frontiers | Frontiers in Horticulture

TYPE Original Research
PUBLISHED 09 February 2026
DOI 10.3389/fhort.2025.1725946

Check for updates

OPEN ACCESS

EDITED BY
Chris Blok,
Wageningen University and Research, Netherlands

REVIEWED BY
Rob Baas,
Plant Research, Netherlands
Alina Stachurska-Swakoń,
Jagiellonian University, Poland

*CORRESPONDENCE
Stefan Irrgang
stefan.irrgang@posteo.de

RECEIVED 15 October 2025
REVISED 15 December 2025
ACCEPTED 22 December 2025
PUBLISHED 09 February 2026

CITATION
Irrgang S, Blievernicht A, Stark TD, Ulrichs C and Förster N (2026) Effect of Sphagnum biomass aqueous extracts on *Lepidium sativum* 'Cresso' seed germination. *Front. Hortic.* 4:1725946. doi: 10.3389/fhort.2025.1725946

COPYRIGHT
© 2026 Irrgang, Blievernicht, Stark, Ulrichs and Förster. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

Effect of Sphagnum biomass aqueous extracts on *Lepidium sativum* 'Cresso' seed germination

Stefan Irrgang[1]*, Armin Blievernicht[1], Timo D. Stark[2], Christian Ulrichs[1] and Nadja Förster[1]

[1]Division Urban Plant Ecophysiology, Thaer-Institute of Agricultural and Horticultural Sciences, Humboldt-Universität zu Berlin, Berlin, Germany, [2]Food Chemistry and Molecular Sensory Science, School of Life Sciences, Technical University of Munich, Munich, Germany

Sphagnum biomass (SBM) is a predecessor of peat and may be the most promising candidate for replacing peat in horticultural growing media. It is the only organic, regrowing material that shares decisive physical and chemical features with peat, which remains the undisputed reference material in horticultural growing media production and use. Despite multiple experimental confirmations of the applicability of SBM for growing media, scattered reports of growth inhibition in plants grown in SBM raise concerns that allelopathic effects may derive from this material. To attribute and quantify potential growth inhibition, a broad sample set of SBM was collected, processed as aqueous extracts (AE_{SBM}), and applied to seeds of *Lepidium sativum* 'Cresso' in a series of laboratory plant assays. The majority of extracts induced significant inhibitory effects on germination and early growth. Using HPLC–MS, secondary metabolites (phenolics) were determined qualitatively and quantitatively. Thirty-eight SBM samples obtained from Sphagnum farming sites and greenhouse-grown material were analyzed. A group of compounds occurred in all samples, defining a core set of phenolic compounds. The complexity of the compound mixture in AE_{SBM} did not allow a clear attribution of the observed effects to individual substances; however, machine learning–based feature selection and importance analysis revealed a clear contribution of two detected compounds. Heat treatment of SBM at 60 and 80 °C significantly reduced the inhibitory effects of the material. Further studies should apply fractionation approaches to evaluate the effects of specific compounds individually.

KEYWORDS

growing medium, growth inhibition, phenolics, plant assay, secondary plant metabolites, Sphagnum biomass, *Sphagnum palustre*

