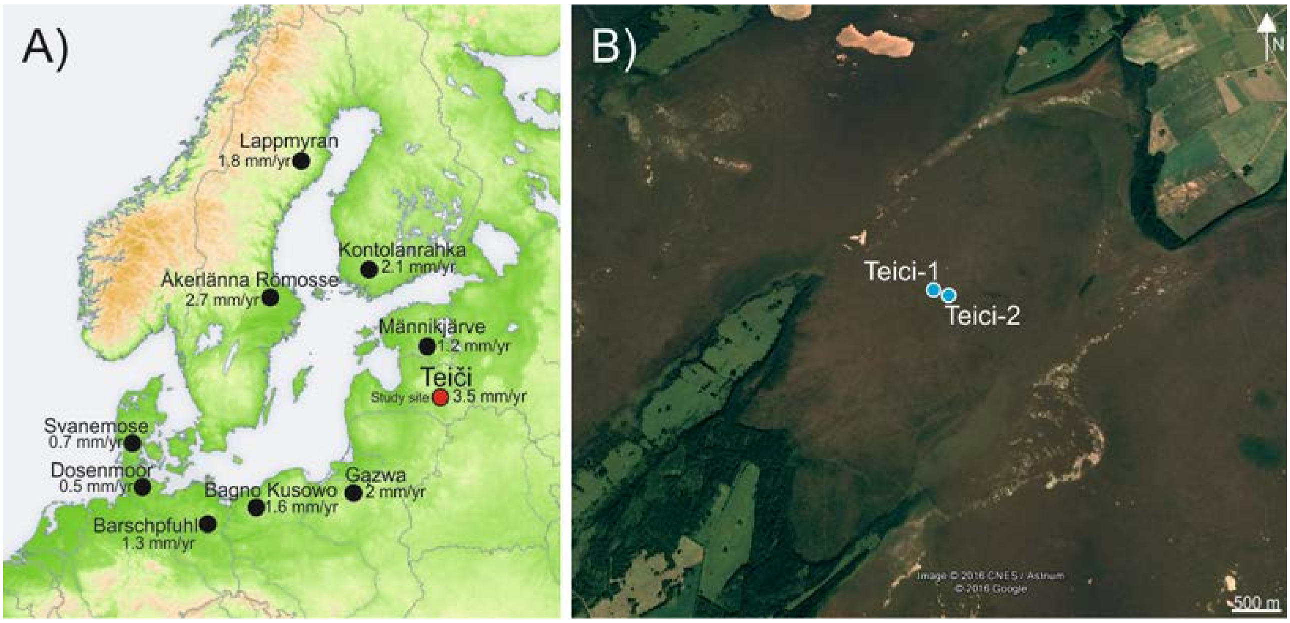

Figure 1. (A) Topographic map of northern central Europe showing the locations of peat bogs discussed in the text. The red dot represents Teici Bog in the eastern Baltic (present study). Average peat accumulation rate over the past 150 years is indicated next to each study site (black dots). References to the accumulation rates are: Männikjärve (Sillasoo *et al*. 2007), Kontolanrahka (Väliranta *et al*. 2007), Lappmyran (van der Linden *et al*. 2008a), Åkerlänna Römosse (van der Linden *et al*. 2008b), Svanemose, Dosenmoor (Barber *et al*. 2004), Barschpfuhl (van der Linden *et al*. 2008c), Bagno Kusowo (Gałka *et al*. 2017) and Gązwa (Gałka *et al*. 2015). (B) Sampling sites for the two cores Teici-1 and Teici-2.

high (Draveniece 2009). In the nearest city Rēzekne (~ 50 km east of Teici), mean annual temperature is +5.2 °C and the mean summer and winter temperatures are +16.9 and -4.1 °C, respectively.

Sampling and lithostratigraphy

Cores Teici-1 (56° 37' 20.67'' N, 26° 26' 26.91'' E) and Teici-2 (56° 37' 17.70'' N, 26° 26' 37.34'' E), containing the uppermost peat deposits of the Siksalas dome of Teici Bog, were retrieved with a Wardenaar corer (Wardenaar 1987) from sites located within a distance of 150 m from each other (Figure 1B). The Siksalas dome was selected for this study after careful evaluation of all possible domes, as the one that was most likely to provide a representative estimate of average peat growth for the entire Teici Bog area. The selection criteria included: shape of the dome with clear margins and dome plateau; location in the middle of the bog massif; similar distances from the centre of the dome to the closest ditches in two opposite directions; dome with no large bog pool(s); ombrotrophic peatland dominated by *Sphagnum* communities. Because the most sensitive stratigraphical record can be found between a hummock and a hollow (De Vleeschouwer *et al*. 2010), the cores were taken from such locations with similar micro- and macro-landscape features (Namatēva 2012). Undisturbed peat profiles 78 cm (Teici-1) and 90 cm (Teici-2) long were obtained, described in the field, wrapped in plastic film, placed horizontally in wooden boxes, and transported to the Institute of Geology at Tallinn University of Technology where they were stored in a cold-room at a constant temperature of 4 °C. Continuous 2 cm^3 subsamples were cut from each monolith in 1-cm increments for further analyses.

The dry weights of sub-samples were determined after oven drying to constant weight (12 hours at 105 °C). The organic matter content of the sediment was determined by loss-on-ignition (LOI) analyses, by combusting the dried samples in a furnace at 550 °C for four hours. The bulk density (g cm^3) was calculated on the basis of LOI for all samples.

High-resolution chronology

A study of environmental impacts on peat formation requires detailed information about the rate of peat growth (accumulation rate), which can best be achieved through high-resolution dating of peat deposits. Accordingly, the chronologies of Cores Teici-1 and Teici-2 were established by ^{14}C AMS dating, spheroidal carbonaceous particles (SCP) and radionuclide dating using naturally occurring ^{210}Pb.

Ombrotrophic peatlands serve as efficient traps of various atmospheric fallout particles. Therefore, we used fuel combustion particles that are man-made pollutants deposited from the atmosphere as an additional indirect dating method for the uppermost peat sequences (Punning & Alliksaar 1997). Analysis of SCP followed the methodology of Rose (1990) and Alliksaar (2000).

In addition to AMS ^{14}C dating and SCP, tephrochronology was used as another independent dating technique. After larger explosive volcanic eruptions, volcanic ash particles or tephra can be dispersed over large areas and deposited in bogs. If accurately identified, these tephra particles provide valuable time and correlation markers. In order to detect and isolate volcanic glass shards, the Teici-1 core was initially sampled and analysed by tephrochronology methods, and results are published in Stivrins *et al*. (2016).

