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Article



Estimation of recent peat accumulation with tree saplings

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Abstract

The purpose of this paper is to develop an approach to estimate peat accumulation rates (PAR) over recent decades based on the age and burial depths of roots from pine sapling and to use the newly developed approach to estimate spatial variations of PAR. To this end, we sampled 120 pine saplings growing in three plots at Rėkyva peatland in Lithuania and accounted for the microtopography around each specimen. In the lab, all saplings were cut into 1-cm segments, sanded and analysed. The counting of annual rings allowed dating the germination of each sapling with a yearly resolution and thus also enabled estimation of peat accumulation. The latter was derived by measuring the distance from the original root collar at germination to the ground level (or peat surface) at the time of sampling. The large number of samples selected from three plots also enabled determination of spatial variations in PAR. We obtain averaged PAR values of 1.6 ± 0.72 cm yr $^{-1}$ across the three plots and over the last decades, but also observe strong spatial heterogeneity in PAR resulting from differences in local hydrology and vegetation. To validate the results, we compared tree-ring derived PAR with radiocarbon-based (14 C) estimates at

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one of the plots. The results are consistent between the two approaches with PAR estimated to 0.8 and 0.79 cm yr⁻¹, respectively, over the last 20 years. We conclude that PAR can be assessed accurately with tree-ring approaches and that they have clear advantages over radiocarbon dating for shorter timescales as they can be replicated more easily. For longer timescales and larger depths (> 15 cm), however, ¹⁴C dating remains the preferred approach.

Keywords

Peat accumulation rates, Tree rings, Boreal peatlands, Scots pine (Pinus sylvestris L.), Lithuania

Introduction

Boreal peatlands play a key role in the global carbon cycle and in climate dynamics (Gorham, 1991; Yu, 2006). Although they cover less than 3% of the Earth's land surface, they represent a significant soil carbon pool and critically vital longterm carbon sinks (Gorham, 1991; Turunen et al., 2002). The role of peatlands as soil carbon pools is fulfilled whenever the rate of accumulation of organic matter exceeds that of decomposition (Belyea and Malmer, 2004; Young et al., 2019). In times of accelerated global warming and widespread wildfires in peatland environments (Hugelius et al., 2020; Witze, 2020), excessive peat extraction and/or peatland drainage, peatlands may well turn into net carbon sources by releasing methane (CH_4) and carbon dioxide (CO_2) to the atmosphere, with severe consequences for global climate (Edvardsson et al., 2016; Fischer et al., 2018; Swindles et al., 2019). Consequently, an improved understanding and the development of approaches that allow quantification of peat accumulation rates (hereafter referred to as PAR) has become key in peatland research.

In the past, radiometric techniques – including radiocarbon (¹⁴C), lead (²¹⁰Pb) and caesium (¹³⁷Cs) – have been employed to estimate PAR (Davies et al., 2018; Kołaczek et al., 2019; Li et al., 2019). As both ¹⁴C and ¹³⁷Cs represent the main radionuclides from radioactive fallout of atmospheric nuclear weapon tests or the 1986 Chernobyl accident (Hua and Barbetti, 2004; Li et al., 2019), they can serve as time markers for peat stratigraphic records and thereby allow quantification of peat accumulation over the last decades (Davies et al.,

2018). For longer timescales (i.e. the last 200 years or so), PAR were estimated by comparing radioactive lead isotope lead-210 excess (²¹⁰Pb) from the in situ decay of radium-226 (or supported ²¹⁰Pb; Appleby and Oldfield 1978; Oldfield et al., 1995; Li et al., 2019). At millennial timescales, finally, radiocarbon (¹⁴C) is the preferred and most frequently used method to estimate PAR (Kilian et al., 2000). In all cases, however, reliable estimates of PAR always need to be based on precise age-depth models and the analysis of several peat cores that have been sampled sequentially. As radiometric dating is expensive, analyses are usually restricted to an estimate of PAR derived from a single core taken at a single point, and thereby prevent assessment of spatial heterogeneity within a peatland complex.

The use of botanical evidence (e.g. tree saplings) has a long tradition in peat accumulation estimation (Backman, 1919; Borggreve, 1889; Heikurainen, 1953; Saarinen, 1933), but has not been used in recent decades. The approach employs the ratio between the depth of peat accumulated above the root plate of a tree sapling and the age of the sapling to derive mean annual PAR (Ohlsson and Dahlberg, 1991). To obtain reliable and accurate results, seed germination needs to take place at the peat surface and growth of saplings needs to be vertically stable. If these conditions are met, PAR can be derived from tree saplings. By contrast to radionuclide dating, a botanical approach would have several advantages as it would (i) benefit from the annual resolution of treering records and thus yields annual PAR, (ii) be easily replicable given the broad extent of forested peatlands (Zoltai and Martikainen, 1996), especially at boreal latitudes (Edvardsson et al., 2015a; Ratcliffe

