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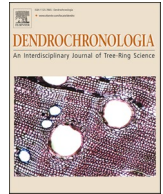
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The timing of wood formation in peatland trees as obtained with different approaches

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ABSTRACT

Dendrometers offer valuable insights into how tree growth responds to climatic variables and physiological processes over the course of a year. Yet, their applicability to extremely slow-growing trees, such as those in peatlands, has been limited due to the intricate and slow nature of growth, therefore rendering interpretation of results complex. In this study, we conducted a comprehensive monitoring of tree wood formation in both peatland and mineral soil ecosystems in southern Sweden (58.37 N, 12.17 E, 75 m asl) in 2021 and 2022, using both band and point dendrometers. To verify and validate the dendrometer data, we also sampled microcores every two weeks during both growing seasons. We find that peatland trees grow at approximately 30 % the rate of their neighbors on mineral soils. The onset of growth among peatland trees typically occurs between mid-May and early June, consistently lagging the start of the growing season in trees on mineral soils by one to three weeks. Notably, growth peaks are synchronized across peatland trees and coincide with the summer solstice. Both types of dendrometers exhibit varying degrees of accuracy depending on the phenological stages measured. They perform well in identifying growth onset and peak but are less effective at detecting growth cessation. Point dendrometers demonstrate superior accuracy as they better capture daily irreversible growth increments. In the case of band dendrometers, growth increments are obscured by greater reversible fluctuations in dead bark tissues. However, they remain valuable for tracking the wood phenology of trees with growth rates exceeding 2 mm/year. Based on our results, for an effective tree monitoring in peatlands, we strongly recommend (1) using point dendrometers and (2) removing the dead bark tissues on monitored trees.

1. Introduction

Pristine peatlands offer a plethora of vital ecosystem services, encompassing carbon sequestration, significant biodiversity support, and crucial roles in freshwater purification (Lolu et al., 2020; MacDonald et al., 2006; Turetsky et al., 2015). Typically, peatlands are characterized by conditions unsuitable for widespread tree encroachment, attributed to nutrient scarcity, water saturation, and low pH levels surrounding tree root systems (Boggie, 1972; Cedro and Lamentowicz, 2011). Currently, peatland tree colonization, as a consequence of climate change, drainage, nitrogen deposition, and alterations in soil and hydrology, is a widespread phenomenon observed across numerous

boreal peatland ecosystems (Edvardsson et al., 2015b; Langdon et al., 2020; Ratcliffe et al., 2017). Once established, trees have the potential to further dry out peat soils (Edvardsson et al., 2016; Holmgren et al., 2015), with potentially profound effects on peatland structure, functioning, hydrology, and ultimately carbon sequestration – by reducing the carbon sink by up to 30 % in peatlands (Holmgren et al., 2015; Malhotra et al., 2020; Ratcliffe et al., 2017; Straková et al., 2012; Strilesky and Humphreys, 2012). However, a solid understanding of interactions between the peatland tree vegetation and hydrology is still critically lacking (Charman et al., 2015; Heijmans et al., 2013; Waddington et al., 2015), partly because multiple questions persist on the actual drivers of peatland tree growth (Dinella et al., 2019; Edvardsson

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et al., 2015b; Smiljanić and Wilmking, 2018). Several standard dendrochronological studies on peatland trees, based on statistical correlation or response function analyses, have been performed without finding a robust and consistent climatic driver of growth, although precipitation and water table appear to have a negative impact on tree growth (Blanchet et al., 2017; Boggie, 1972; Cedro and Lamentowicz, 2011; Edvardsson et al., 2015b; Edvardsson and Hansson, 2015; Linderholm et al., 2002), thus complicating possible climatic reconstructions (but see Tamkevičiūtė et al., 2018).

Hence, a gap exists in comprehending how peatland trees respond to environmental factors. The monitoring of wood formation, i.e., the study of intra-annual growth fluctuations, provides a unique opportunity to uncover the climatic factors influencing growth through ecophysiological mechanisms (Daudet, 2004; Deslauriers et al., 2007; Rathgeber et al., 2016; Steppe et al., 2015; Zweifel et al., 2006). The primary methods used to investigate the patterns and timing of wood formation involve (i) pinning techniques through which controlled wounds are regularly induced to trees during the growing season (Seo et al., 2007), (ii) taking multiple samples from the cambium layer using microcores (Prislan et al., 2013; Rossi et al., 2006b) and (iii) the use of dendrometers (De Swaef et al., 2015; Deslauriers et al., 2003). Several types of dendrometers exist, but band and point dendrometers are the most used. Band dendrometers consist of a flexible band or belt that is wrapped around a tree's stem. The band is equipped with sensors that detect changes in tension as the stem diameter varies. They have been widely used, especially in forestry research, because they are cheap and easy to install (Deslauriers et al., 2007; Miller et al., 2023; Obojes et al.,

2018). Point and LVDT (Linear Variable Differential Transformer) dendrometers (we refer to point dendrometers in both cases in this article) measure the linear displacement of a rod or probe in contact with the tree's stem (Deslauriers et al., 2003; Etzold et al., 2022; Zweifel et al., 2006). Concerns have been raised about the reliability of dendrometers in monitoring wood formation as opposed to the microcore approach which offers a more direct but also more time-consuming alternative (Chan et al., 2016; Mäkinen et al., 2008). Indeed, dendrometer measurements are strongly influenced by the changing water status of the stem, which may mask crucial phenological events such as the onset and cessation of wood formation or the timing of maximum growth (Oberhuber et al., 2020; Oberhuber and Gruber, 2010). Although the limitations of dendrometers are well known, only few studies compared results with microcore data (Chan et al., 2016; Cruz-García et al., 2019; Mäkinen et al., 2008), especially when it comes to compare the two main types of dendrometers (Corell et al., 2014; Wang and Sammis, 2008). We identified only one published research on the use of (band) dendrometers in peatlands (Smiljanić and Wilmking, 2018), and no studies using point dendrometers. However, Edvardsson et al. (2016) demonstrated that these devices can provide important information on the functioning of peatland ecosystems.

Therefore, a methodological study is essential to evaluate the feasibility of different techniques such as microcoring or band and point dendrometers to monitor wood formation phenology of peatland trees. Based on the above considerations, we designed a study through which we assessed wood formation phenology of peatland trees during two consecutive years as obtained with (i) microcoring, (ii) band and (iii)