1 Introduction

The use of peat in horticultural growing media is strongly connected to the release of significant amounts of CO_2 (He and Roulet, 2023). Peat is one of the largest carbon sinks in nature (Hugelius et al., 2020), but through oxidation, stored carbon is released into the atmosphere after extraction from natural sites. The replacement of peat as a main constituent of growing media is a major challenge in horticultural science, since no other available regrowing material provides the same set and combination of advantageous properties. Currently, compost, coconut products, and wood fibers are mainly utilized as peat substitutes. All of them are, in principle, suitable for use in growing media but exhibit important disadvantages. Compost is often not available in consistently high quality. The extensive use of coir and coir pith is questionable, since it relies on a byproduct of coconut production and must be processed and transported with a corresponding use of resources. Wood fibers can improve the properties of growing media but are not suitable as a main constituent. A highly relevant exception among peat substitutes is Sphagnum biomass (SBM). It consists mainly of plant biomass from the bryophyte genus *Sphagnum*. Widespread use of this resource is only possible through agricultural and horticultural cultivation of *Sphagnum*, since the genus is under nature conservation in Germany, and extensive exploitation of natural sites counteracts sustainability goals. SBM contains dead plant parts of the bryophyte genus *Sphagnum* and can be used to produce Sphagnum growing media (SGM). Since degraded plants of this genus resemble the main fraction of most horticulturally used peat, SBM can be considered a peat precursor. Like peat, SBM has a low pH, high air content and water-holding capacity, minor nutrient content, and low nitrogen fixation rates. Several trials have demonstrated the excellent feasibility of SBM as growing media (Emmel, 2008; Blievernicht et al., 2012; Müller and Glatzel, 2021; Tommila et al., 2022). Nonetheless, in some cases, allelopathic effects of SBM (Emmel and Kennett, 2007) or aqueous extracts of SBM (AE_{SBM}) have been observed (Michel et al., 2011; Hamard et al., 2019). This can occur with SBM harvested from natural and semi-natural habitats or from laboratory cultivation. Reported effects include growth depression (Emmel, 2008), leaf chlorosis, leaf necrosis, and, in some cases, plant death (Irrgang et al., 2018). In addition to allelopathic effects of processed *Sphagnum*, similar effects have been observed in natural habitats, where *Sphagnum* suppresses the growth of vascular plants as well as other *Sphagnum* species (van Breemen, 1995). It is worth noting that the effects of AE_{SBM} on vascular plants can range from growth-promoting to strong growth inhibition (Bibtex-Key Chiapusio et al., 2013).

Allelopathic effects of *Sphagnum* are not limited to vascular plants. Inter-specific allelopathic effects within the genus have also been reported. These effects differ among species and can be either growth-promoting or inhibitory (Ingerpuu and Vellak, 2013; Liu et al., 2019, 2023), depending on the species involved. A distinct experimental attribution of individual compounds to symptoms of germination or growth inhibition has not yet been established. *Sphagnum* contains a variety of phenolic substances (Rasmussen et al., 1995), some of which may possess allelopathic effects. *p*-Hydroxybenzoic acid (*p*HBA) is one of two enzymatic degradation products of *trans*-sphagnum acid (*t*SphA; *p*-hydroxy-β-[carboxymethyl]-cinnamic acid) (Wilschke, 1989). *p*HBA can disturb root growth (Huang et al., 2020), as well as root development and water uptake (Yan et al., 2022). Other compounds typically contained in *Sphagnum* include *p*-coumaric acid (*p*CA) and *trans*-cinnamic acid (*t*CA) (Wilschke et al., 1989). These substances have also been reported to exert allelopathic effects. *p*CA can cause reduced water utilization, transpiration, and leaf expansion in cucumber (Blum and Thomas, 2005), whereas *t*CA has shown inhibitory effects on lettuce germination (Li et al., 1993).

Although most substances occurring in ethanolic and methanolic extracts of *Sphagnum* have been identified, phenolic profiles of aqueous *Sphagnum* extracts remain largely unexplored (Chiapusio et al., 2018). Most experiments on secondary metabolites of SBM have been conducted using strong solvents such as ethanol or methanol, often in combination with heat application to yield maximum compound concentrations. Under non-laboratory conditions in natural stands or horticultural production systems, where problems with SBM have been observed, such solvents are unlikely to occur. Therefore, the composition of water-based extracts is more relevant for understanding processes in the root-substrate system involving SBM.

To safeguard a reliable quality of SBM for widespread use in horticultural growing media in the future, a clear cause-and-effect relationship between SBM and allelopathic effects must be identified. This study aims to test whether water-soluble phenolics or phenolic acids cause inhibitory effects on *Lepidium sativum* under controlled laboratory conditions. Furthermore, it seeks to attribute these effects to one or multiple substances to facilitate quality assessment in SGM production.