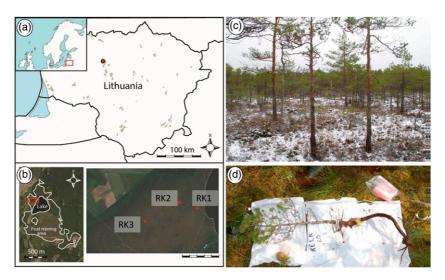


Figure 1. (a) Location of the Rékyva peatland complex (red dot) in Lithuania with other large Lithuanian peatland complexes shown in grey, (b) Overview of the study site with the limits of the peatlands shown in white. The red rectangle and the red dots indicate the location of the three plots (RKI, RK2 and RK3) where pine saplings and peat cores were sampled, (c) Illustration of a forested patch within Rékyva peatland colonized by *Pinus sylvestris* and (d) Detail view of a sapling extracted from plot RKI with the characteristic concave deformation at the stem-root transition. For interpretation of the references to colours in this figure legend, refer to the online version of this article.

et al., 2017); and as it would (iii) have a much better cost-benefit ratio compared to other analytical procedures that have been employed traditionally to estimate PAR. Nonetheless, several sources of uncertainties must be mentioned, as they could bias quantification of PAR from tree saplings: (i) the number of rings of a tree sapling at the peat surface will only rarely correspond to the real age of a tree, (ii) changes in surface elevation can be caused by the presence of a tree sapling and the microenvironment it creates and (iii) seeds can be uplifted in the peat. However, these elements have not been considered in the pioneer studies.

The aim of this paper, therefore, is to present an improved methodology, accounting for the above-mentioned potential inaccuracies, to enable quantification of local PAR more reliably with peat burial depths of calendar-dated roots of pine saplings. We hypothesize that the inclusion of these sources of uncertainties will provide more robust PAR estimations. To this end, we test the reliability of the improved botanical approach independently by comparing our results with data obtained from

radiometric measurements based on ¹⁴C. Furthermore, given the high spatial replicability of the samples analysed, we also show how the approach based on tree sapling offers insights into the spatial variability of PAR in a complex peatland ecosystem, and how these differences can be ascribed to variations in hydrology and/or vegetation.

Material and methods

Study site and sampling strategy

The Rėkyva peatland complex is located in central northern Lithuania (55°51′ N, 23°15′ E, 130 m a.s.l.; Figure 1(a)) and covers an area of 2608 ha. It is composed of six bogs amongst which the Aukštelkė bog is the last remaining natural area and thereby preserved under a strict reserve status. Like in many boreal peatlands, the bog surface has been colonized by trees, generally Scots pine (*Pinus sylvestris* L.) (Edvardsson et al., 2015a, b). During fieldwork, 120 pine saplings growing on peat soils with a thickness > 3 m were hand-picked in three squared plots of

20 x 20 m each. The plots (named RK1, RK2 and RK3) are located in the western part of the Rėkyva peatland complex, c. 100 (RK1), 300 (RK2) and 600 m west of Lake Rėkyva (Figure 1(b)).

In the field, the current peat surface level was marked on each sapling with a tape. Then, the microtopography around each sapling was recorded (see Conceptual model for the quantification of peat accumulation with tree saplings). Afterwards, each sapling (including the root system) was manually extracted. After extraction, the aerial part of the saplings was cut with a saw roughly 5 cm above the current ground level. Only the roots, root collar and lowermost part of the stem were considered for analysis and stored in plastic bags to avoid drying. We also recorded the relative position, size and diameter of each tree within the plots as additional information. To compare tree-ring-based estimates of PAR, peat sequences containing the uppermost metre of peat were extracted from the centre of each of the three plots (RK1, RK2 and RK3) with a Wardenaar peat corer. These peat cores were then used to reconstruct a radiocarbon (14C) based age-depth model.

Peat accumulation derived from tree (ring) analysis

The tree-ring-based approach allows quantification of PAR between the germination of the sapling and its removal. It is based on the age of the sapling (At; in yrs) and peat layer depth accumulated since germination (Pa; in cm). In their most simplified version, PAR can be estimated directly in the field as the ratio between peat thickness measured at the level of the stem base of saplings and the number of whorls as a proxy for tree age. Yet, this approach is known to suffer from major inaccuracies as the counting of whorls leads almost systematically to an underestimation of the real age of saplings (Van der Burght et al., 2012). Besides, peat profiles in the immediate surroundings of stems are known to be influenced by tree growth (see Conceptual model for the quantification of peat accumulation with tree saplings). For these reasons, we propose a series of major methodological improvements to enable quantification of both At and Pa in a way that minimizes biases in the estimation of PAR.