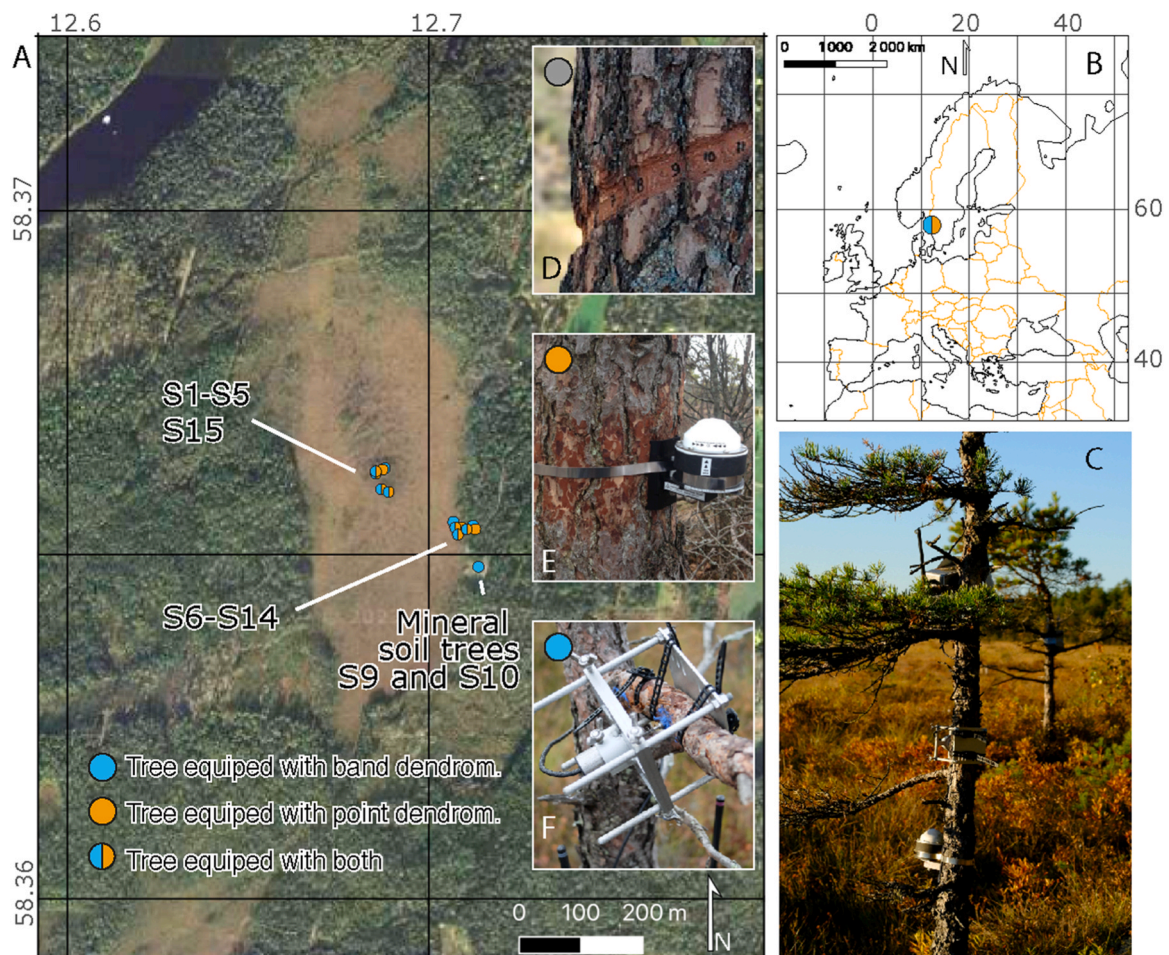


Fig. 1. Location and overview of the Mycklemossen peatland monitoring site in southern Sweden (A, B, C). Location of monitored trees (S1-S15) is indicated (A). Examples of trees monitored with microcore samples (D), a band dendrometer (E), and a point dendrometer (F).

point dendrometry. In addition, nearby mineral soil trees were monitored to highlight variations in wood phenology depending on soil/hydrological conditions and potential challenges specific to peatland tree growth.

2. Methods

2.1. Study site

Tree monitoring took place at Mycklemossen, an ombrotrophic mire with oligotrophic bog-like vegetation in southern Sweden (58.37 N, 12.17 E, 75 m asl, Fig. 1A-B). The site is part of the Skogaryd Research Catchment and Swedish Infrastructure for Ecosystem Science network. Mean annual air temperature and total precipitation are 6.9 °C and

901 mm (1981–2010), respectively, at the nearest weather station located 11 km to the east of the study site. The site consists of a mosaic of drier hummocks and wetter hollows, with local peat deposits extending down to 6 m below the surface (Wallin et al., 2015). The hollows are composed of various *Sphagnum* species, primarily *S. rubellum*, *S. fallax* and *S. austinii* and *Rhynchospora alba*, while the hummocks are dominated by *Eriophorum vaginatum*, *Calluna vulgaris* and *Erica tetralix* (Kelly et al., 2021). Tree species are present in driest hummocks, locally forming forest-like vegetation dominated by *Pinus sylvestris*.

2.2. Microcore sampling and laboratory work

We carefully selected 10 mature *P. sylvestris* tree individuals growing on peat, strategically sampling from both the center and the edge of the

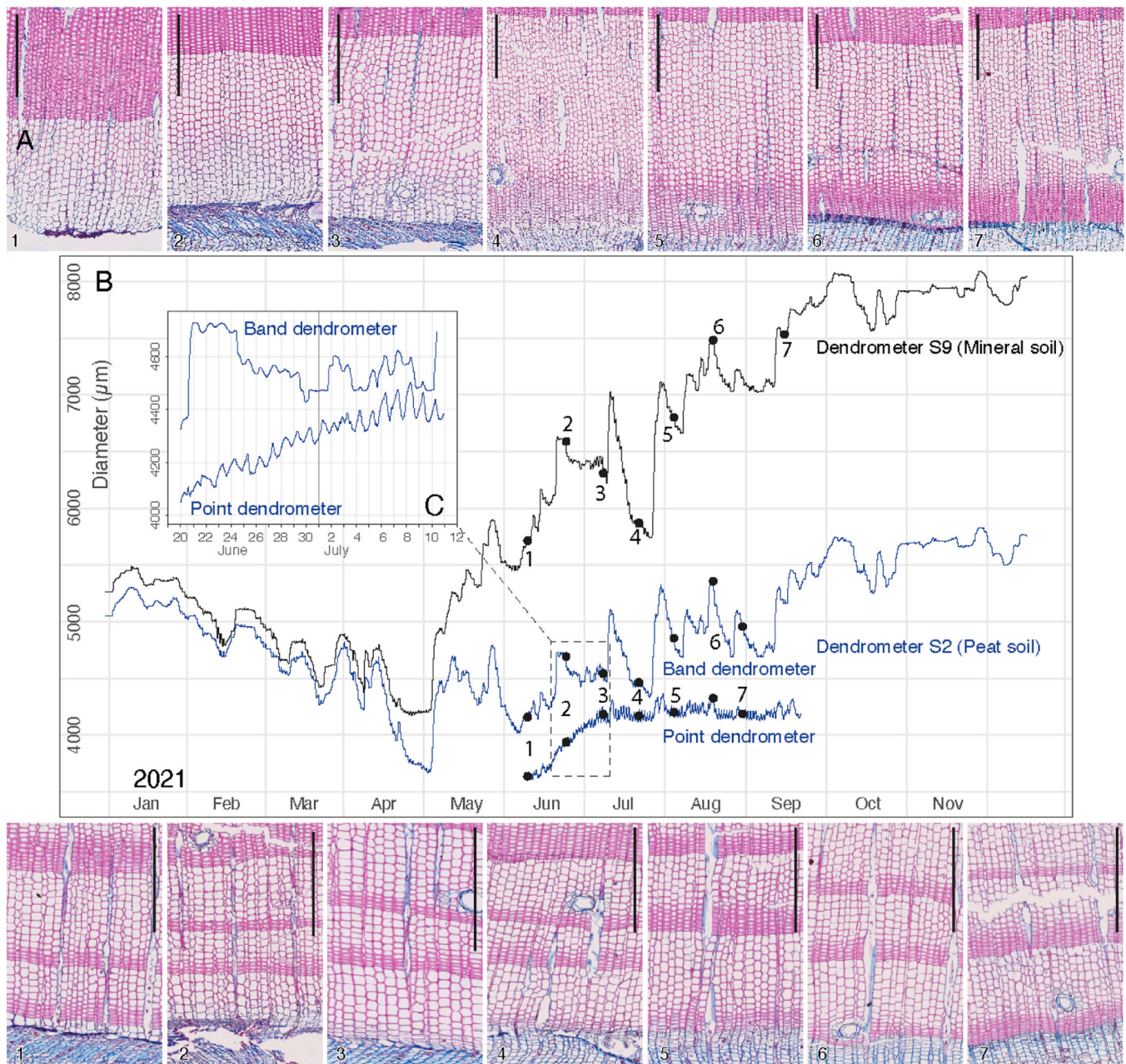


Fig. 2. Examples of the growth seasonal course of two trees derived from microcores, growing on mineral soils (upper panel) and on peat soils (lower panel), respectively (A). The SDV curves of the band dendrometers (SDV_b) are shown in black for mineral soil tree S9 and in blue for peatland tree S2 (B). The numbered points indicate the date the microcores were sampled, and the numbers can be seen on the cross-section images. The SDV of a point dendrometer (SDV_p) is shown for peat tree S2 (B, C). The SDV curves of point and band dendrometers are compared over a shorter time window (C).