2 Materials and methods

2.1 Plant material

The plant material used for the experiments originated from a Sphagnum farming site (SFS), a semi-natural site, and greenhouse cultivation and represented different growing systems. Thirty-eight samples were grouped into four topic-specific subsets, which also facilitated the conduction of plant assays. All samples were taken from the upper 20 cm of *Sphagnum* carpets. All non-*Sphagnum* plants were avoided, and residues were removed.

Gravitational water was allowed to drain from the samples before storage in bags, except for sample SFS-Hank S (water squeezed out). Bags were transported cooled on ice to the laboratory and stored at −80 °C until further processing.

Seasonal variation—The first subset included samples taken monthly from a German experimental SFS in Lower Saxony (near the municipality of Hankhausen; 8.148079, 53.228851, 8.393726, 53.299492 [EPSG:4326]; cf. Supplementary Material for a map of

10.3389/fhort.2025.1725946

the SFS). The selected field on the farming site is surrounded by a main ditch for water supply. The ditch is filled through an inflow on the eastern field margin, and water can leave the ditch through an outflow on the opposite side. The harvested SBM contained a mixture of *Sphagnum* species (*S. palustre*, *S. papillosum*, *S. fimbriatum*). One sample per month was taken in 2017 at the same position on site, except during periods with permanent frost (January and December).

Spatial variation—Samples for this subset were taken in early April 2018 at the same SFS in Hankhausen as the monthly samples, along a transect line following an east–west direction. The distance between sampling points on the transect line was 25 m. At each sampling point, three subsamples were taken and pooled: one along the line and two located 50 cm to the left and right of the transect line.

Cultivation environment—This subset comprises different variants of the same SBM as in the sample sets described above from the SFS. The respective sample treatments are listed in Table 1. In addition, a reference SBM sample was included as a positive control. This material originated from a semi-natural production site near the municipality of Aitoneva (Finland) and was harvested sustainably. It has been proven feasible for use in growing media in extensive scientific trials (Irrgang et al., 2018). The material was already processed (dried and sieved) and consisted of *S. fuscum* and *S. rubellum*.

Post-harvest treatment—The effect of post-harvest treatment was assessed using two mono-specific samples of *S. palustre*. The samples originated from material collected in the Netherlands in 2010 (*S. palustre* mono-specific sample 1, Pm1; 5.977936, 52.692115, 6.082306, 52.739741 [EPSG:4326]) and in Norway in 2012 (*S. palustre* mono-specific sample 2, Pm2; 10.772095, 59.508720, 11.016541, 59.598663 [EPSG:4326]). Plants were cultivated in a greenhouse in polystyrene plastic trays for 12 months before sample acquisition. After lyophilization and milling, samples were treated at four different temperature levels (20, 40, 60, and 80 °C). Temperatures were maintained for 24 h in a drying oven (UT6200, Heraeus Instruments).

TABLE 1 Sample treatments for the cultivation environment sample set. Sphagnum farming site Hankhausen (Lower Saxony, Germany); AIT-FIN = Aitoneva (Pirkanmaa, Finland).

Sampling origin	Treatment	Abbrev.
SFS-Hank	Harvested on-site in June 2016 gravitation water removed	G
SFS-Hank	Harvested in June 2016, SBM firmly squeezed at harvest	S
SFS-Hank	Harvested on-site in June 2016 near inflow	O-IF
SFS-Hank	Harvested on-site in June 2016 near outflow	O-OF
SFS-Hank	Transferred from field margin to greenhouse off-site (2016) and harvested (2017)	GH-FM
SFS-Hank	Transferred from field near inflow to greenhouse off-site (2016) and harvested (2017)	GH-IF
SFS-Hank	Transferred from field near outflow to greenhouse off-site (2016) and harvested (2017)	GH-OF
AIT-FIN	SBM harvested in municipality of Aitoneva (Finland) processed (dried and sieved) for growing media production	AIT

2.2 Extraction

Plant material was prepared for extraction and chemical analysis via lyophilization (Alpha 1–4 LSCplus, CHRIST). To obtain a fine, homogeneous powder, SBM was first cut using a household rotary cutter (Moulinette S, MOULINEX) for 10–15 s and subsequently ball-milled (MM400, RETSCH) for 30 s with a frequency of 30 Hz.