For the upper section, radionuclide dating by means of ^{210}Pb was applied. The common ^{210}Pb dating technique involves measurements of the naturally occurring radioisotope ^{210}Pb (half-life 22.26 years) together with its parent isotope ^{226}Rn in order to determine the content of unsupported ^{210}Pb, i.e. the ^{210}Pb deposited from the atmosphere. The radionuclide activities were measured by gamma spectrometry at the Gamma Dating Centre Copenhagen, University of Copenhagen, Denmark. The ^{210}Pb-based chronologies were calculated using a CRS (Constant Rate of Supply) model (Appleby & Oldfield 1983). The accuracy of CRS-based chronologies depends strongly on proper assessment of the activity of unsupported ^{210}Pb in the deeper part of the profile. Therefore, the activity below 38.5 cm in Teici 1 and 32.5 cm in Teici 2 was calculated on the basis of a regression of unsupported ^{210}Pb *versus* cumulative mass as outlined by Appleby (2001).

Combined chronologies for both cores were produced using Bayesian age-depth modelling software Bacon 2.2 (Blaauw & Christen 2011). Bacon 2.2 divides a core into a large number of thin vertical sections and models the accumulation rate of each section (Blaauw & Mauquoy 2012). Individual ^{14}C calibration was carried out by using the IntCal13 calibration dataset (Reimer *et al*. 2013) with a 2σ (95.4 %) confidence level. All this was performed in the R environment (version 3.0.3) (R Core Team 2015).

In order to compare Teici peat accumulation rates with regional ones, we selected high-resolution peat studies from all over northern central Europe (Figure 1) and, by using their original dating data, estimated peat accumulation rates for the years 1866 to 1999 AD. The time beyond 2000 AD was excluded to minimise the potential bias or incorrect boost in average peat accumulation rate (PAR) due to the top-most live section. All the dates were re-calibrated using the newest version of the IntCal13 calibration dataset and the age-depth models made in Bacon 2.2.

Local vegetation composition

Plant macrofossils were analysed at 1-cm intervals in contiguous 25 cm³ samples. The samples were washed and sieved under a current of warm water over 0.25-mm mesh screens, then the whole of each sample was analysed with the help of a stereoscopic microscope. Carpological (fossil) remains and vegetative fragments (leaves, rootlets, epidermis) were identified using the available identification key (Mauquoy & van Geel 2007) and, thus, the percentages of fossils of individual vascular plant species were determined. The volume percentages of different vegetative remains and *Sphagnum* sections were estimated in increasing steps of 5 %. The relative proportions of the taxonomic sections of *Sphagnum* were estimated under the microscope on two 32 × 32-mm cover glasses on the basis of the branch leaves. The identification of *Sphagnum* at species level was performed separately on the basis of stem leaves using specialist keys (Hölzer 2010, Laine *et al*. 2011) and recent material. Moss and vascular plant nomenclature follow Laine *et al*. (2011) and Mirek *et al*. (2002), respectively. The results, presented in the form of diagrams of plant macroremains, were prepared in the C2 graphics programme (Juggins 2003). *Sphagnum fuscum* and *S. capillifolium* have been reported together due to the difficulty of differentiating them in the fossil state, particularly when the stem leaves are missing (Hölzer 2010; Gałka *et al*. 2013, 2014).

Water level changes

Subfossil testate amoebae were extracted from 3–4 cm^3 sample volumes at 1-cm intervals. The samples were prepared by sieving and back-sieving (Booth *et al*. 2010). A minimum of 150 testate amoebae *per* sample were identified at 200–400 times magnification according to published identification keys (Ogden & Hedley 1980, Mazei & Tsyganov 2006).

Reconstruction of the water table depth based on testate amoebae was carried out using C2 software (Juggins 2003) and the transfer function developed for northern Poland by Lamentowicz & Mitchell (2005) and Lamentowicz *et al*. (2008). This training dataset and transfer function was applied here because no analogue has been produced separately for the Baltic countries, and climatically similar northern Poland is the closest region where such a transfer function has been developed.

Record of historical climate

Instrumental records of monthly air temperature and precipitation over the last 150 years (1866–2013) from the city of Tartu in south Estonia (190 km from the study area) were obtained from the Estonian Institute of Hydrology and Meteorology. A long-term instrumental climate record is also available from Riga (150 km from the study area), but climate data from Tartu were used because Tartu is more similar to the Teici region in that it is more influenced by continental climate than Riga. The earliest instrumental records closer to Teici are available for only the last 50 years from the city of Rēzekne, which displays similar climatic trends to those at Tartu. To characterise the climate of each year, we used the average summer temperature (average for June, July and August), the average winter temperature (average for December, January and February), summer precipitation (sum of precipitation in June, July and August) and winter precipitation (sum of precipitation in December, January and February).

Drainage history

Using the known periods of drainage (first drainage at the end of the 1920s, second drainage since the 1960s, dams to restore the water level in 1999), we divided the study period into four 'drainage periods', namely: natural (prior to 1925), weak drainage (1925–1960), strong drainage (1960–1999), and restored water level (after 1999).

Statistical analyses

We used variation partitioning (Borcard *et al*. 1992) to investigate how peat accumulation is associated with the four groups of explanatory variables: (1) climate (summer and winter temperature and precipitation); (2) drainage (four 'drainage periods': natural, weak drainage, strong drainage and restored); (3) peat composition (the Hellinger-transformed cover percentages of the ten most abundant peat-forming taxa); and (4) other sediment characteristics (water table depth, density, organic matter content, moisture content, site identity). Because the two cores used in our study might also differ in ways that are not described by the factors mentioned above, we also included site identity (Teici-1 or Teici-2) among the variables in 'other sediment characteristics'. In each group of explanatory variables, only the significant variables derived from the model selection procedure (with backward selection of variables in linear models with PAR as a response variable) were included in the variation partitioning. The significance levels of the individual effects of the four partitions (peat composition, climate, drainage, other sediment characteristics) were estimated with Monte Carlo permutation tests (999 randomisations). All statistical analyses were carried out in the R environment (R Core Team 2015) using the package "vegan" (Oksanen *et al*. 2013) for variation partitioning.

The upper part of the sediment core, which includes the living parts of *Sphagnum* mosses, has somewhat different characteristics and should be used with caution in statistical analyses and interpretation (van der Linden *et al*. 2014, Swindles *et al*. 2015). This was also evident from our results (see Results and Discussion sections). Therefore, we excluded from the variation partitioning analysis the uppermost 10 cm (acrotelm), which reflects the period after 1999. Three drainage periods (natural, weak and strong drainage) were used as dummy variables in the variation partitioning analysis.

RESULTS

Peat accumulation rates (PAR) and climate characteristics

The sequences studied consist of *Sphagnum* peat. The acrotelm is estimated to comprise the top 10 cm of the peat, which is not permanently saturated with water. In this layer, peat is still being degraded by aerobic bacteria (van der Linden *et al*. 2008a). Age-depth models for the sediment sequences we studied are presented in Figures 2 (Teici-1) and 3 (Teici-2).