Improvements of the age determination of the tree. Each year, woody plants develop growth rings in their stems and roots because of the meristematic nature of growth (Erktan et al., 2018). In temperate climates, the growth cycle is annual, but the number of annual rings will vary along the stem and roots as a result of their elongation (Pardé and Bouchon, 1994). In previous work, the total number of annual rings has simply been counted at peat surface. However, the innermost rings that are visible at this height within the plant will not necessarily represent the year at which the plant germinated, as the accumulating peat may bury the initial root collar and the lowermost segments of the stem. Therefore, to assess exact germination dates of pine saplings, we prepared cross-sections from each of the 120 saplings at ~ 1 cm intervals from the current peat level towards the root and the stem (i.e. above and below the current peat surface), resulting in 1755 analysed cross-sections. All cross-sections were sanded with gradually finer sandpaper until all ring boundaries become clearly visible to be then counted under a stereomicroscope. For each section, the number of annual rings was noted, and the largest number of rings was considered as the germination age (Figure 2). Increment cores were processed similarly, and tree ring counted to approximate average age of individual trees.

Conceptual model for the quantification of peat accumulation with tree saplings. The microtopography of peatland surfaces is affected by the presence of pine saplings. The presence of saplings will influence growth conditions of mosses growing around their stems; likewise, deformations can be induced by the pressure exerted by root plates as they exceed the unconfined shear strength of the surrounding soil (Ballesteros-Cánovas et al., 2013; Bodoque et al., 2015). The presence of saplings will also result in strong concavity at the stem-root transition. Despite its control on peat accumulation (Pa), the influence of saplings on microtopography around their stems has been neglected, therefore resulting in a systematic underestimation of PAR in past studies. To remove

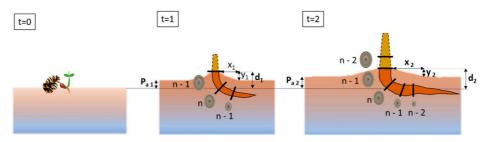


Figure 2. Concept of the tree-ring-based quantification of peat accumulation rates (PAR). At the initial stage (t=0), a seed germinates at the peat surface, radicles protrude from the covering structures and the stem system starts to elongate. In a subsequent stage (t=1), the sapling has developed a primary root and a stem system. At the same time, peat that accumulated between t=0 and t=1 (P_{a1}) will start to bury the stem partially (d_1), but also to deform the root system. Later (t=2), the tree has grown further, and peat continues to accumulate, burying the stem further (d_2). At the same time, mosses start to growth around the stem and small hummocks can form, thereby changing microtopography. For interpretation of the references to colours in this figure legend, refer to the online version of this article.

this bias and to account for microtopography around saplings, we adopted a three-step procedure to estimate PAR more accurately.

In the field, we recorded the level of the peat surface $(x_1, Figure 2)$. In a second step, we measured the horizontal distance between the root collar of the sapling and the unaffected peat surface surrounding it (defined here as X_2). We then measured the vertical distances between the root collar and the tape marking the current peat surface (d_2) . Peat accumulation is obtained by subtracting the amount of super-elevated mosses (Y_2) growing around the stem from d_2 (Figure 2). For each sample, the procedure was repeated for the four compass directions.

Radiocarbon dating

Peat cores have been taken at each of the three plots (RK1, RK2 and RK3). After visual inspection of the stratigraphic sequences, core RK2 was considered to be most susceptible (more homogeneous sample) to provide a detailed age-depth model for the most recent decades to centuries. Subsamples from peat sequence RK2 were thus prepared for radiocarbon (¹⁴C) dating at the Laboratory of Nuclear Geophysics and Radioecology of the Nature Research Centre in Lithuania. A total of 24 samples, each 1 cm in thickness, were taken from the peat core (see Table 1). Radiocarbon content in bulk organics after physico-chemical pre-treatment was measured by

liquid scintillation counting (LSC) of ¹⁴C beta decay in benzene produced from peat carbon (Petrošius and Mažeika, 2004; Skripkin and Kovalyukh, 1994). All ¹⁴C dates were then calibrated to calendar ages with the IntCal13 dataset (Reimer et al., 2013) and the post-bomb peak atmospheric NH1 curve (Hua et al., 2013) using the software OxCal v4.3.1 (Bronk Ramsey, 2001).

Statistical analysis

PARs were estimated for individual saplings and at the scale of plots. In a first step, we characterized the distribution of tree ages, peat accumulation and PAR in the 3 plots with descriptive statistical analyses. To test for the significance of differences between findings for individual saplings and at the plot scale, the non-parametric Friedman test () was used at the 95% least significance difference (LSD). Sprent and Smeeton, 2016

Results

Botanical approach based on pine saplings

The 120 pine saplings (40 per plot) show an average age of 22.2 ± 5.2 years. Substantially older saplings were found in RK2 (35.3 \pm 7.4 years), whereas the youngest individuals were found in RK1 (12.5 \pm 2.9 years), sapling ages in RK3 were close to average

Table 1. Overview of radiocarbon dated peat samples with lab identification number, average depth of samples (between
the upper and lower boundaries of the analysed sample), radiocarbon activity, calibrated ages and corresponding numbers of
years, as well as estimated peat accumulation rate (PAR). The line shows the location of a likely hiatus.