Extract preparation—Two grams of ball-milled plant powder were mixed with 26 mL distilled water in a 50 mL tube. The sealed tube was vortexed for 10 s and then transferred to a rack positioned on an automated shaker for 24 h (250 Mot/min). The rack was covered with laboratory aluminum foil to avoid photochemical effects within the extracts. After removal from the shaker, tubes were again vortexed for 10 s. Immediately afterward, extracts were purified by centrifugation and filtration. In the first step, tubes were centrifuged at 5,000 rpm for 5 min. The supernatant was filtered using folded cellulose filters (Macherey+Nagel, diameter 110 mm). The extract was used for plant assays, and 2 mL was retained for HPLC analysis. This aliquot was further filtered using 0.22 µm Spin-X tubes (Costar, Corning, New York, NY, United States) by centrifugation at 10,000 rpm for 10 min (Megafuge X1R, Thermo Scientific/Heraeus, Germany).

2.3 *Lepidium sativum* 'Cresso' - plant assays

Experimental setup—Assays were conducted batchwise, grouped according to the sample sets described above. Ninety-six–well plates with flat bottoms were used. Each well contained one seed of *Lepidium sativum* 'Cresso' (LsC). Fifty microliters of AE_{SBM} from the respective treatment or distilled water (control treatment) was added to each well. Each plate contained a uniform treatment in all 96 wells, representing 96 biological replicates in one technical replicate. Controls (distilled water) were repeated five times in every sample set (rep = 5, n = 96) to confirm uniform germination of the seeds used. Well plates were tightly covered with transparent, stretchable polyethylene foil. Plates were incubated at 24 °C for 72 h in an *in vitro* growing room (20 µmol s^{-1} m^{-2}; VALOYA L28-NS12 LED pipes). The experiment was stopped after 72 h by cooling the plates to 1 °C, and plates were kept cooled until measurement of radicle and hypocotyl length (initiated immediately after the end of the experiment).

Radicle and hypocotyl length—Seeds and seedlings were removed individually from wells and positioned under a microscope (ETD-201, BRESSER) at 10-fold magnification. Images of all seeds and seedlings were acquired (MikroCam SP 5.0l, BRESSER). Measurements of radicle and hypocotyl length

were performed using ImageJ 1.54j (RRID: SCR_003070). Radicles and hypocotyls were traced using the multipoint tool and then automatically measured. A calibration image with an appropriate scale was taken after each well plate (96 images) to ensure consistency in length determination.

2.4 Analytics

HPLC–MS—All extracts (10 µL) were analyzed by HPLC (Ultimate 3000 equipped with an autosampler WPS-3000TR, pump LPG-3400RS, column compartment TCC-3000RS, and diode array detector DAD-3000RS; Thermo Scientific, Germany) as described previously by Förster et al. (2023). Reversed-phase chromatography was performed on an Acclaim PolarAdvantage C16 column (3 µm, 120 Å, 2.1 × 150 mm, Thermo Scientific), protected by a pre-column (5 µm, 120 Å, 2 × 10 mm, Thermo Scientific), at a flow rate of 0.4 mL/min and a column temperature of 35 °C, using eluents (A) H_2O (0.5% formic acid) and (B) 40% acetonitrile. The gradient program was as follows: 0–1 min, 0.5% B; 1–10 min, 0.5%–40% B; 10–12 min, 40% B; 12–18 min, 40%–80% B; 18–20 min, 80% B; 20–24 min, 80%–100% B; 24–30 min, 100% B; 30–34 min, 100%–0.5% B; and 34–39 min, 0.5% B. Quantification of phenolic compounds was conducted at 290 nm using a photodiode array detector against the internal standard 4-methoxycinnamic acid (1 mM; Sigma-Aldrich, Germany). Commercially available standards of individual compounds were used as references (*p*-coumaric acid, sphagnum acid). Relative response factors of compounds with similar chemical structures were applied to correct for differences in absorbance.