High-resolution chronology indicates a similar pattern of peat accumulation, with increased rate towards the upper section, for both cores. The Teici-2 core covers a longer time period than Teici-1 because the Teici-2 sediment core was longer. Altogether, 27 samples consisting exclusively of *Sphagnum* stems were dated by AMS ^{14}C in the Poznan Radiocarbon Laboratory, Poland (Poz) (see Appendix). The cores were also analysed for their content of the isotopes ^{137}Cs and ^{241}Am (Table A5 in the Appendix) which are both related to nuclear weapons testing with a maximum in 1963 and, for ^{137}Cs, also the Chernobyl accident in 1986. However, the content of ^{241}Am was generally below detection limits and the content of ^{137}Cs did not show any marked peaks or trends consistent with the known history of release of this isotope into nature. This indicates that, in agreement with the findings of e.g. Appleby *et al*. (1997), ^{137}Cs is mobile in deposits with very high organic content. Therefore, both isotopes were considered to be useless as chronological markers in the deposits.

On average, the PAR of Teici-1 was 4 mm yr^{-1}

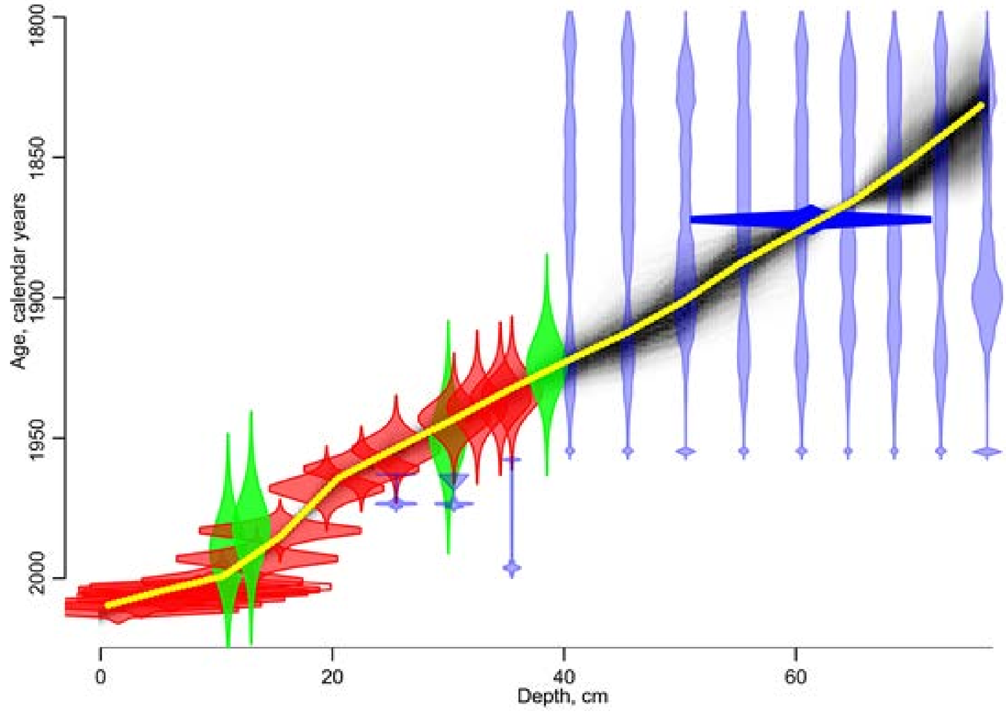

Figure 2. Age-depth model for the Teici-1 sequence (Stivrins *et al*. 2016). The age-depth model is based on ^{14}C AMS (purple), radionuclide ^{210}Pb (red), spheroidal carbonaceous particles (green) and tephra from the Askja eruption of 1875 (dark blue). The yellow curve shows the weighted mean ages for all depths, and greyscales show uncertainties (darker grey indicates more certain section).

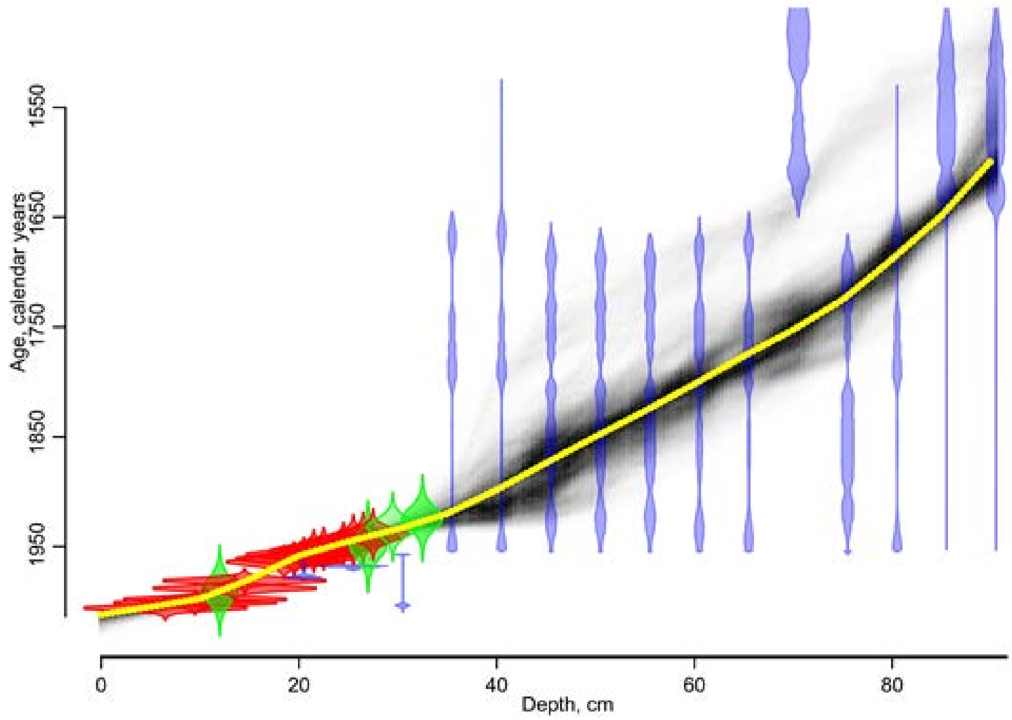

Figure 3. Age-depth model for the Teici-2 sequence. The age-depth model is based on ^{14}C AMS (purple), radionuclide ^{210}Pb (red) and spheroidal carbonaceous particles (green). The yellow curve shows the weighted mean ages for all depths, and greyscales show uncertainties (darker grey indicates more certain section).

from 1830 AD to 1965 AD. Then, after a minor decrease, it increased sharply to 10 mm yr^{-1} after 2000 AD (Figure 4). Meanwhile for Teici-2 the PAR was 2 mm yr^{-1} from 1866 AD to 1915 AD and, as for Teici-1, the accumulation rate increased steeply at 2000 AD. The uppermost increase can probably be explained by the presence of living *Sphagnum* and low compression of the peat. The sediment is highly organic in nature, as expected (Figure 4). Water level reconstructions for both sites, based on testate amoebae, indicate that the deepest water table level (15–16 cm below the surface) prevailed from 1996/1999 up to the present time. Temperatures show an increasing trend over the last 150 years (Figure 4).