mire to ensure representation of the entire peatland. Additionally, we included one individual growing on mineral soil, to provide a comparative reference. The decision to sample only one tree outside the peatland was based on the examination of dendrometric curves spanning several years, which revealed remarkably similar growth patterns. This contrasts with the observed strong interindividual variability among peatland trees. Trees with injuries were avoided. Due to the small stem diameters (between 6 and 20 cm) for peatland trees, we avoided sampling the same trees two years in a row. Consequently, five different individuals with comparable diameters were sampled in 2021 and 2022. By contrast, the same mineral soil tree was sampled over two consecutive years. Wood samples (microcores) of 2 mm in diameter by 15–20 mm in length were collected bi-weekly from mid-May to October from the selected trees using a Trephor tool and following an ascendant spiral starting at breast height (Rossi et al., 2006a, see Fig. 1D). Microcores collected in the field were stored in ethanol solution (50 % in water). Microcores were dehydrated before being embedded in paraffin. Finally, transverse sections of 12 μm were cut using a rotary microtome (Fig. 2A), stained with safranin and astra blue dyes and finally mounted on slides (Schweingruber and Poschold, 2005).

2.3. Dendrometric data acquisition

Stem diameter variation (SDV, see Fig. S2, S3 and S4) was monitored across 10 trees in 2021 and 13 trees in 2022 of *P. sylvestris* growing on peat, along with two additional individuals growing on mineral soil at the edge of the mire (Fig. 1A and Table S4). Ten trees were equipped with band dendrometers (DRL26, EMS, Brno, Fig. 1E) and ten with point dendrometers (Pepiapi, INRAE, Fig. 1F) consisting of an LVDT sensor connected to a data logger. Finally, each microcored tree was also equipped with at least one dendrometer. In most cases, it was not possible to fit both types of dendrometers on the same tree because the point dendrometers cannot be attached to trees with stem or branch diameters greater than 7 cm (see Fig. 1C for an example of a tree monitored with both types of dendrometers), whereas the minimum diameter for the band dendrometers with the used base plate is 8 cm. In total, five individuals were initially equipped with both types of dendrometers. However, the point dendrometer situated on a mineral soil tree experienced a breakdown, reducing the count to four. Before installing the dendrometers, the dead outermost layers of bark were partly removed without damaging living tissues, so as to reduce hygroscopic fluctuations due to the shrinking and swelling of bark tissues (Oberhuber et al., 2020). In the case of dendrometers, the rod of the sensor was sealed with silicone to the stem to prevent water loss through evaporation (Oberhuber et al., 2020). Stem diameter variation from band (SDV_b) and point (SDV_p) dendrometers were recorded at hourly resolution (Fig. 2BC).

2.4. Wood phenological stages extraction (onset, peak and growth cessation)

Microcores can help to determine the onset and cessation of cambial growth based on the number of enlarging tracheids. In spring, when at least one horizontal row of cells was observed in the enlarging phase, xylem formation was considered to have begun (Deslauriers et al., 2008). In cases where timings occurred between two sampling dates, we used a modeling approach to determine the exact date. Specifically for growth onset, we extrapolated the missing data by fitting a straight line and determined the date corresponding to the first modeled row of tracheids formed. In late summer, when no more cells were observed in the enlargement phase, radial growth was considered complete. We chose not to place the cessation of growth at the end of the cell wall thickening phase as in other studies (Deslauriers et al., 2008; Gruber et al., 2010) because we were seeking for a comparison with dendrometric data and dendrometers that are not sensitive to this phenological stage. To determine the growth peak, we fitted a Gompertz function over

the total number of tracheids produced at each date. The maximum slope's timing corresponding to the growth peak was finally extracted.

To extract the growth onset and cessation dates from the dendrometer time series, we first applied the zero growth method of Zweifel et al. (2016), assuming no growth during periods of stem shrinkage and used the R package treenetproc (Knüsel et al., 2021). Because we observed a large increase in diameter in winter due to hygroscopic effects in dead bark tissues swelling when the water table is high in winter, we removed SDV from October to April 20 (see Fig. S1). During the growing season, accumulated growth appears as a step-like line that increases during periods when the stem diameter exceeds an earlier maximum. Thus, growth onset was detected when stem diameter in spring reaches the maximum value in the previous growing season. Growth onset and growth cessation are defined here as when SDV reaches 5 % and 95 % of annual growth, respectively (Etzold et al., 2022; Knüsel et al., 2021). In addition, we calculated the growth rate by dividing the increase in stem diameter by the number of days between two diameter swelling events ($\mu\text{m}\cdot\text{day}^{-1}$). The growth peak corresponds to the highest growth rate. Finally, data for onset, peak, and cessation of growth were compared between the three different methods (microcoring, band, and point dendrometry).

3. Results

3.1. Wood phenology derived from cell counting

Microcoring samples (Figs. 3 and 4, Table S1) of peatland trees show that the first row of tracheids was formed on June 4 (DOY 155.6 \pm 2.88 days) in 2021 and on May 16 (DOY 136 \pm 1 day) in 2022. For the mineral soil tree, growth started systematically earlier, on May 6 (DOY 126) and 7 (DOY 127), in 2021 and 2022, respectively. The last enlarging tracheid of peatland trees was detected, with greater variability among trees than for the growth onset, on July 24 (DOY 205.4 \pm 7.57) and September 2 (DOY 245.2 \pm 9.96) in 2021 and 2022, respectively. Thus, growing season length was the same or longer for trees on mineral soils (89 and 106 days in 2021 and 2022, respectively) than for trees on peat soils (50 and 109 days in 2021 and 2022, respectively). However, the growth peaks occurred at similar timings among trees and years, namely around the summer solstice (Table S2). The tree that grows on mineral soil produced an average of 43 rows of tracheids per year, which is significantly more than trees growing on peat soil ($n = 15$) (Fig. 3).

3.2. Wood phenology derived from dendrometers

Point dendrometer data show regular daily oscillations and regularly increasing SDV patterns similar to the curves obtained from cell counting (Fig. 2C). By contrast, the SDV extracted from the band dendrometers shows strong and irregular oscillations (Fig. 2C), where it is difficult to detect growth, especially in individuals with low growth rates where no growth trend is noticeable on SDV curves during the growth period, even when cell counting shows a clear growth trend (i.e., S1, S4, and S5, Fig. 4). SDV_b, sometimes temporarily decreases, even when tracheid rows are formed, while SDV_p increases in the same period of time (i.e., between June 22 and July 21, 2021, for band dendrometers S2 and S9, see Fig. 2).