Phenolics and phenolic acids were identified based on retention times and specific UV spectra (*trans*-sphagnum acid and *cis*-p-coumaric-acid glucuronide), as well as mass spectrometry. MS/MS analysis was performed by electrospray ionization (ESI) using a Thermo Scientific LXQ ESI ion trap mass spectrometer (RRID: SCR_018701; negative ion mode). Mass spectra were recorded in the range m/z 50–1,000. Instrument control and data processing were performed using Thermo Xcalibur (RRID: SCR_014593; version 2.2 SP1.48).

Since not all detected peaks could be identified, compound contents could not be calculated using compound-specific response factors; therefore, response factors for unknown compounds were set to 1.

2.5 Statistical and data analysis

Data processing and basic statistical analyses were conducted using the KNIME Analytics Platform (version 5.3.0; RRID: SCR_006164). Further statistical analyses and visualization were performed using R (version 4.1.2; RRID: SCR_001905) and RStudio (version 2024.12.1; RRID: SCR_000432). Results of the plant assays were tested for normality (Shapiro–Wilk test) and homoscedasticity (Levene's test). Due to violations of both assumptions, the Kruskal–Wallis test followed by Dunn's *post hoc* test was applied.

Feature selection and importance—All machine learning analyses were performed using the R package mlr3 (Machine Learning in R—Next Generation; RRID: SCR_025562). For reproducible random number generation, the seed was set to 2005. Data were split into 67% training and 33% test sets. The model was trained using a regression random forest learner ("regr.rpart"). Feature selection included resampling with repeated cross-validation (three repeats and four folds). Feature importance was extracted from the learner's intrinsic importance measure.

3 Results

3.1 Plant assays

Symptoms of growth inhibition—A majority of the seeds and seedlings treated with AE_{SBM} showed symptoms of reduced germination and growth inhibition. Frequently observed symptoms ranged from germination arrest after imbibition to normally developed plants. Examples of common symptoms are shown in Figure 1, including a representative example of control plants. Inhibition symptoms were mostly not consistently present across all replicates within individual plates. Control plants developed a distinct radicle and hypocotyl with well-developed cotyledons during the 72 h experiment.

Seasonal variation—Plants grown in extracts from monthly collected samples (2017) showed broad variation in median radicle and hypocotyl length (Figure 2). All prepared extracts significantly inhibited *Lepidium sativum* 'Cresso' (LsC) growth. Extracts from April and June showed the strongest inhibitory effects, particularly on hypocotyl development. Extracts from May, August, and October also belonged to the group with severe inhibitory effects. Extracts from March and September showed the weakest effects among the sampled months in 2017. Overall, the summer months—except July, which showed a opposing tendency—exhibited strong inhibitory effects, whereas effects were mitigated in early spring and autumn.

Spatial variation—Treatment with extracts from transect samples collected in April 2018 resulted in stronger inhibitory effects than the sample taken in April 2017 (subset seasonal variation). All samples along the transect line exhibited strong inhibitory effects on radicle and hypocotyl growth and differed markedly from the control treatment, as shown in Figure 3. The most severe effects on radicle growth originated from extracts taken at distances of 100 m and 150 m from the start of the transect. Effects on hypocotyl growth exceeded those on radicle development at most sampling points along the transect. In contrast to assays using monthly samples, transect assays produced a noticeably higher number of outliers per plate.

Cultivation environment—Extracts of the SBM reference material from the Aitoneva region in Finland (AIT) showed no significant inhibition of radicle growth and only minor inhibition of hypocotyl development (Figure 4). In contrast, extracts from samples collected at the SFS showed inhibitory effects. AE_{SBM} from June 2016 samples where only gravitational water was