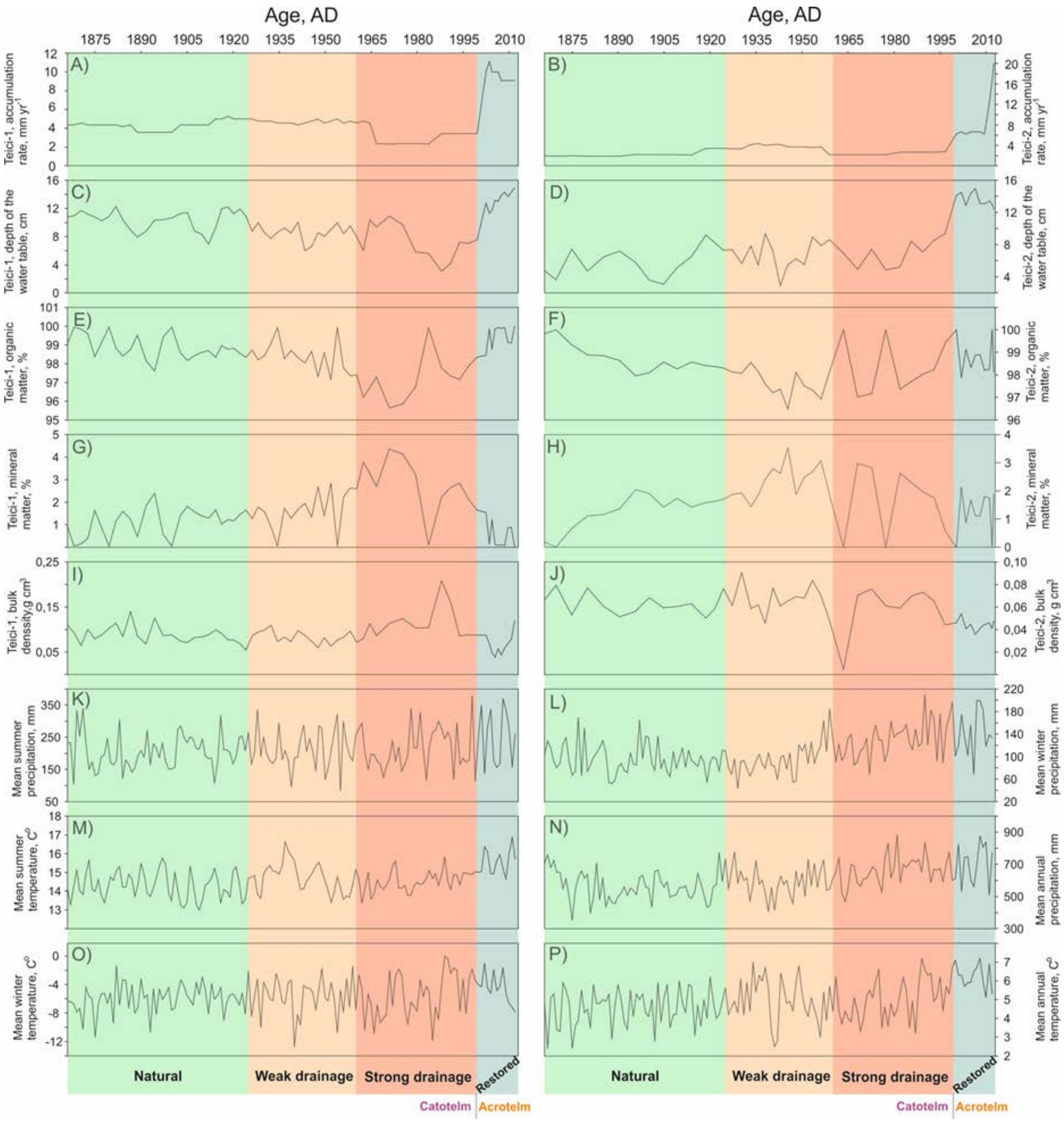

Figure 4. Peat characteristics and climate data. Results from Teici-1 and Teici-2: (A, B) peat accumulation rate, mm yr^{-1}; (C, D) depth of the reconstructed water table, cm; (E, F) organic matter, %; (G, H) mineral matter, %; (I, J) bulk density, g cm^{-3}. Climate variables for Tartu, Estonia over the last 150 years: (K) mean summer precipitation, mm; (L) mean winter precipitation, mm; (M) mean summer temperature, °C; (N) mean annual precipitation, mm; (O) mean winter temperature, °C; (P) mean annual temperature, °C.

 DOI: 10.19189/MaP.2016.OMB.262

Local vegetation composition

Four development phases of the local vegetation were delimited on the basis of drainage periods (Figure 5). In Teici-1 the natural phase was characterised by domination of *Sphagnum balticum*, *Sphagnum cuspidatum*, *Sphagnum majus* and *Sphagnum capillifolium*. Although the presence of *Andromeda polifolia*, *Ericaceae* and *Oxycoccus microcarpus* suggests that the bog surface was periodically dry, the vegetation composition indicates very wet conditions. After minor drainage in 1920–1930, the same plant species dominated but there were variations in percentage composition. *Sphagnum capillifolium*, *Sphagnum balticum*, *Sphagnum majus* and *Sphagnum fuscum* still dominated, indicating wet conditions, but an increase of *Oxycoccus microcarpus* and *Andromeda polifolia* shows that the bog surface was drier than before.

During the strong drainage phase 1960–1999 *Sphagnum* species still dominated the vegetation although *Sphagnum cuspidatum* and *Sphagnum majus* disappeared, indicating a decrease in the distribution of bog pools. *Sphagnum magellanicum*, *Sphagnum balticum* and *Sphagnum fuscum* were the prevalent *Sphagnum* species in Teici-1. Overall, the composition of the vegetation still indicates wet conditions. *Rhynchospora alba* appeared for the first time in 1990, and the role of *Sphagnum magellanicum* increased after rewetting in 1999.

Sphagnum balticum, Sphagnum magellanicum and *Sphagnum majus* were the dominant peat-forming species in the upper part of Teici-2 under conditions of both strong drainage and restored water level. The composition of the vegetation indicates the occurrence of dry periods even after rewetting. *Sphagnum balticum*, *Sphagnum capillifolium* and *Sphagnum magellanicum* are the main peat-forming species at present.

Environmental variables associated with peat accumulation rate

Backward selection of climate variables showed that only winter precipitation was significantly negatively associated with the PAR, indicating that PAR was lower in years with high winter precipitation. The periods of natural and weak drainage conditions had significantly higher PAR than the period of strong drainage. In the case of peat composition, high abundance of *Sphagnum fuscum*/*capillifolium*, *Sphagnum majus* and Ericaceae was associated with higher PAR, and high abundance of *Sphagnum magellanicum* was associated with lower PAR. Teici-1 had higher PAR than Teici-2. In addition, water table depth was significantly positively associated with PAR.