The onset of growth determined by point dendrometers closely followed the growth onset extracted from cell counting with a small delay of $+5 \pm 5.17$ days (Figs. 5 and 6). In comparison, band dendrometers show more inconsistent results regarding growth onset (-10 ± 5.17). Growth onset timings were found systematically earlier than those obtained from microcore analyses in 2021, but later in 2022, with high variability among trees (Fig. 6). The growth peak was more accurately determined with point dendrometers (-2 ± 7.17) as compared to band dendrometers ($+9 \pm 47.2$). However, growth cessation was determined inaccurately for both types of dendrometers (Fig. 6) (-33 ± 34.2 and 27

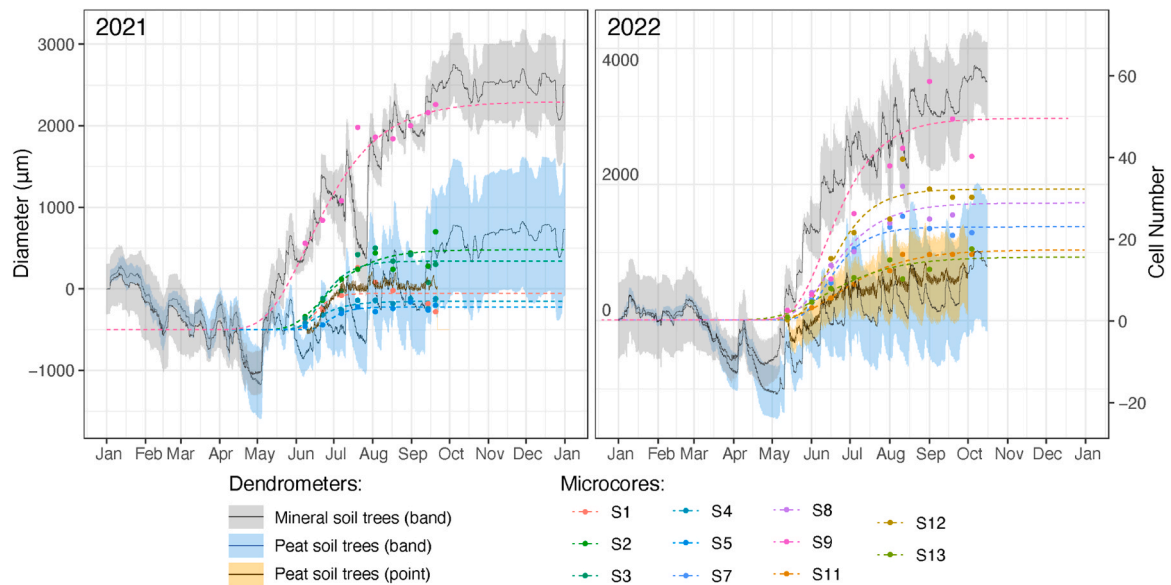


Fig. 3. Overview of the microcore, band, and point dendrometer data set for 2021 and 2022. Mean stem diameter variations (SDV) are shown for band dendrometers for mineral soil trees (black line), band dendrometers for peatland trees (blue line), and point dendrometers (yellow line) with their 95 % confidence intervals. Colored dots indicate the cumulative number of tracheid rows for all sampled trees over the growing season, fitted by a Gompertz model (colored dashed lines).

± 32.7 for point and band dendrometers, respectively). Interestingly, the time lags between the wood phenological timings from the band dendrometers and the microcores are much smaller for the trees that have higher growth rates (see Fig. S5), especially for the mineral soil tree, which has a lag of only -1 day and $+4$ days for the observed growth onset in 2021 and 2022, respectively.

4. Discussion

4.1. Specificity of growth timings on peatland environments

According to dendrochronological studies, the growth of peatland trees is mainly related to the hydrology of the peatland, i.e., the variability of the water table and the subsequent availability of oxygen and nutrients due to soil aeration (Boggie, 1972; Edvardsson et al., 2016; Linderholm, 1999). Therefore, the peatland trees' main environmental limiting factor differs from trees growing on mineral soils (Edvardsson et al., 2015a; Linderholm et al., 2002; Rimkus et al., 2019; Smiljanić and Wilmking, 2018). Our study indicates notable differences between peat and mineral soil trees, first in terms of overall wood productivity (number of cells produced annually) and, second in the timing of growth phenology, particularly growth onset. Interestingly, unlike the trees on mineral soils, which started growing at approximately the same time in both years, the onset of growth in peatland trees was systematically delayed (30 days in 2021 and 10 days in 2022), suggesting that a local factor specific to the peatland was constraining growth onset. However, these differences between peatland and surrounding trees should be viewed with caution, as our sampling strategy has limitations (i.e. unbalanced monitoring of trees in peat vs. mineral soils). However, the almost identical results obtained using microcores and dendrometers for the two mineral soil trees give us confidence in the representativeness of our sampling. While it would be valuable in future studies to examine more peatlands across different regions to validate our findings, it is noteworthy that Smiljanić and Wilmking (2018) also reported shorter growing seasons for peatland trees compared to nearby trees in their study site in Finland. This indicates a potential consistency in the observed patterns between different peatlands and across regions.

In peatland ecosystems, if the high water table could limit tree growth, soil temperature, which is generally lower in peat soils than in

mineral soils, could also play a role (Lieffers and Rothwell, 1987; Malhotra et al., 2020). It is well known that growth peaks in temperate and boreal regions occur quasi-simultaneously around the time of maximum daylength (Gruber et al., 2009; Rossi et al., 2006b). This result was reaffirmed in our study, as the maximum growth rates were found around the summer solstice in all trees, both soil types, and both years. However, the cessation of growth (based on cell enlargement) varies from tree to tree. This could be due to the specific microconditions of each tree, and control factors may differ from year to year. These may include photoperiod, a temperature threshold, the onset of wood formation, drought (Mu et al., 2023), and also a rising water table in the case of peatland trees. Since we found a much shorter growing season in 2021 than in 2022, the timing of growth onset, and thus the length of the growing season, does not appear to be a determining factor in the timing of growth cessation. Overall, our results differ slightly from those of Smiljanić and Wilmking (2018), the only comparable study on peatland trees. The main differences are that they found a comparable timing for the onset of wood formation in trees on mineral and peat soils, but, more importantly, they evidenced a very early timing for the cessation of growth (around the summer solstice).

Finally, our findings underscore the potential of dendrometric studies in peatland tree research, which can be conducted on a larger spatial and temporal scale compared to the labor-intensive practice of tree microcoring. They also highlight the potential difficulties of such a study, mainly due to the very low growth rates observed in these ecosystems.

4.2. Dendrometry in peatland environments

Our results point to differences between the two types of dendrometers. SDV obtained from point dendrometers are more consistent with the results of the microcoring technique than band dendrometers. SDV_b shows a combination of large, irregular amplitudes and smaller daily fluctuations. The large fluctuations undoubtedly correspond to reversible fluctuations in the stem related to hygroscopic movements in the elastic tissues outside the cambium and especially in the dead tissues of the bark (Delapierre et al., 2023; Oberhuber et al., 2020), probably because the bark could not be completely removed around the stem. Additionally, due to the small stature of the trees, the dendrometers were in close proximity to the water table, potentially facilitating water