10.3389/fhort.2025.1725946

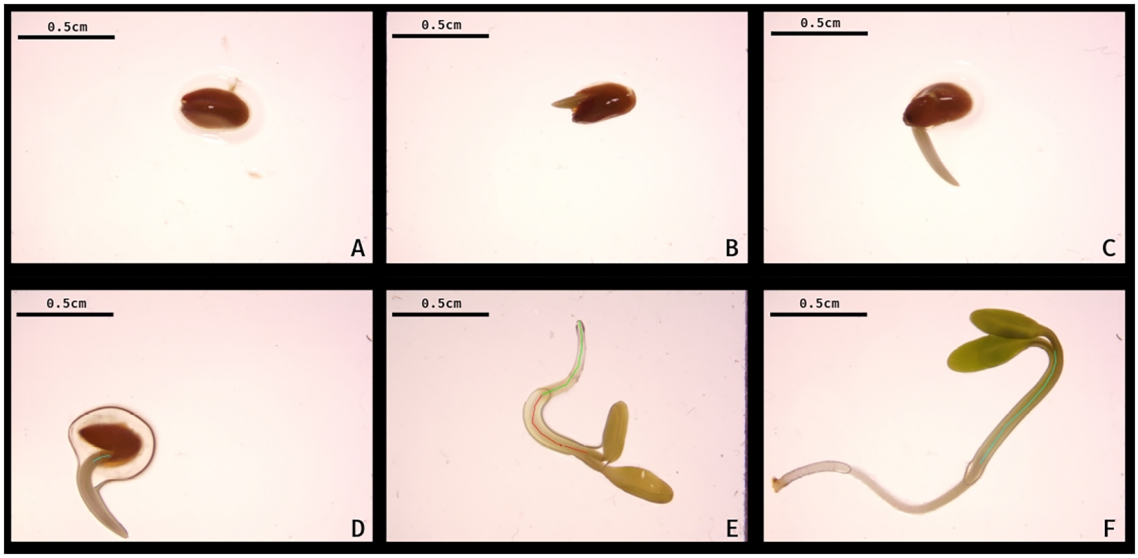


FIGURE 1
(A) Early stop - Seed is welled but neither radicle nor hypocotyl are visible. **(B)** Tipped - Only tip of radicle is emerged. **(C)** Half way - Radicle is developed but reduced in length; hypocotyl is not visible. **(D)** Low growth - Radicle is developed but reduced; Hypocotyl is visible but reduced. **(E)** Reduced chlorophyll - As D symptom but with distinct chlorosis of cotyledons. **(F)** Control treatment - Typical plant development after 72 h without treatment of AE_{SBM}.

allowed to drain (G) showed a markedly strong inhibitory effect on LsC seeds. Extracts of squeezed (S) SBM from June 2016 showed significantly lower inhibitory effects, resulting in greater mean radicle and hypocotyl length. Twelve months of greenhouse cultivation of SBM harvested from the inflow (GH-IF) and outflow (GH-OF) areas of the SFS did not result in significantly reduced inhibition, except for hypocotyl length in treatment GH-OF.

Post-harvest heat treatment—Heat treatment reduced the inhibitory effects of extracts prepared from Pm1 (*S. palustre*) (cf. Figure 5). Although not statistically significant, extracts from Pm2 also showed a tendency toward decreased inhibition of radicle and hypocotyl development. The inhibitory effects of the two mono-specific samples differed significantly. With stepwise increases in treatment temperature, inhibitory effects decreased. For Pm1, radicle and hypocotyl development of LsC seeds did not differ significantly from the control when extracts were prepared from SBM heated to 60 and 80 °C.

3.2 HPLC-MS analysis

Peak profiles differed considerably between sample subsets. Samples from the 2018 transect contained the most diverse spectrum of compounds. AE_{SBM} prepared from heat-treated samples cultivated in the greenhouse were composed of fewer substances. Peaks of the different subsets are summarized in Table 2 in order of appearance throughout the HPLC run. A proportion of the detected peaks showed overlapping signals, which justified grouping them accordingly.

Peak PK10 and PK17 were identified as *cis-p*-coumaric-acid glucuronide (*cp*CouAG) and *trans*-sphagnum acid (*t*SphA), respectively, and were used for naming the corresponding groups. *t*SphA shares the fragments 177 and/or 133 with PK05, PK06, and PK07 and defines group A. *Cis-p*-coumaric-acid glucuronide shares the fragments 163 and/or 119 with PK09, PK11, PK19, PK20, and PK21 and defines group B. PK02 and PK12 share fragment 191 and constitute group C. Extracts induced symptoms described in Section 1 across all four sample sets. Peaks detected across all sample sets were grouped into a core peak group, comprising six peaks: PK05, PK09, PK10, PK15, PK17, and PK19 (Table 2). Peak PK15 was detected by HPLC but was not ionized in negative mode (nor in positive mode) in MS and lacked a fragmentation pattern.