Sample ID (cm)	Depth (± Iσ)	¹⁴ C activity (AD / no. yrs)	Calibrated age (cm/yr)	PAR
2597	2.2	103.85±0.59	2008±1 / 6±1	0.37 ± 0.06
2598	3.85	107.75±0.57	2003±2 / 12±2	0.35 ± 0.07
2599	5.75	107.36±0.77	2004±3 / 10±3	0.58 ± 0.19
2600	7.65	108.24±0.72	2002±3 / 12±3	0.64 ± 0.17
2602	11.25	III.57±0.62	1996±3 / 19±3	0.63 ± 0.11
2603	12.75	112.87±0.67	1994±3 / 21±3	0.64 ± 0.10
2604	14.25	113.81±0.67	1992±2 / 22±2	0.65 ± 0.06
2604	14.25	113.81±0.67	1992±2 / 22±2	0.65 ± 0.06
2605	15.75	113.65±0.75	1993±3 / 22±3	0.75 ± 0.11
2606	17.40	119.05±0.66	1986±2 / 28±2	0.62 ± 0.04
2609	23.75	122.32±0.75	1984±2 / 31±2	0.79 ± 0.05
2610	25.35	99.01±0.46	1870±66 / 144±66	0.18 ± 0.10
2625	27.00	94.27±0.47	1440±45 / 574±45	0.05 ± 0.01
2626	28.60	91.99±0.45	1368±28 / 646±28	0.04± 0.01
2622	31.95	90.98±0.46	1242±52 / 772±52	0.04± 0.01
2623	33.80	90.62±0.42	1225±55 / 790±55	0.04± 0.01
2629	38.95	89.98±0.46	1206±59 / 808±59	0.05± 0.01
2630	40.45	89.96±0.47	1206±60 / 808±60	0.05± 0.01
2612	43.45	89.58±0.52	1142±106 / 872±106	0.05± 0.01
2615	46.45	89.53±0.43	I127±93 / 887±93	0.05± 0.01
2616	49.45	89.09±0.43	I106±83 / 908±83	0.05± 0.01
2617	50.80	88.72±0.62	1090±102 / 924±102	0.05± 0.01
2620	55.15	87.18±0.67	898±123 / 1116±123	0.05± 0.01
2621	56.65	87.33±0.52	944±82 / 1070±82	0.05± 0.01

 $(19.1 \pm 6.1 \text{ yrs})$. The age distribution between plots is consistent with the range of ages found for mature trees, namely, 43-85, 93-186 and 47-60 years for RK1, RK2 and RK3, respectively. The diameter of saplings at the level of the root collar was 10.5 \pm 3.9 mm on average. We observed largest diameters in RK2 (26.5 \pm 6.8 mm) and much smaller diameters in RK1 and RK3 (with 9.0 \pm 2.5 and 10.5 \pm 4.0 mm, respectively). Figure 3 shows relations between the diameter at the level of the root collar and the age of saplings. In all plots, significant correlations (p < .05) exist between these parameters. Stronger and more significant correlations were found for RK1 (r = 0.89, p < .001) and RK3 (r = 0.78, p < .001) as compared to RK2 (r = 0.39, p = 0.012). The distribution of vertical distances measured between the present-day peat surface and the original root collar (d_2 in Figure 4) are comparable among the three plots and are on average 29.0 ± 10.0 cm at RK1, 29.1 ± 9.4 cm at RK2 and 28.9 ± 9.34 cm at RK3.

The microtopography of the peat surface surrounding the tree sapling $(y_2 \text{ and } X_2 \text{ in Figure 4})$ was measured in the vertical and horizontal orthogonal directions and was 7.7 ± 14.5 and 31.3 ± 18.6 cm on average, respectively. Horizontal distances differ significantly between plots (p-value = 0.0001 x^2 = 25.41, df = 5). By contrast, higher, albeit limited differences (p-value = $=0.1225 \text{ x}^2 = 8.6834, \text{ df} = 5$) were found in terms of vertical distances. Higher values were observed at RK2 (9.4 \pm 11.2 cm), values at RK1 (6.4 \pm 10.1 cm) and RK3 (7.3 \pm 8.5 cm) were lower. Interestingly, vertical and horizontal orthogonal distances did not correlate significantly with sapling ages ($r^2 = 0.0078$). Based on the germination ages of the 120 Scots pine saplings and bias-corrected peat accumulation – taking possible deformation into account - we obtain an average peat accumulation rate (PAR) for the Rėkyva peatland complex of 1.6 ± 0.72 cm yr⁻¹. The highest PAR's values are found close to the lake

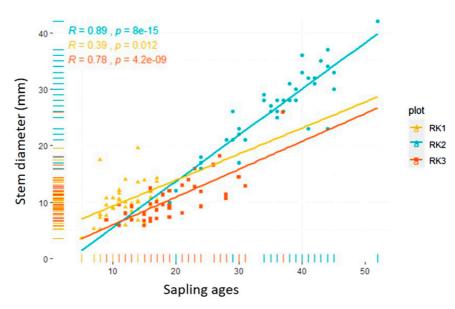


Figure 3. Relationship between stem diameter and sapling ages at plots RK1 (yellow triangles), RK2 (blue dots) and RK3 (red squares). For interpretation of the references to colours in this figure legend, refer to the online version of this article.