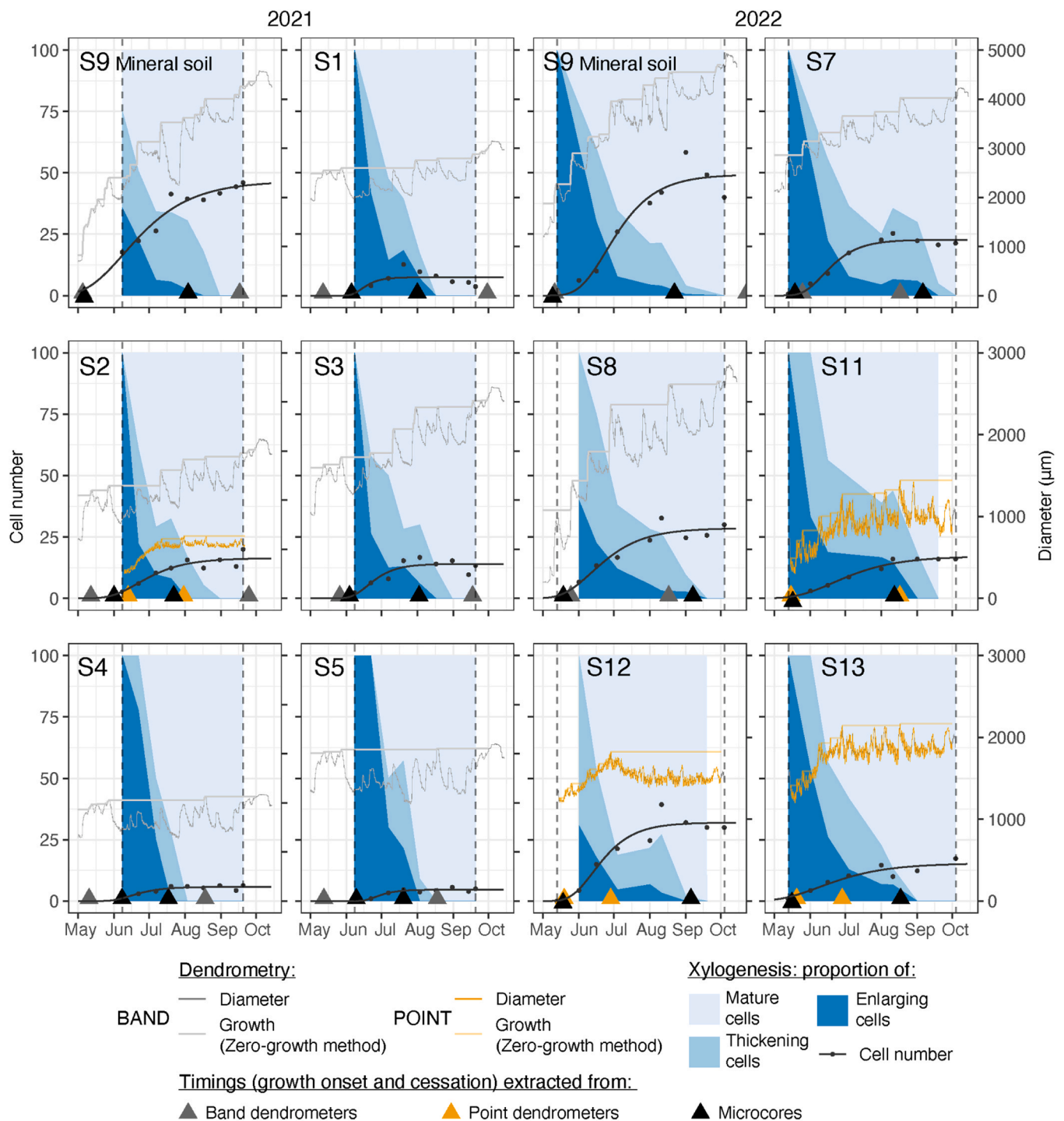


Fig. 4. Black dots show the cumulative number of tracheid rows fitted with a Gompertz model (black line) for each microcored tree in 2021 and 2022. Dark, medium, and light blue areas indicate the proportion of enlarging, thickening, and mature tracheids, respectively, to their total number. Dark grey lines indicate SDV derived from band dendrometers. Light grey lines correspond to growth increments determined by the Zero-growth method. SDV and growth increments determined by point dendrometers are shown in orange. Colored triangles show the timings of growth onset and cessation determined with microcores (black), band dendrometers (grey), and point dendrometers (orange). At least one enlarging cell was the threshold used to assess growth onset and cessation from microcores. For the dendrometric curves, the onset and cessation of growth were determined when the SDV reached 5% and 95% of the total growth, respectively.

transfer between the peat and the bark through capillary processes. Daily cycles corresponding to the sequence of (1) contraction, (2) recovery, and potentially (3) irreversible growth described by Downes et al. (1999) and Deslauriers et al. (2003) are more evident in SDV_p than in SDV_b. This explains the agreement between the phenological timings obtained with SDV_p (growth onset and peak timings) and the microcore analyzes. Compared to a band dendrometer, it is easier to properly

remove the bark when installing point dendrometers, since the contacts between the dendrometer and the stem are significantly reduced. This explains the reduction of reversible hygroscopic noise in the final SDV_p curves. For band dendrometers, the high amplitude reversible fluctuations seem to mask the irreversible growth, especially for slow growing peatland trees (with radius increase < 2 mm). This explains the difference in phenological growth timing extracted from SDV_b compared to

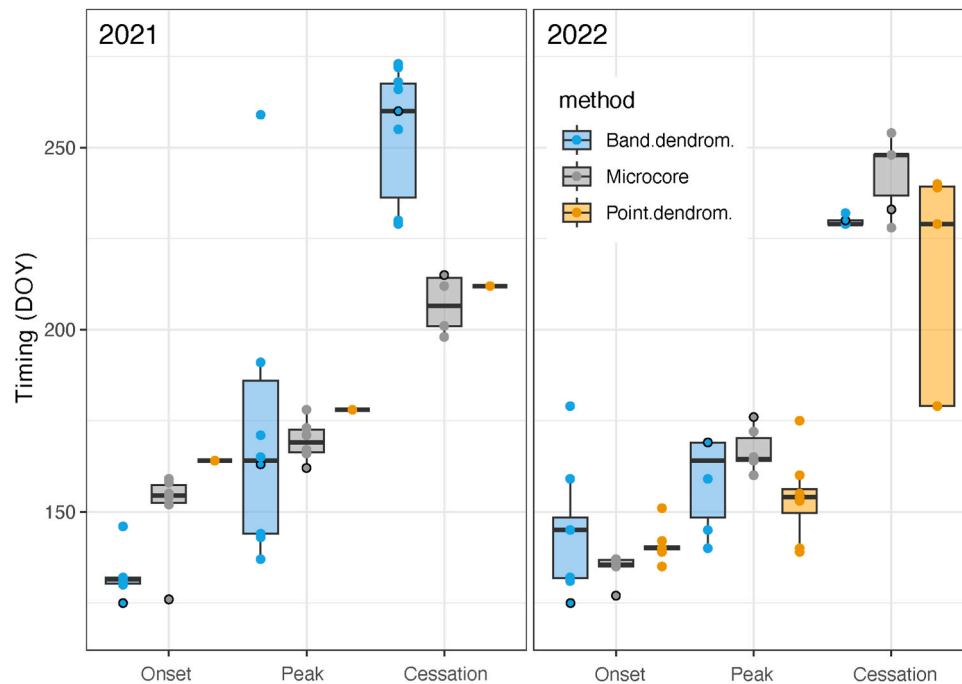


Fig. 5. Phenology of wood formation (growth onset, peak and cessation) extracted from microcores, band, and point dendrometers (in grey, blue, and orange, respectively) for 2021 and 2022. The points corresponding to the reference mineral soil trees are circled in black.

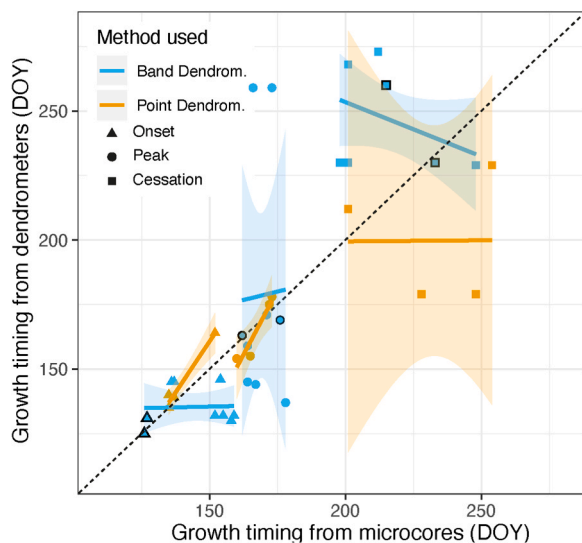


Fig. 6. Growth onset (triangles), peak (circles), and cessation (squares) timings extracted from band (in blue) and point dendrometers (in orange) compared to cell counting (microcores). The points corresponding to the reference mineral soil trees are circled in black.

the microcore analysis. In this context, without isolating the reversible hygroscopic signal, it is challenging to use SDV_b to extract phenological timing, and even more so to analyze hydroclimatic drivers of growth, which can lead to misleading results, as pointed out by Oberhuber et al. (2020).