DISCUSSION

Drainage has a long-term effect

The results of variation partitioning suggest that drainage explains a substantial part (20 %) of the variation in peat growth rate (Table 1, Figure 6). This, combined with the results of linear modelling, reveals that the peat had a positive growth balance under natural conditions and minor drainage (4 mm) and under strong drainage (2.8 mm) (Table 1). As expected, strong drainage leads to a reduction in peat growth. The closest ditch to both sampling points is 1 km away, and it is evident from our results that drainage did not have an immediate impact. The water table did not fall immediately after the drainage events (Figure 4) and the effect on peat growth had a time lag of 9–17 years. It is also worth noting that our reconstructions of water table depth based on testate amoebae give long-term information about water level changes and do not show short-term fluctuations (Swindles *et al*. 2015). Nevertheless, testate amoebae reflect changes in water table depth that could not be obtained in any other way.

Water table depth was positively associated with peat growth rate (Table 1), explaining 44 % of the variation together with site differences such as peat bulk density, organic matter content, moisture content, water table depth and site identity. An even greater proportion (as much as 59 %) of the variation in PAR was explained by the local vegetation (Table 1, Figure 6). Given that peat in Teici is formed mainly from *Sphagnum* species that are known to be closely dependent on water table depth, it is no surprise to see such a high proportion of variance explained by these factors, which reflect differences in water level regime. For instance, abundant *Sphagnum balticum*, *Sphagnum fuscum* and *Sphagnum magellanicum* in raised bogs usually indicates a relatively high water level (Väliranta *et al*. 2007, Laine *et al*. 2011, Gałka *et al*. 2017). In this regard, the study of Paal *et al*. (2016) about the impact of drainage on the vegetation of transitional mires in Estonia shows that *Sphagnum* species are sensitive to changes in water level regime. These authors found that *Sphagnum* species are sensitive to drainage even at a distance of 400 m from the drainage ditch. Besides, *Sphagnum* species become more common if the minimum water level in transitional mires is higher than 50 cm below the soil surface. In Teici Bog, the water level did not fall more than 15–16 cm below the surface and our sampling locations are twice as far from the nearest ditch. Nevertheless, based on variation partitioning analysis, we detect a clear drainage impact on peat growth. Although drainage also influences rather

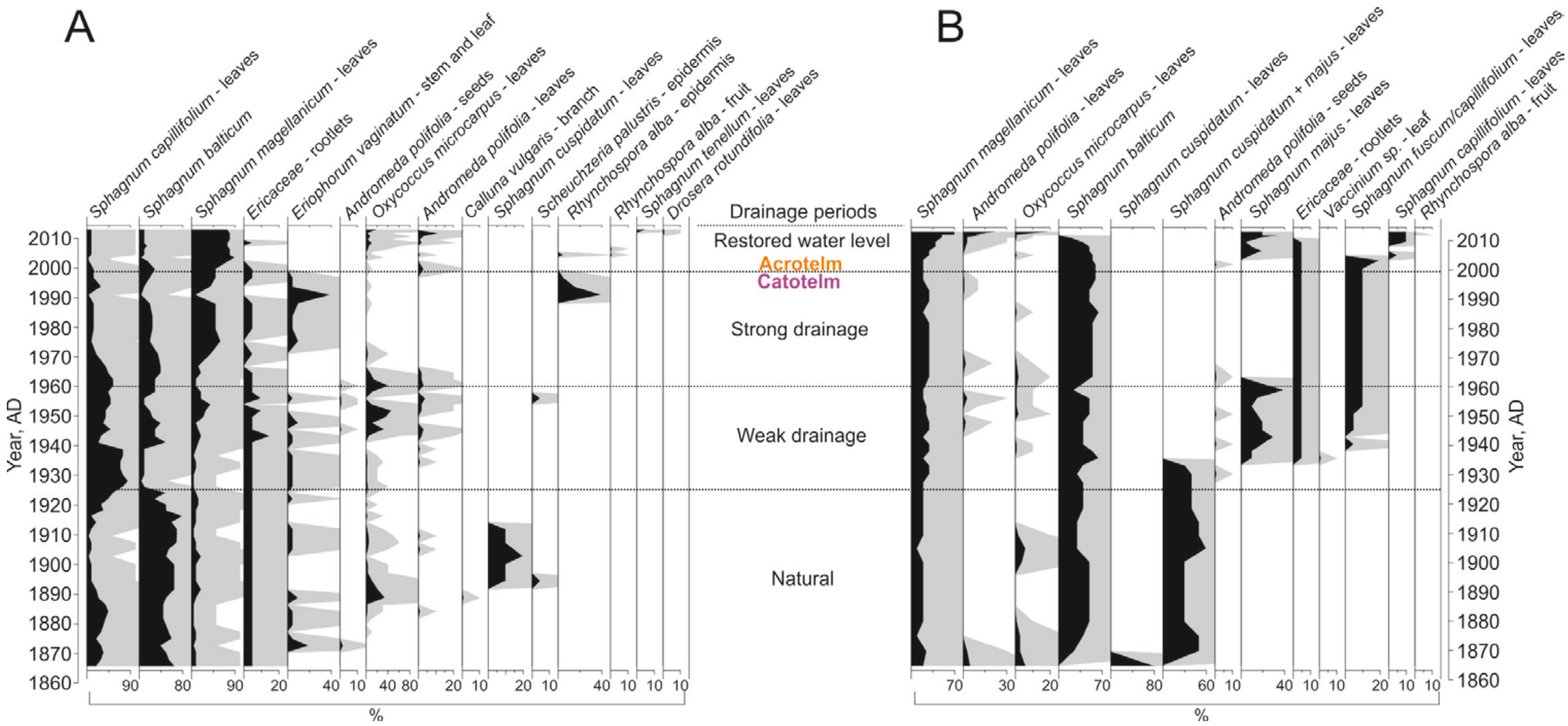

Figure 5. Plant macrofossils in the peat sequences of Teici-1 (A) and Teici-2 (B). Zonation according to drainage periods. Acrotelm and catotelm position is also indicated.

Table 1. Results of the linear models. Explanatory variables that were significantly associated with peat accumulation rate (PAR) are listed in four groups (climate, drainage, peat composition or other sediment characteristics). The uppermost 10 cm is excluded. The sign of association (+/–) and significance level (*** $p < 0.001$; ** $p < 0.01$, * $p < 0.05$) are given. In cases of association with the categorical variables "Drainage" and "Site", the letters (A and B) denote significantly different ($p < 0.05$) groups according to the Tukey *post hoc* test and the sign shows whether the average accumulation rate of one group is higher (+) or lower (–) than the average of the other group.