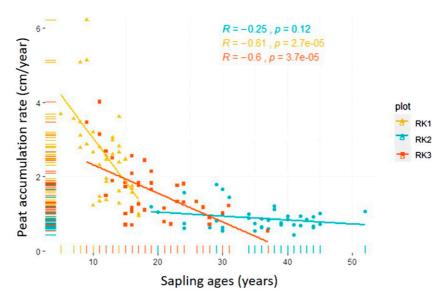


Figure 4. Relationship between estimated peat accumulation rates and sapling age. For interpretation of the references to colours in this figure legend, refer to the online version of this article.

in plot RK1 with 2.4 ± 1.0 cm yr⁻¹, the lowest values were obtained in plot RK2 with 0.8 ± 0.3 cm yr⁻¹. Values at plot RK3 $(1.6 \pm 0.7 \text{ cm yr}^{-1})$ were virtually identical with the mean PAR of the full dataset.

According to the Friedman test at LSD 95%, means obtained at the three plots are statistically different ($x^2 = 53.9$, df = 2 and p-value = $1.9e^{-12}$, Figures 4 and 5).

Age-depth modelling and peat accumulation based on radiocarbon analyses

A total of 24 samples were extracted from the uppermost 58 cm of the peat core sampled in plot RK2 and subsequently dated by radiocarbon (¹⁴C). As can

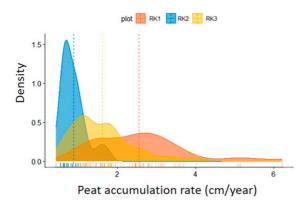


Figure 5. Distributions of peat accumulation rates at each of the plots. For interpretation of the references to colours in this figure legend, refer to the online version of this article.

be seen in Table 1, analyses yielded the highest ¹⁴C activity at a depth of 23.75 cm, and a decline in activity as one goes both upwards and downwards in the stratigraphic record. It can thus be assumed that the uppermost 23.75 cm of the record represent peat accumulation during a period following the 1963 bomb peak and today while the sequence below 25.35 cm was formed before 1963. However, the significant gap in time the 14C ages show also indicates that there is a hiatus at a depth comprised between 23.75 and 25.35 cm, which means that the actual bomb peak is missing. All ¹⁴C-samples were initially used to construct the age-depth model and to estimate changes in peat accumulation rates over time (Figure 6(a)). Between 1984 and today, PARs were in the range of 0.35 ± 0.07 to 0.79 ± 0.05 cm yr⁻¹ (Table 2; Figure 6(b) and (c)). By contrast, at depths > 24 cm, significantly lower PAR values were obtained, often in the order of 0.05 ± 0.01 cm yr⁻¹. Due to the presence of the hiatus described above, we limited analysis to the upper 23.75 cm of the peat sequence when comparing PARs calculated with the ¹⁴C method and the tree saplings.

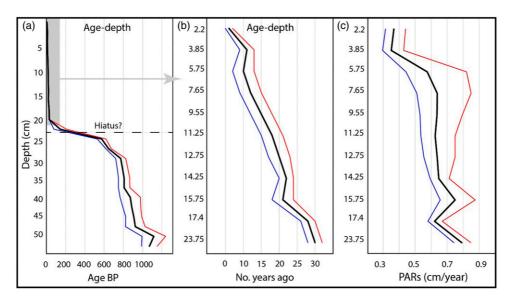


Figure 6. (a) Age-depth model based on a radiocarbon (¹⁴C) dated peat sequence from plot RK2. (b) Age-depth model for the peat sequence above the possible hiatus at a depth between 23.75 and 25.35 cm bellow the peat surface. (c) Peat accumulation rates (PAR) for the uppermost 23.75 cm. For interpretation of the references to colours in this figure legend, refer to the online version of this article.

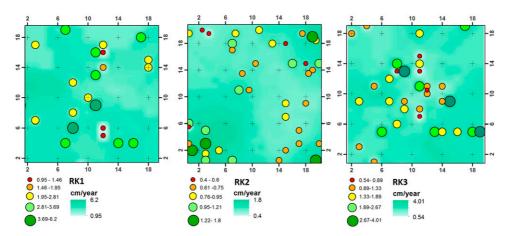


Figure 7. Interpolation of peat accumulation rates with an Inverse Distance Weighting approach in plots RK1, RK2 and RK3. Interpolation based on IDW method and computed in ArcGis 10.3. For interpretation of the references to colours in this figure legend, refer to the online version of this article.