Growth onset obtained from SDV_p was consistently observed at comparable or only later timings (+5 days) than in microcores, consistent with the findings of Gruber et al. (2009). This is in contrast to other comparative studies (Chan et al., 2016; Mäkinen et al., 2008), where dendrometers indicated the onset of growth with a systematic advance compared to the microcoring results, which in their case was explained by stem pre-growth rehydration and/or bark growth. Peak growth was

also well detected by point dendrometers, in agreement with Gruber et al. (2009). However, discrepancies between growth cessation data obtained from SDV_p and microcores are greater than those previously found in the literature (Gruber et al., 2009; Mäkinen et al., 2008). Since the dendrometers were placed at a certain distance above the place where the microcores were sampled, it is possible that the higher part of the tree is subjected to greater dehydration than the lower part of the stem (Charrier et al., 2017), which could explain the discrepancy between the timing of growth cessation determined by the two methods. Moreover, due to its costliness and time-consuming nature, we opted for bi-weekly microcore sampling intervals in our study. Consequently, despite the approximation of the timings between two sampling dates by a modeling approach, inaccuracies may persist in the determination of the critical growth timings. It should also be considered that the threshold of 95 % of total growth used to extract the end of growth from the dendrometric data is arbitrary and could explain these discrepancies between the two methods.

4.3. Recommendations

For future monitoring of trees in peatlands, we highly recommend employing point dendrometers because of their accuracy and the minimal issues they present in dealing with fluctuations related to dead bark tissue. The key advantage of point dendrometers lies in their ability to facilitate the removal of dead bark layers specifically at the point of contact between the dendrometer rod and the tree stem. This process is notably more straightforward compared to the laborious task of scraping dead bark from the entire circumference of the trunk, as required by band dendrometers. It is worth noting that our recommendations align closely with those proposed by Oberhuber et al. (2020).

However, several multi-annual SDV records on peatland trees are available in several countries from band dendrometers (Augustaitis, 2021; Smiljanić and Wilmking, 2018). We believe that this dataset could be used to extract information on wood formation phenology by following some recommendations. First and foremost, our research suggests that determining the timing of wood formation in trees with an annual ring width exceeding 2 mm can be readily achieved through the

analysis of band dendrometer data. Secondly, the most reliable method for identifying the onset of growth is to use exceedance of the maximum diameter of the previous growing season (April to October) as a reference point. It is crucial to exclude winter months (November to March) from considerations, as reversible bark swelling during this period may mask growth increments during the following growing season. Thirdly, one potential solution to isolate the cambial growth signal would be to distinguish actual irreversible growth from reversible swelling and contraction of elastic tissues. This distinction can be effectively achieved by integrating moisture-related data, such as water table depth in peatlands, to identify hygroscopic patterns within SDV. Furthermore, considering the monitoring of standing dead trees with intact bark as it has been done by Oberhuber et al. (2020), represents another way to extract irreversible growth, since dead trees does not show irreversible growth.

5. Conclusion

In summary, our study (1) offers essential guidelines for the accurate monitoring of cambial growth within peatland environments. It also (2) uncovers contrasting phenological characteristics and wood growth rates in peatland trees when compared to those growing on mineral soils, thereby highlighting the influence of peatland-specific conditions.

Our results suggest a delayed growth and shorter growing seasons experienced by peatland trees compared to mineral soil trees. This observation may contribute to understanding the varied climate-growth relationships reported in dendrochronological literature between these two environments (Dinella et al., 2021; Edvardsson et al., 2015a). Visual observations of cell enlargement by microcores sampling, here performed for the first time in peatland environment, allow us to emphasize the limitations of band dendrometry and encourage the use of point dendrometers in future studies. Band dendrometers provide noisy and complex records where water content of dead bark tissue interferes with growth increments. In contrast, point dendrometers, when properly utilized, can provide valuable insight into the response of peatland trees to climate. We believe that our recommendations also apply to peatland trees in other biomes and even in any highly constrained ecosystem where stress keeps tree growth rates very low.

It is important to acknowledge the inherent limitations of our research, including the relatively small sample size of microcore sampling and tree monitoring. In particular, a focused investigation on the growth differences between trees growing within and outside the peatland would be essential to confirm our results. Nevertheless, our work remains a good starting point for better use of existing dendrometric data and for future monitoring of trees in such a poorly studied and complex environment, which holds immense ecological significance.

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Markus Stoffel reports financial support was provided by Swiss National Science Foundation.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2024.126210.

References

- Augustaitis, A., 2021. Intra-annual variation of stem circumference of tree species prevailing in hemi-boreal forest on hourly scale in relation to meteorology, solar radiation and surface ozone fluxes. *Atmosphere* 12, 1017. <https://doi.org/10.3390/atmos12081017>.
- Blanchet, G., Guillet, S., Calliari, B., Corona, C., Edvardsson, J., Stoffel, M., Bragazza, L., 2017. Impacts of regional climatic fluctuations on radial growth of Siberian and Scots pine at Mukhrino mire (central-western Siberia). *Sci. Total Environ.* 574, 1209–1216. <https://doi.org/10.1016/j.scitotenv.2016.06.225>.
- Boggie, R., 1972. Effect of water-table height on root Development of Pinus contorta on Deep Peat in Scotland. *Oikos* 23, 304. <https://doi.org/10.2307/3543168>.
- Cedro, A., Lamentowicz, M., 2011. Contrasting responses to environmental changes by pine (*Pinus sylvestris* L.) growing on peat and mineral soil: an example from a Polish Baltic bog. *Dendrochronologia* 29, 211–217. <https://doi.org/10.1016/j.dendro.2010.12.004>.
- Chan, T., Hölttä, T., Berninger, F., Mäkinen, H., Nöjd, P., Mencuccini, M., Nikinmaa, E., 2016. Separating water-potential induced swelling and shrinking from measured radial stem variations reveals a cambial growth and osmotic concentration signal. *Plant Cell Environ.* 39, 233–244. <https://doi.org/10.1111/pce.12541>.
- Charman, D.J., Amesbury, M.J., Hinchliffe, W., Hughes, P.D.M., Mallon, G., Blake, W.H., Daley, T.J., Gallego-Sala, A.V., Mauquoy, D., 2015. Drivers of Holocene peatland carbon accumulation across a climate gradient in northeastern North America. *Quat. Sci. Rev.* 121, 110–119. <https://doi.org/10.1016/j.quascirev.2015.05.012>.
- Charrier, G., Nolf, M., Leitinger, G., Charra-Vaskou, K., Losso, A., Tappeiner, U., Améglio, T., Mayr, S., 2017. Monitoring of freezing dynamics in trees: a simple phase shift causes complexity. *Plant Physiol.* 173, 2196–2207. <https://doi.org/10.1104/pp.16.01815>.
- Corell, M., Girón, I.F., Galindo, A., Torrecillas, A., Torres-Sánchez, R., Pérez-Pastor, A., Moreno, F., Moriana, A., 2014. Using band dendrometers in irrigation scheduling. *Agric. Water Manag.* 142, 29–37. <https://doi.org/10.1016/j.agwat.2014.04.005>.
- Cruz-García, R., Balzano, A., Cufar, K., Scharnweber, T., Smiljanić, M., Wilmking, M., 2019. Combining Dendrometer Series and Xylogenesis Imagery—DevX, a simple visualization tool to explore plant secondary growth phenology. *Front. For. Glob. Change* 2, 60. <https://doi.org/10.3389/fgc.2019.00060>.
- Daudet, F.-A., 2004. Experimental analysis of the role of water and carbon in tree stem diameter variations. *J. Exp. Bot.* <https://doi.org/10.1093/jxb/eri026>.
- De Swaef, T., De Schepper, V., Vandegehuchte, M.W., Steppe, K., 2015. Stem diameter variations as a versatile research tool in ecophysiology. *Tree Physiol.* 35, 1047–1061. <https://doi.org/10.1093/treephys/tpv080>.
- Delapierre, F., Fonti, P., Lischke, H., Moos, C., 2023. A method to quantify and account for the hygroscopic effect in stem diameter variations. *Front. For. Glob. Change* 6, 1167542. <https://doi.org/10.3389/fgc.2023.1167542>.
- Deslauriers, A., Morin, H., Urbinati, C., Carrer, M., 2003. Daily weather response of balsam fir (*Abies balsamea* (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Québec (Canada). *Trees - Struct. Funct.* 17, 477–484. <https://doi.org/10.1007/s00468-003-0260-4>.
- Deslauriers, A., Rossi, S., Anfodillo, T., 2007. Dendrometer and intra-annual tree growth: what kind of information can be inferred? *Dendrochronologia* 25, 113–124. <https://doi.org/10.1016/j.dendro.2007.05.003>.
- Deslauriers, A., Rossi, S., Anfodillo, T., Saracino, A., 2008. Cambial phenology, wood formation and temperature thresholds in two contrasting years at high altitude in southern Italy. *Tree Physiol.* 28, 863–871. <https://doi.org/10.1093/treephys/28.6.863>.
- Dinella, A., Giammarchi, F., Prendin, A.L., Carrer, M., Taroni, G., 2021. Xylem traits of peatland Scots pines reveal a complex climatic signal: a study in the Eastern Italian Alps. *Dendrochronologia* 67, 125824. <https://doi.org/10.1016/j.dendro.2021.125824>.
- Dinella, A., Giammarchi, F., Taroni, G., 2019. Are living peatland trees a reliable natural archive for climate reconstruction? *IAWA* 40, 366–379. <https://doi.org/10.1163/22941932-40190228>.
- Downes, G., Beadle, C., Worledge, D., 1999. Daily stem growth patterns in irrigated *Eucalyptus globulus* and *E. nitens* in relation to climate. *Trees* 14, 102–111. <https://doi.org/10.1007/PL00009752>.
- Edvardsson, J., Hansson, A., 2015. Multiannual hydrological responses in Scots pine radial growth within raised bogs in southern Sweden. *Silva Fenn.* 49 <https://doi.org/10.14214/sf.1354>.
- Edvardsson, J., Rimkus, E., Corona, C., Šimanasienė, R., Kažys, J., Stoffel, M., 2015a. Exploring the impact of regional climate and local hydrology on *Pinus sylvestris* L. growth variability – a comparison between pine populations growing on peat soils