Group of explanatory variables	Variables	Adjusted R^2
Climate	– Winter precipitation (*)	0.03
Drainage	Natural A (+) Weak drainage A (+) Strong drainage B (–) (***)	0.20
Peat composition	+ *Sphagnum fuscum*/*capillifolium* (***) – *Sphagnum magellanicum* (***) + *Sphagnum majus* (*) + Ericaceae (**)	0.59
Other sediment characteristics	+ Water table depth (***) Site Teici-1 A (+) Site Teici-2 B (–) (***)	0.44

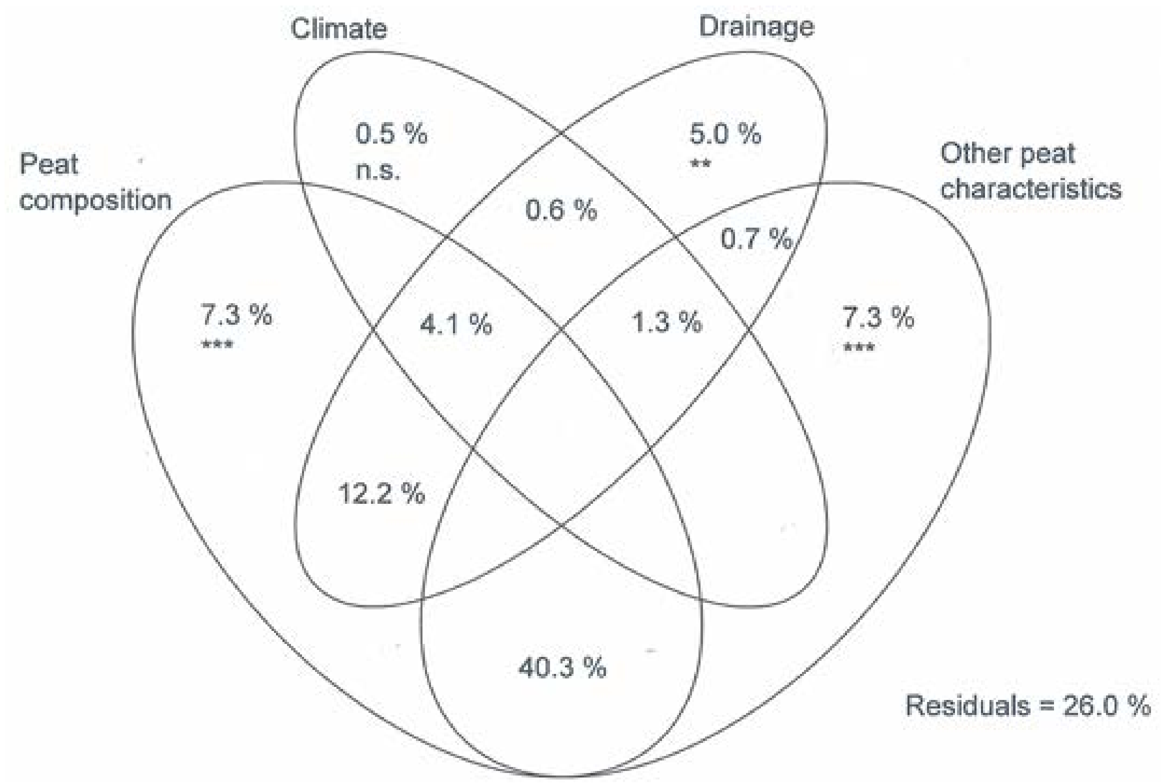

Figure 6. Venn plot of the variation partitioning results showing the percentage of variance in PAR explained by different sets of factors. The factors included within different groups are given in Table 1. The significances of individual fractions are obtained from Monte Carlo permutation tests and are given as *** $p < 0.001$, ** $p < 0.01$, n.s. $p > 0.05$.

remote peatland communities, we do not see replacement of the dominant *Sphagnum* by other transitional mire species. In theory, we would expect that the response of wet habitats (with *Sphagnum cuspidatum*, *Sphagnum majus* or *Sphagnum balticum*) to drainage would be an increase in cover of *Sphagnum magellanicum* or *Sphagnum capillifolium*. In a dry habitat, *Sphagnum capillifolium* could remain dominant after drainage because it is more tolerant of relatively dry conditions.

Our explanatory variables together explain 74 % of the variation in peat accumulation and only 26 % of the residue is unexplained. Therefore, we can be quite confident that we have included the most important factors influencing peat growth in our analyses. However, we expected a larger effect of climate on peat accumulation rate in our analyses—we found that only 0.5 % of the variation was explained by this factor and it was not significant (Figure 6). Based on the linear models, winter precipitation was the only variable that had a significant negative relationship with PAR (Table 1) indicating that more precipitation in winter slows down peat growth. This finding contradicts the study of Dorrepaal *et al*. (2003) who report enhanced growth of *Sphagnum* (particularly *Sphagnum fuscum*) with increasing precipitation. *Sphagnum fuscum* is abundant in Teici-2 and not in Teici-1, indicating micro-landscape differences between the two sites. Although the two sampling sites represent the same landscape and vegetation features at the present time, it is evident that they have developed in slightly different ways over the last 150 years and this legacy is no longer evident except in peat cores.

Peat accumulation rate during the last 150 years in Europe

Average PAR for the last 150 years in Teici was 3.5 mm yr^{-1}. However, Teici-1 had a higher PAR of 4 mm yr^{-1} and Teici-2 a lower PAR of 3 mm yr^{-1}. In comparison with other high-resolution and high-precision studies from Europe (Figure 1), Teici had the highest PAR. In Europe, peat growth rates appear to have no clear spatial trend, suggesting an influence of more local drivers in each bog. For example, van der Linden *et al*. (2008c) evaluated the relative contributions of climate change and human impact on vegetation change and peat accumulation in the ombrotrophic bog Åkerlänna Römosse in central Sweden. Based on visual interpretation, van der Linden *et al*. (2008c) concluded that climate change (precipitation and evaporation) control bog surface wetness. Meanwhile, a high-resolution study of the Finnish raised bog Kontolanrahka by Väliranta *et al*. (2007) revealed that wet and dry shifts were driven not only by climate but also by local factors. Indeed, in our study, local factors such as drainage and vegetation change explained more variation in peat growth than climate.

Our study shows that the local vegetation composition and dominant *Sphagnum* species significantly influence PAR. The increment of each species can vary due to local aspects such as humidity, water table depth and interspecific competition. On average, the increment can be as high as 27 and 41 mm yr^{-1} for living *Sphagnum capillifolium* and *Sphagnum majus* (Breeuwer *et al*. 2008, Hájek 2009), and even higher for *Sphagnum cuspidatum* (91 mm yr^{-1}). For *Sphagnum fuscum* and *Sphagnum magellanicum* it is 10–15 and 15–20 mm yr^{-1} (Loisel *et al*. 2012). The dominance of *Sphagnum capillifolium*, *Sphagnum majus* and *Sphagnum cuspidatum* overlaps with the time of increased peat growth in Teici (Figures 4 and 5).