Discussion

In this study, we employed a botanical approach to reconstruct and quantify peat accumulation rates (PAR) at annual to decadal scales in a Lithuanian peatland colonized by Scots pines. Based on the analysis of 120 P. sylvestris saplings and accurate micro-topographic measurements around the trees that have been hand-picked for analyses, we provide a retrospective estimate of PAR at three plots (20 \times 20 m) in the Rèkyva peatland complex. Even if the suitability and potential of the tree-ring-based approach have been demonstrated previously by Ohlson and Dahlberg (1991), it has not been employed widely ever since. In addition, we review this approach critically and propose methodological improvements to (i) determine the exact year of sapling germination with dendrochronological analyses and (ii) to characterize variations in peat microtopography around the saplings. Using the results of PAR at the level of individual trees (with a mean PAR of 1.6 ± 0.72 cm yr⁻¹), we also demonstrate the potential of interpolation approaches in estimating mean accumulation rates at the plot scale and point to strong heterogeneity in PAR occurring within small surfaces. The improved approach presented in this paper expands our understanding of peat evolution over the last decades and with high spatial resolution.

Comparing botanical and radiocarbon-based estimates of peat accumulation

Comparisons between tree-ring and radiocarbonbased estimates of PAR were performed in this work at plot RK2. To this end, we used the uppermost 24 cm of the peat core for which recent, radiocarbonbased PAR could be obtained (Table 2, Figure 7(a)). Below this level, accumulation rates drop drastically. We explain these changes with (i) the compression of peat with increasing depth, (ii) the degradation of organic matter, as well as with (iii) a likely hiatus in the record. The likely interruption of accumulation restricted comparison to the uppermost part of the peat sequence, equivalent to a peat depth of 23.75 cm and an age reconstructed at 30 ± 2 years. As the average age of pine saplings was c. 25 years and as their roots only rarely exceeded depths of 24 cm, the relative short radiocarbon-based series is not considered to influence comparison in any way.

Interestingly, PAR values reconstructed with the tree-ring and radiocarbon-based approaches yield virtually identical results with 0.8 ± 0.3 and 0.79 ± 0.05 cm yr⁻¹, respectively. In comparison to other studies (Table 1), the PAR can be considered high. Nonetheless, it should be emphasized that the depth for which the comparison is valid only applies to the uppermost layers of the peat sequence

(at depths < 25 cm), whereas other approaches employing ¹⁴C-based age-depth models clearly reach larger depths to extend farther back in time.

Comparison between the two techniques also shows that the radiocarbon-based approach more easily captures minor variations in the PAR with increasing depth (Figure 7(c)). In future studies, we suggest to divide pine sapling material into different subgroups according to root depths, in such a way depth-dependent calculation of PAR could be realized with the botanical approach as well. To do so, much more material would be needed to obtain statistically significant results and with enough relevance for larger parts of a peatland. By contrast, we argue that a key strength of the fine-tuned botanical approach lies in the possibility of obtaining spatially explicit results, as we could show clearly with the different PAR reconstructed between the three plots (RK1-3).

Improvements of the botanical-based peat accumulation assessment

At the scale of the plots analysed, we find an average PAR over the last 20 years ranging between 0.8 (RK2) and 2.4 (RK1) cm yr⁻¹. These results are thus similar to the PAR estimated by Ohlson and Dahlberg (1991) in hummock and lawn communities (0.3– 2 cm yr⁻¹) based on a tree-ring approach covering a comparable time period. By contrast, our values are significantly higher than those obtained at longer (up to millennial) timescales and based on ¹⁴C and ¹³⁷Cs dating (~2.1 mm y⁻¹ in Craft and Richardson (2008), 0.2 mm yr⁻¹ in Drexler et al. (2017) and 0.03 mm yr⁻¹ in Whitehead and Oaks (1979). These discrepancies probably result from the spatiotemporal resolution of different approaches. Indeed, the botanical approach exclusively provides estimates of peat accumulation above the root plate. This portion of the peat corresponds to the acrotelm, that is, the upper organic soil layer affected by fluctuating groundwater tables and characterized by high permeability, high hydraulic conductivity and abundant peat-forming aerobic microorganisms (Morris et al., 2011). As the examined roots barely reached beyond 25 cm peat depth (with a maximum

~36 cm), we have to consider this as the maximum depth for which saplings from the three plots can provide information about. By contrast, age-depth and PAR models based on the ¹⁴C method can also provide insights on the catotelm, that is, on a layer which is permanently below the level of the groundwater table, characterized by compacted peat layers and dominated by abundant anaerobic microorganisms (Morris et al., 2011).