- and mineral soils in Lithuania. *Plant Soil* 392, 345–356. <https://doi.org/10.1007/s11104-015-2466-9>.
- Edvardsson, J., Šimanas, R., Taminskas, J., Baužienė, I., Stoffel, M., 2015b. Increased tree establishment in Lithuanian peat bogs — insights from field and remotely sensed approaches. *Sci. Total Environ.* 505, 113–120. <https://doi.org/10.1016/j.scitotenv.2014.09.078>.
- Edvardsson, J., Stoffel, M., Corona, C., Bragazza, L., Leuschner, H.H., Charman, D.J., Helama, S., 2016. Subfossil peatland trees as proxies for Holocene palaeohydrology and palaeoclimate. *Earth-Sci. Rev.* 163, 118–140. <https://doi.org/10.1016/j.earscirev.2016.10.005>.
- Etzold, S., Sterck, F., Bose, A.K., Braun, S., Buchmann, N., Eugster, W., Gessler, A., Kahnen, A., Peters, R.L., Vitasse, Y., Walthert, L., Ziemińska, K., Zweifel, R., 2022. Number of growth days and not length of the growth period determines radial stem growth of temperate trees. *Ecol. Lett.* 25, 427–439. <https://doi.org/10.1111/ele.13933>.
- Gruber, A., Strobl, S., Veit, B., Oberhuber, W., 2010. Impact of drought on the temporal dynamics of wood formation in *Pinus sylvestris*. *Tree Physiol.* 30, 490–501. <https://doi.org/10.1093/treephys/tpq003>.
- Gruber, A., Zimmermann, J., Wieser, G., Oberhuber, W., 2009. Effects of climate variables on intra-annual stem radial increment in *Pinus cembra* (L.) along the alpine treeline ecotone, 503–503 *Ann. Sci.* 66. <https://doi.org/10.1051/forest/2009038>.
- Heijmans, M.M.P.D., van der Knaap, Y.A.M., Holmgren, M., Limpens, J., 2013. Persistent versus transient tree encroachment of temperate peat bogs: effects of climate warming and drought events. *Glob. Change Biol.* 19, 2240–2250. <https://doi.org/10.1111/gcb.12202>.
- Holmgren, M., Lin, C.-Y., Murillo, J.E., Nieuwenhuis, A., Penninkhof, J., Sanders, N., van Bart, T., van Veen, H., Vasander, H., Vollebregt, M.E., Limpens, J., 2015. Positive shrub-tree interactions facilitate woody encroachment in boreal peatlands. *J. Ecol.* 103, 58–66. <https://doi.org/10.1111/1365-2745.12331>.
- Wang, J., Sammis, T.W., 2008. New automatic band and point dendrometers for measuring stem diameter growth. *Appl. Eng. Agric.* 24, 731–742. <https://doi.org/10.13031/2013.25361>.
- Kelly, J., Kljun, N., Eklundh, L., Klemetsson, L., Liljebladh, B., Olsson, P.-O., Weslien, P., Xie, X., 2021. Modelling and upscaling ecosystem respiration using thermal cameras and UAVs: application to a peatland during and after a hot drought. *Agric. For. Meteorol.* 300, 108330. <https://doi.org/10.1016/j.agrformet.2021.108330>.
- Knüsel, S., Peters, R.L., Haeni, M., Wilhelm, M., Zweifel, R., 2021. Processing and extraction of seasonal tree physiological parameters from stem radius time series. *Forests* 12, 765. <https://doi.org/10.3390/f12060765>.
- Langdon, S.F., Doviak, M., Leopold, D.J., 2020. Tree encroachment varies by plant community in a large boreal peatland complex in the boreal-temperate ecotone of Northeastern USA. *Wetlands* 40, 2499–2511. <https://doi.org/10.1007/s13157-020-01319-z>.
- Lieffers, V.J., Rothwell, R.L., 1987. Effects of drainage on substrate temperature and phenology of some trees and shrubs in an Alberta peatland. *Can. J. For. Res.* 17, 97–104. <https://doi.org/10.1139/x87-019>.
- Linderholm, H.W., 1999. Climatic and anthropogenic influences on radial growth of Scots pine at hanvedsmossen, a raised peat bog, in south central Sweden. *Geogr. Ann.* Ser. A, Phys. Geogr. 81, 75–86. <https://doi.org/10.1111/j.0435-3676.1999.00050.x>.
- Linderholm, H.W., Moberg, A., Grudd, H., 2002. Peatland pines as climate indicators? A regional comparison of the climatic influence on Scots pine growth in Sweden. *Can. J. For. Res.* 32, 1400–1410. <https://doi.org/10.1139/x02-071>.
- Lotu, A.J., Ahluwalia, A.S., Sidhu, M.C., Reshi, Z.A., Mandotra, S.K., 2020. Carbon sequestration and storage by wetlands: implications in the climate change scenario. In: Upadhyay, A.K., Singh, R., Singh, D.P. (Eds.), *Restoration of Wetland Ecosystem: A Trajectory Towards a Sustainable Environment*. Springer, Singapore, Singapore, pp. 45–58. https://doi.org/10.1007/978-981-13-7665-8_4.
- MacDonald, G.M., Beilman, D.W., Kremenetski, K.V., Sheng, Y., Smith, L.C., Velichko, A.A., 2006. Rapid Early Development of Circumarctic Peatlands and Atmospheric CH₄ and CO₂ Variations. *Science* 314, 285–288. <https://doi.org/10.1126/science.1131722>.
- Mäkinen, H., Seo, J.-W., Nöjd, P., Schmitt, U., Jalkanen, R., 2008. Seasonal dynamics of wood formation: a comparison between pinning, microcoring and dendrometer measurements. *Eur. J. For. Res.* 127, 235–245. <https://doi.org/10.1007/s10342-007-0199-x>.
- Malhotra, A., Brice, D.J., Childs, J., Graham, J.D., Hobbie, E.A., Vander Stel, H., Feron, S.C., Hanson, P.J., Iversen, C.M., 2020. Peatland warming strongly increases fine-root growth. *Proc. Natl. Acad. Sci. U. S. A.* 117, 17627–17634. <https://doi.org/10.1073/pnas.2003361117>.
- Miller, T.W., Stangler, D.F., Larysch, E., Honer, H., Puhlmann, H., Schindler, D., Jung, C., Seifert, T., Rigling, A., Kahle, H.-P., 2023. Later growth onsets or reduced growth rates: What characterises legacy effects at the tree-ring level in conifers after the severe 2018 drought? *Sci. Total Environ.* 854, 158703. <https://doi.org/10.1016/j.scitotenv.2022.158703>.