Human-induced impact on bogs has been recorded all over northern central Europe. Periods of drier bog communities with the reappearance of charcoal suggest human interference in Denmark and northern Germany (Barber *et al*. 2004). In this area PAR for the last 150 years was only 0.5–0.7 mm yr^{-1} (Figure 1). Another rather similar site is Barschpfuhl Bog in north-east Germany (PAR 1.3 mm yr^{-1}), where afforestation with fast-growing conifers and drainage for agricultural purposes resulted in lowering of the water table, changes in surface vegetation and increased decomposition of the peat (van der Linden *et al*. 2008b). Human activities *via* drainage within and close to the bog Männikjärve in Estonia were significant during the last century (Sillasoo *et al*. 2007) and are the most likely reason for the average PAR of 1.2 mm yr^{-1}. The higher PARs of Bagno Kusowo Bog (1.6 mm yr^{-1}) and Gązwa Bog (2 mm yr^{-1}) in north-western and north-eastern Poland are probably due to exceptional hydrology as well as peatland size and the thickness of the peat layer (making the bog difficult to drain) (Gałka *et al*. 2015, 2017). But why, then, is PAR so high in Teici Bog if drainage influence is apparent? Another potentially controlling aspect of PAR can be the size of the bog. The extent of the whole Teici bog complex is 14,000 ha, and that of the Siksalas dome where we obtained our results is 880 ha. In comparison, the area of Åkerlänna Römosse is 104 ha, Kontolanrahka 880 ha, Barschpfuhl 6.2 ha, Männikjärve 263 ha, Lappmyran 13 ha and Gązwa 280 ha. The results from Swedish, Finnish and Latvian sites suggest that a larger bog has a larger capacity to grow and local climatic conditions have a bigger influence (Figure 1). As there is no strong correlation with historical climate records, we can also speculate that the large bog area has buffered the influence of climate change over the last 150 years. In addition, our results reveal that drainage affected peat growth with a time lag and, if Teici Bog were smaller, we would probably have detected an immediate effect. To test our hypotheses, a comparative study including bogs of different sizes would be required.

Growth of living *Sphagna* is not the same as peat accumulation rate

Our results show that PAR has increased abruptly since 2000. It can be assumed that the installation of dams in 1999 (Bergmanis *et al*. 2002) increased *Sphagnum* growth. From a conservation point of view, this result is a great success. However, it is probably too early to determine whether or not the dams that have been installed at Teici are effective for the whole bog ecosystem. While they can show immediate changes locally around the rewetted ditches, it may be some time before the changes positively influence the central part of the dome. A high peat growth signal can be misleading as the upper part of the profile represents the acrotelm where *Sphagnum* is alive and the peat itself is less compacted. It is worth noting that *Sphagnum magellanicum*, which has been the dominant species since 2000, is also one of the largest *Sphagnum* species. Many studies have shown that more than a few years is needed to evaluate the ecological effectiveness of a restoration measure (Montoya *et al*. 2012, Daza Secco *et al*. 2016) because peat is not formed until several decades after the living surface vegetation dies off. Therefore, the whole sequence cannot be evaluated in the same manner at this point; in our analysis, we had to exclude the living part of the acrotelm.

CONCLUSIONS

The results of variation partitioning explained 74 % of the variation in peat accumulation rate and left only 26 % unexplained. Our study shows, further, that local vegetation composition significantly influences the peat accumulation rate. The linear models revealed that under natural conditions, minor drainage and even strong drainage influences, peat has a positive accumulation balance of 2–4 mm *per* year. We also found that drainage systems can impact peatland communities across a considerable distance. Drainage has a delayed impact—the water table is not lowered immediately after a drainage event and the effect on peat growth has a time lag of 9–17 years. A low correlation with the historical climate record suggests that the bog area has buffered the influence of climate change over the last 150 years. This study also helps us to understand which *Sphagnum* species are more tolerant of water level changes. This could be helpful, for instance, when planning *Sphagnum* farming or peatland rehabilitation projects.

ACKNOWLEDGEMENTS

Our research was supported by the Estonian Ministry of Education and Research (PUT1173) and the Latvian Peat Association. This study was carried out in co-operation with Projects ETF9031, IUT 1-8 and EBOR. Thanks to Uldis Ozols for valuable support during the fieldwork.

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Submitted 07 Nov 2016, revision 30 Jan 2017
Editor: Ab Grootjans

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Appendix

Table A1. AMS ^{14}C-based dates of the Teici-1 sequence (Stivrins *et al*. 2016).

Depth (cm)	Lab. no.	^{14}C age	yr calBP	yr calAD (2σ range)
25 – 26	Poz-58406	144.61 ± 0.40 pMC	-2963 ± 22	1960 – 1975
30 – 31	Poz-58407	143.98 ± 0.38 pMC	-2928 ± 21	1960 – 1975
35 – 36	Poz-58408	111.44 ± 0.31 pMC	-870 ± 22	1960 – 2000
40 – 41	Poz-58409	135 ± 25 BP	274 – 9	1675 – 1940
45 – 46	Poz-58411	125 ± 25 BP	270 – 10	1680 – 1940
50 – 51	Poz-58412	80 ± 25 BP	260 – 30	1690 – 1920
55 – 56	Poz-58413	120 ± 25 BP	270 – 10	1680 – 1940
60 – 61	Poz-58414	125 ± 25 BP	270 – 10	1680 – 1940
64 – 65	Poz-58415	100 ± 25 BP	265 – 25	1690 – 1930
68 – 69	Poz-58416	100 ± 30 BP	270 – 15	1680 – 1935
72 – 73	Poz-58417	125 ± 25 BP	270 – 10	1680 – 1940
76 – 77	Poz-58418	65 ± 25 BP	255 – 30	1695 – 1920

Table A2. AMS ^{14}C-based dates of the Teici-2 sequence (this study).

Depth (cm)	Lab. no.	^{14}C age	yr calBP	yr calAD (2σ range)
19 – 20	Poz-59163	132.05 ± 0.41 pMC	-2233 ± 25	1960 – 1980
24 – 25	Poz-59164	161.99 ± 0.48 pMC	-3875 ± 24	1965 – 1970
29 – 30	Poz-59205	107.59 ± 0.4 pMC	-588 ± 30	1960 – 2005
34 – 35	Poz-59343	200 ± 30 BP	300 – -5	1650 – 1955
39 – 40	Poz-59607	210 ± 35 BP	310 – -5	1640 – 1955
44 – 45	Poz-59208	140 ± 30 BP	280 – 5	1670 – 1945
49 – 50	Poz-59209	135 ± 30 BP	280 – 10	1670 – 1940
54 – 55	Poz-59211	130 ± 30 BP	275 – 10	1675 – 1940
59 – 60	Poz-59212	160 ± 30 BP	285 – -5	1665 – 1955
64 – 65	Poz-59213	180 ± 30 BP	295 – -5	1655 – 1955
69 – 70	Poz-59215	370 ± 30 BP	500 – 320	1450 – 1630
74 – 75	Poz-59216	115 ± 30 BP	270 – 10	1680 – 1940
79 – 80	Poz-59217	205 ± 35 BP	310 – -5	1640 – 1955
84 – 85	Poz-59218	325 ± 30 BP	470 – 310	1480 – 1640
89 – 90	Poz-59219	320 ± 30 BP	465 – 305	1485 – 1645

Table A3. Teici-1 core: AMS ^{14}C dates and $\delta^{13}C$ values. Material: *Sphagnum* stems; AMS date: 20.1.2014.