We are also aware that the main limitation of our approach is the neglection of a potential uplift of the pine seed prior to germination. It is thus possible that the seed could be affected by a relative vertical uplift movement as a result of peat accumulation during its first years. We could equally assume that this movement continues until the resistive strength of the root anchorage system exceeds the axial uprooting forces exerted by the soil (Coutts, 1986) and peat accumulation. Albeit this phenomenon has been neglected so far, it could have an impact on the reliability of estimates of peat accumulation and obviously on PAR. Ohlson and Dahlberg (1991) assumed that the vertical position of the seed remains stable and that a downward movement can be excluded for saplings with limited weight.

The development of the taproot, either short and thick or long and thin, is crucial for anchorage (Crook et al., 1997; Stokes, 1999), and the taproot thus acts as a stake in the soil anchoring the tree into the ground (Danquechin Dorval et al., 2016; Ennos, 1993). Although the maximum elongation of roots is controlled by environmental factors (Erktan et al., 2018; Toca et al., 2019), observations on root development in pine trees suggest that taproot length can reach 20 cm after only one year with lateral roots developed at depths exceeding 5–6 cm. In the case of 4-5-year old pine saplings growing in shade and lakewood sand, taproot lengths ranged from 38 to 60 cm (Everett, 1935). Similar taproot extensions have been reported in a wide range of environments (Iversen et al., 2018; Lyr and Hoffmann, 1967; Mattsson, 1986; Stevens, 1931), all suggesting that after 1-2 years, root plate development could be enough to limit or to hinder vertical uplift.

Another source of uncertainty is related to the depth of the peat soil at the time of seed germination, as it can directly affect estimation of PAR. Field

observations indicate that a majority of pine saplings at the study site germinate at depths ranging from 1– 3 cm, thus suggesting that the uppermost portion of the sphagnum carpet can constitute an optimal place for successful germination (Groeneveld et al., 2007). By contrast, if pine seeds germinate deeper in the acrotelm, they will likely be overgrown by sphagnum mosses, annihilating the probability of survival (Okland and Ohlson, 1998; Zackrisson and Ohlson, unpublished). Based on the above considerations and comparing total accumulation (29 \pm 16cm) with germination depth (1–3 cm), measurements could overestimate accumulation depths by up to 9.5%. Finally, we also observe a dependency of PAR with tree age (Figure 4). We agree with Ohlson and Dahlberg (1991) that higher PAR measured in plots with younger trees could reflect the dissimilar influence of compaction and decay processes, as the latter tend to decrease as one goes back in time.

Improvements and limitations of botanical peat accumulation assessments

The botanical approach presented here clearly goes one critical step beyond earlier work (Backman, 1919; Borggreve, 1889; Heikurainen, Ohlson and Dahlberg, 1991; Saarinen, 1933) as it includes two major improvements, that is the (i) determination of the year of germination and (ii) a quantification of peat accumulation since germination, including changes in microtopography next to stems. The exact determination of germination dates is crucial as a deviation of \pm 3 years would bias the resulting PAR at the study site by up to 30% on average. Obviously, this bias would even be higher should younger pine saplings be included for analysis. Unlike Ohlson and Dahlberg (1991) who estimated germination by counting tree rings at peat surface, we analysed cross-sections – cut at 1-cm intervals – from both the stem and the roots. This approach not only allowed identification of the section with the maximum number of rings, but also enabled accurate quantification of the distance to the current peat surface. Despite its clearly added value, we are aware of remaining limitations of our approach, mostly related to the detection of transition stem-root sections which can be very challenging in root systems that are highly influenced by peat dynamics as was systematically the case at our study site (Figure 1(d)).

Microtopographic deformation of peat soils at the vicinity of stems results from the pressure exerted by the root system and the growing stem (Ballesteros-Canovas et al., 2013; Bodoque et al., 2015). If the pressure exerted by the growing stem and expanding roots exceed the unconfined shear strength of the surrounding soil, the latter will be displaced and a small bulge, referred to as hummock (Nungesser, 2003), will form around the stem. Therefore, if microtopographic variations around the saplings is neglected, PAR would be overestimated by c. 10%. Even if smaller errors could be expected in parental soils, the low bulk density and higher hydraulic conductivity of acrotelm found in peatland complexes clearly pledges for a systematic inclusion of precise microtopographic data in future PAR studies. In this paper, microtopography was estimated with field measurements including the length, width and height of small peat hummocks along four compass directions. In the future, studies would most likely get even better results by including high-resolution surveying techniques such as photogrammetry with Terrestrial Laser Scanning (Bodoque et al., 2017). As both sources of uncertainties inherent to previous work can represent up to 40% of the estimated PAR, we demonstrated here why they should be accounted for systematically in future estimates relying on treering records of saplings. Moreover, comparisons between PAR in plot RK2 using our improved botanical approach and the radiocarbon-based approach prove quite nicely that the corrections for microtopographic variations and seed uplift indeed yield very reliable results.