- Mu, W., Wu, X., Camarero, J.J., Fu, Y.H., Huang, J., Li, X., Chen, D., 2023. Photoperiod drives cessation of wood formation in northern conifers. *Glob. Ecol. Biogeogr.* 32, 603–617. <https://doi.org/10.1111/gcb.13647>.
- Oberhuber, W., Gruber, A., 2010. Climatic influences on intra-annual stem radial increment of *Pinus sylvestris* (L.) exposed to drought. *Trees* 24, 887–898. <https://doi.org/10.1007/s00468-010-0458-1>.
- Oberhuber, W., Sehr, M., Kitz, F., 2020. Hygroscopic properties of thin dead outer bark layers strongly influence stem diameter variations on short and long time scales in Scots pine (*Pinus sylvestris* L.). *Agric. For. Meteorol.* 290, 108026. <https://doi.org/10.1016/j.agrformet.2020.108026>.
- Obojes, N., Meurer, A., Newesely, C., Tasser, E., Oberhuber, W., Mayr, S., Tappeiner, U., 2018. Water stress limits transpiration and growth of European larch up to the lower subalpine belt in an inner-alpine dry valley. *New Phytol.* 220, 460–475. <https://doi.org/10.1111/nph.15348>.
- Prislan, P., Gričar, J., de Luis, M., Smith, K.T., Čufar, K., 2013. Phenological variation in xylem and phloem formation in *Fagus sylvatica* from two contrasting sites. *Agric. For. Meteorol.* 180, 142–151. <https://doi.org/10.1016/j.agrformet.2013.06.001>.
- Ratcliffe, J.L., Creevy, A., Andersen, R., Zarov, E., Gaffney, P.P.J., Taggart, M.A., Mazei, Y., Tsyganov, A.N., Rowson, J.G., Lapshina, E.D., Payne, R.J., 2017. Ecological and environmental transition across the forested-to-open bog ecotone in a west Siberian peatland. *Sci. Total Environ.* 607–608, 816–828. <https://doi.org/10.1016/j.scitotenv.2017.06.276>.
- Rathgeber, C.B.K., Cuny, H.E., Fonti, P., 2016. Biological basis of tree-ring formation: a crash course. *Front. Plant Sci.* 7. <https://doi.org/10.3389/fpls.2016.00734>.
- Rimkus, E., Edvardsson, J., Kažys, J., Pukienė, R., Lukošūnaitė, S., Linkevičienė, R., Corona, C., Stoffel, M., 2019. Scots pine radial growth response to climate and future projections at peat and mineral soils in the boreo-nemoral zone. *Theor. Appl. Clim.* 136, 639–650. <https://doi.org/10.1007/s00704-018-2505-6>.
- Rossi, S., Anfodillo, T., Menardi, R., 2006a. Trephor: A New Tool for Sampling Microcores from tree stems. *IAWA J.* 27, 89–97. <https://doi.org/10.1163/22941932-90000139>.
- Rossi, S., Deslauriers, A., Anfodillo, T., Morin, H., Saracino, A., Motta, R., Borghetti, M., 2006b. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. *New Phytol.* 170, 301–310. <https://doi.org/10.1111/j.1469-8137.2006.01660.x>.
- Schweingruber, F.H., Poschold, P., 2005. Growth Rings in Herbs and Shrubs: life span, age determination and stem anatomy. *For. Snow Landsc. Res.* 79, 195–415.
- Seo, J.-W., Eckstein, D., Schmitt, U., 2007. The pinning method: from pinning to data preparation. *Dendrochronologia* 25, 79–86. <https://doi.org/10.1016/j.dendro.2007.04.001>.
- Smiljanić, M., Wilmking, M., 2018. Drivers of stem radial variation and its pattern in peatland Scots pines: a pilot study. *Dendrochronologia* 47, 30–37. <https://doi.org/10.1016/j.dendro.2017.12.001>.
- Steppe, K., Sterck, F., Deslauriers, A., 2015. Diel growth dynamics in tree stems: linking anatomy and ecophysiology. *Trends Plant Sci.* 20, 335–343. <https://doi.org/10.1016/j.tplants.2015.03.015>.
- Straková, P., Penttilä, T., Laine, J., Laiho, R., 2012. Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter decomposition: consequences for accumulation of organic matter in boreal peatlands. *Glob. Change Biol.* 18, 322–335. <https://doi.org/10.1111/j.1365-2486.2011.02503.x>.
- Strilesky, S.L., Humphreys, E.R., 2012. A comparison of the net ecosystem exchange of carbon dioxide and evapotranspiration for treed and open portions of a temperate peatland. *Agric. For. Meteorol.* 153, 45–53. <https://doi.org/10.1016/j.agrformet.2011.06.006>.
- Tamkevičiūtė, M., Edvardsson, J., Pukienė, R., Taminskas, J., Stoffel, M., Corona, C., Kibirkštis, G., 2018. Scots pine (*Pinus sylvestris* L.) based reconstruction of 130 years of water table fluctuations in a peatland and its relevance for moisture variability assessments. *J. Hydrol.* 558, 509–519. <https://doi.org/10.1016/j.jhydrol.2018.01.067>.
- Turetsky, M.R., Benscoter, B., Page, S., Rein, G., Van Der Werf, G.R., Watts, A., 2015. Global vulnerability of peatlands to fire and carbon loss. *Nat. Geosci.* 8, 11–14. <https://doi.org/10.1038/ngeo2325>.
- Waddington, J.M., Morris, P.J., Kettridge, N., Granath, G., Thompson, D.K., Moore, P.A., 2015. Hydrological feedbacks in northern peatlands: hydrological feedbacks in northern peatlands. *Ecohydrol* 8, 113–127. <https://doi.org/10.1002/eco.1493>.
- Wallin, M.B., Weyhenmeyer, G.A., Bastviken, D., Chmiel, H.E., Peter, S., Sobek, S., Klemetsson, L., 2015. Temporal control on concentration, character, and export of dissolved organic carbon in two hemiboreal headwater streams draining contrasting catchments: temporal control on stream doc. *J. Geophys. Res. Biogeosci.* 120, 832–846. <https://doi.org/10.1002/2014JG002814>.
- Zweifel, R., Haeni, M., Buchmann, N., Eugster, W., 2016. Are trees able to grow in periods of stem shrinkage? *New Phytol.* 211, 839–849. <https://doi.org/10.1111/nph.13955>.
- Zweifel, R., Zimmermann, L., Zeugin, F., Newbery, D.M., 2006. Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. *J. Exp. Bot.* 57, 1445–1459. <https://doi.org/10.1093/jxb/erj125>.