Sample code	Sample name	C (mg)	pMC	^{14}C age (years)	$\delta^{13}C$ (AMS)	Current (μA)
Poz#2-58406	25 – 26	1.77	144.61 ± 0.40	-2964 ± 22	-22.2 ± 0.3	39.6
Poz#2-58407	30 – 31	2.56	143.98 ± 0.38	-2929 ± 21	-29.4 ± 0.2	34.3
Poz#2-58408	35 – 36	2.02	111.44 ± 0.30	-871 ± 21	-30.5 ± 0.3	32.4
Poz#2-58409	40 – 41	2.34	98.34 ± 0.29	134 ± 23	-25.0 ± 0.5	37.9
Poz#2-58411	45 – 46	2.82	98.48 ± 0.30	123 ± 24	-28.5 ± 0.2	34.4
Poz#2-58412	50 – 51	2.37	99.01 ± 0.29	79 ± 23	-26.6 ± 0.4	37.7
Poz#2-58413	55 – 56	2.94	98.49 ± 0.29	122 ± 23	-22.9 ± 0.3	38.5
Poz#2-58414	60 – 61	3.42	98.45 ± 0.30	125 ± 24	-26.8 ± 0.3	35.2
Poz#2-58415	64 – 65	3.86	98.77 ± 0.30	99 ± 24	-26.4 ± 0.4	36.3
Poz#2-58416	68 – 69	4.01	98.76 ± 0.36	100 ± 29	-29.0 ± 0.1	30.8
Poz#2-58417	72 – 73	4.95	98.46 ± 0.31	124 ± 25	-28.6 ± 0.3	33.2
Poz#2-58418	76 – 77	4.46	99.22 ± 0.31	62 ± 25	-28.7 ± 0.4	34.0

Note from the Poznan AMS dating laboratory: the $\delta^{13}C$ values determined cannot be used for palaeoecological reconstructions. The reason is that $\delta^{13}C$ was measured in the GRAPHITE prepared from the samples, and the graphitisation process introduces significant isotopic fractionation. The second point is that the AMS spectrometer (unlike a normal mass spectrometer) introduces fractionation too. Therefore, $\delta^{13}C$ values reflect the original isotopic composition in the sample only very roughly. Nevertheless, $\delta^{13}C$ measurement is fully suitable for the fractionation correction of $^{14}C/^{12}C$ ratios that Poznan laboratory always do.

Table A4. Teici-2 core: AMS ^{14}C dates and $\delta^{13}C$ values. Material: *Sphagnum* stems; AMS date: 9.12.2013.

Sample code	Sample name	C (mg)	pMC	^{14}C age (years)	$\delta^{13}C$ (AMS)	Current (μA)
Poz-59163	TE II 20	1.26	132.05 ± 0.41	-2234 ± 24	-20.9 ± 0.2	28.9
Poz-59164	TE II 25	2.32	162.00 ± 0.48	-3876 ± 23	-22.6 ± 0.4	27.1
Poz-59205	TE II 30	2.19	107.59 ± 0.40	-588 ± 29	-20.2 ± 0.7	24.2
Poz-59343	TE II 35	2.33	97.54 ± 0.34	200 ± 28	-25.8 ± 0.2	24.5
Poz-59207	TE II 40	3.68	97.41 ± 0.40	210 ± 32	-23.3 ± 0.7	22.6
Poz-59208	TE II 45	1.69	98.25 ± 0.34	141 ± 27	-22.8 ± 0.3	24.0
Poz-59209	TE II 50	2.13	98.32 ± 0.32	136 ± 26	-21.5 ± 0.3	22.0
Poz-59211	TE II 55	1.87	98.38 ± 0.35	131 ± 28	-24.8 ± 0.4	22.2
Poz-59212	TE II 60	1.84	98.00 ± 0.32	162 ± 26	-25.3 ± 0.2	22.5
Poz-59213	TE II 65	2.54	97.79 ± 0.34	179 ± 27	-25.0 ± 0.4	25.0
Poz-59215	TE II 70	2.06	95.52 ± 0.33	368 ± 27	-28.6 ± 0.3	26.0
Poz-59216	TE II 75	2.01	98.55 ± 0.34	117 ± 27	-31.3 ± 0.3	25.1
Poz-59217	TE II 80	1.45	58.11 ± 0.23	4360 ± 31	-28.3 ± 1.2	16.1
Poz-59218	TE II 85	2.03	96.01 ± 0.34	327 ± 28	-26.0 ± 0.2	24.2
Poz-59219	TE II 90	1.37	96.12 ± 0.34	317 ± 28	-25.4 ± 0.3	24.4

Note from the Poznan AMS dating laboratory: the $\delta^{13}C$ values determined cannot be used for palaeoecological reconstructions. The reason is that d13C were measured in the GRAPHITE prepared from the samples, and the graphitisation process introduces significant isotopic fractionation. The second point is that the AMS spectrometer (unlike normal mass spectrometer) introduces fractionation too. Therefore, $\delta^{13}C$ values reflect the original isotopic composition in the sample only very roughly. Nevertheless, $\delta^{13}C$ measurement is fully suitable for fractionation correction of $^{14}C/^{12}C$ ratios that Poznan laboratory always do.

Table A5. Radiometric data for Teici-1 core.

Depth (cm)	^{210}Pb tot (Bq kg^{-1})	^{210}Pb sup (Bq kg^{-1})	^{210}Pb unsup (Bq kg^{-1})	^{137}Cs (Bq kg^{-1})	^{241}Am (Bq kg^{-1})
1.5	376 ± 52	13 ± 10	363 ± 52	148 ± 9	0
3.5	479 ± 56	0	479 ± 56	115 ± 7	0
5.5	691 ± 64	3 ± 4	688 ± 64	72 ± 5	0
7.5	459 ± 33	9 ± 2	450 ± 33	54 ± 3	0
8.5	445 ± 40	0	445 ± 40	52 ± 4	0
9.5	419 ± 48	0	419 ± 48	44 ± 6	0
10.5	527 ± 55	8 ± 15	518 ± 57	41 ± 6	0
13.5	481 ± 37	0	481 ± 37	44 ± 4	0
15.5	447 ± 39	0	447 ± 39	47 ± 4	0
19.5	233 ± 32	0	233 ± 32	43 ± 6	31 ± 18
22.5	161 ± 21	5 ± 1	156 ± 21	137 ± 8	0
25.5	149 ± 21	0	149 ± 21	45 ± 6	0
30.5	112 ± 17	3 ± 6	109 ± 18	31 ± 5	0
32.5	52 ± 9	4 ± 7	48 ± 11	26 ± 4	8 ± 13
34.5	72 ± 12	0	72 ± 12	20 ± 4	0
35.5	77 ± 11	4 ± 7	74 ± 13	17 ± 3	0
38.5	92 ± 15	9 ± 1	84 ± 15	16 ± 4	0