Potential implications of the improved approach

Provided a careful estimation of the biases, the method presented here is particularly interesting as it enables quantification of peat accumulation retrospectively with a high spatio-temporal resolution in an environment where trees become increasingly abundant (Edvardsson et al., 2015a; Rattcliff et al., 2017). From a temporal perspective, the approach provides estimates of PAR for short (i.e. few years) to intermediate (i.e. few decades) timescales, and therefore for a period that is rarely covered by isotope approaches. Furthermore, the tree-ring-based approach allows calculations and comparisons between PAR (i) over a surface (e.g. a plot) and (ii) between zones of a peatland with different hydrological conditions or different vegetation types. This is in contrast to traditional age-depth models that have been used to calculate peat accumulation from stratigraphic sequences, as they were normally based on single point datasets taken from complex, and often quite heterogenous peatland ecosystems. Here, the spatialization of accumulation values at the scale of plots or entire peatlands provides us with unique opportunities to understand environmental changes that can be related to water drainage, climatic fluctuations and/or vegetation evolution. At Rekyva peatland complex, large variations have been observed between the three plots analysed. Thus, a direct improvement of the botanical approach is the capability to use the larger number of observation (in comparison with radiocarbon-based approach) and study the spatial heterogeneity of peat accumulation based on interpolation methods. As example, spatial differences in peat accumulation are shown in Figure 7, where RK1 (and to a lesser degree also RK3) shows a more heterogeneous behave than RK2 (based on range values). We can thus hypothesize that the rapid peat accumulation values computed at plot RK1 could be controlled by the comparably wetter peat surface conditions in the vicinity of the lake (Figure 1(b)). These moister conditions, when compared to RK2 and RK3, may have favoured moss growth and could have been detrimental for colonizing trees. In comparison, relatively dry conditions may have controlled the moderate PAR estimated at plot RK2. The relatively large and old trees observed in this area may have played a role in water-table conditions as well: as the trees get larger and the tree stand becomes more dense, the trees consume more water, which logically results in drier peat surface conditions and, therefore, decreased moss growth (Limpens et al., 2014).

Such increases of vascular plants, foremost pine trees, have been observed in many boreal peatlands (Edvardsson et al., 2015a; Ratcliff et al., 2017; Wang et al., 2015). The increase of trees on peat surfaces may

cause drier peat surface conditions and thereby decreased peat accumulation and carbon storage (Edvardsson et al., 2016; Limpens et al., 2014). Here, the modified tree sapling approach developed may also be relevant when it comes to compare peat accumulation in areas with different tree size and age, as well as with tree-stand densities - thereby assisting in the documentation of likely impacts of tree colonization on PAR. The observed differences in PAR and vegetation between plots RK1 and RK2 show the potential of the botanical approach for such studies quite clearly. Given the rather limited cost of the approach in terms of field sampling and time-series analysis, high replication is theoretically possible. Yet, accounting for the destructive character of the approach, a trade off should be found between exhaustive replication and the preservation of saplings. In this study, we picked 40 trees per plot which allowed us to derive highly resolved interpolated maps. In this regard, different covariables relating to soil parameters, peat morphology or tree characteristics could be included in a statistical model that would allow interpolation of PAR at the peatland scale. Such analyses will be relevant for peatland managers to identify hotspots for restoration of the ecological value of degraded ecosystems (Duberstein et al., 2016; Wurster et al., 2016). As such, our results demonstrate many added values and greatly improved reliability of the botanical approach employing pine saplings to reconstruct PAR. They also provide a new application of treering research in peatlands.

Conclusions

Comparisons between the improved botanical approach using pine saplings and peat microtopography and the radiocarbon-based application used to estimate PAR agree on the rate of accumulating peat for the recent past and for the layers located above the roots of the sapling analysed. The average depth of saplings used in this study was c. 15 cm and the average age of the plants around 20 years, and thus agree with values observed in other boreal peatlands. For greater depths or longer timescales, any estimation of PAR will have to rely on traditional methods using lead (210 Pb) or radiocarbon (14 C) dating.

In conclusion, our approach has also shown that microtopography of the peat surface around saplings

as well as the exact determination of germination ages are essential to quantify peat accumulation rates reliably at short-to medium-term scales. At the plot level, based on the improved methodology, we show heterogeneous peat accumulation rates and hypothesize that differences could be connected to hydrological conditions. Due to its low cost and high replicability, the botanical approach also has a clear potential for upscaling of results using statistical and interpolation models. These findings provide enough evidence that tree saplings can help in assessing vertical accumulation, a parameter that has been discarded traditionally in peatland research. The systematic application of the botanical approach could not only improve our understanding of PAR more systematically, but also open the door to gain more detailed insights into the effect of changing environmental factors on peat evolution.

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