Seasonal variation—The total content of the core peak group (TPC_{core}) varied over the annual cycle, as shown in Figure 6. The lowest TPC_{core} was detected in March. In November, a nearly fourfold higher TPC_{core} marked the maximum value among the sampled months. *t*SphA (PK17) dominated the composition of all samples and was followed by PK15. The remaining peaks (PK05, PK09, PK10, and PK19) occurred at markedly lower levels. *t*SphA content was lowest in March, increased until August, and decreased again until October. The highest *t*SphA content was observed in November.

Spatial variation—In samples from the SFS collected in April 2018, variation along the transect was observed. Comparable to the April 2017 sample from the same field, *t*SphA and PK15 were the most prominent peaks. The content of *t*SphA varied more strongly than that of PK15 across the field. *t*SphA exceeded the content of all other peaks in all samples. Maximum TPC_{core} was observed at 175 m, whereas the lowest TPC_{core} was measured at 100 m. The *t*SphA content at 175 m was more than twice as high as that at 50 m. Although present in lower

10.3389/fhort.2025.1725946

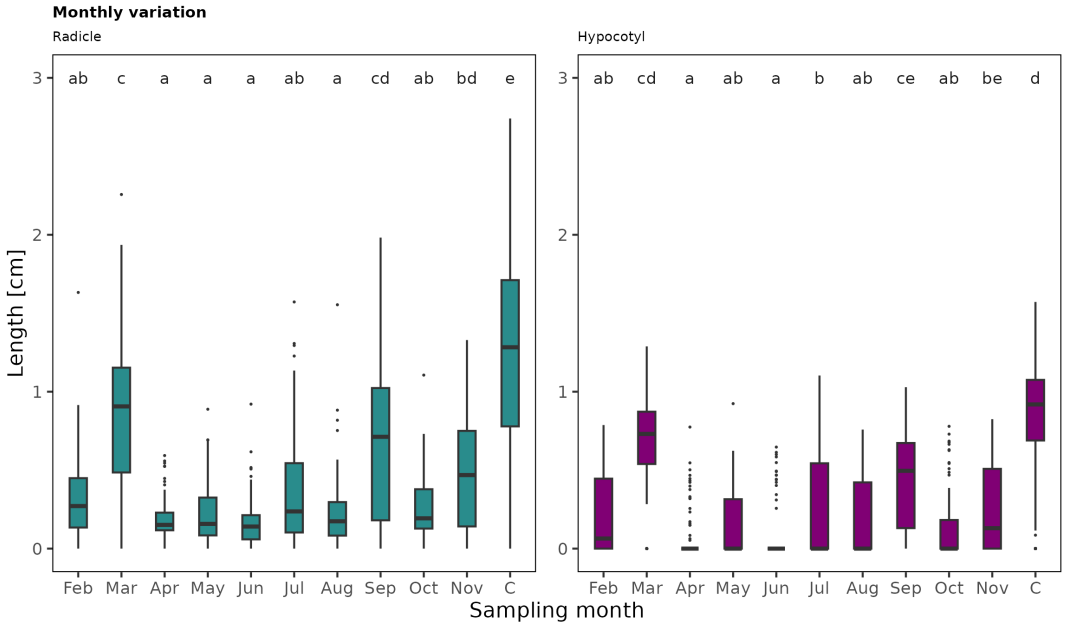


FIGURE 2
Median, distribution, and interquartile-range of radicle and hypocotyl length (cm) of LsC treated with extracts prepared from SBM sampled monthly throughout 2017 at the Hankhausen Sphagnum farming site (Lower Saxony, Germany). Control treatment (C). Different letters indicate statistically significant differences ($P < 0.05$) between means, as determined by Dunn's test as a *post hoc* test following the Kruskal–Wallis test ($n_{treatment} = 96$, $n_{control} = 480$).

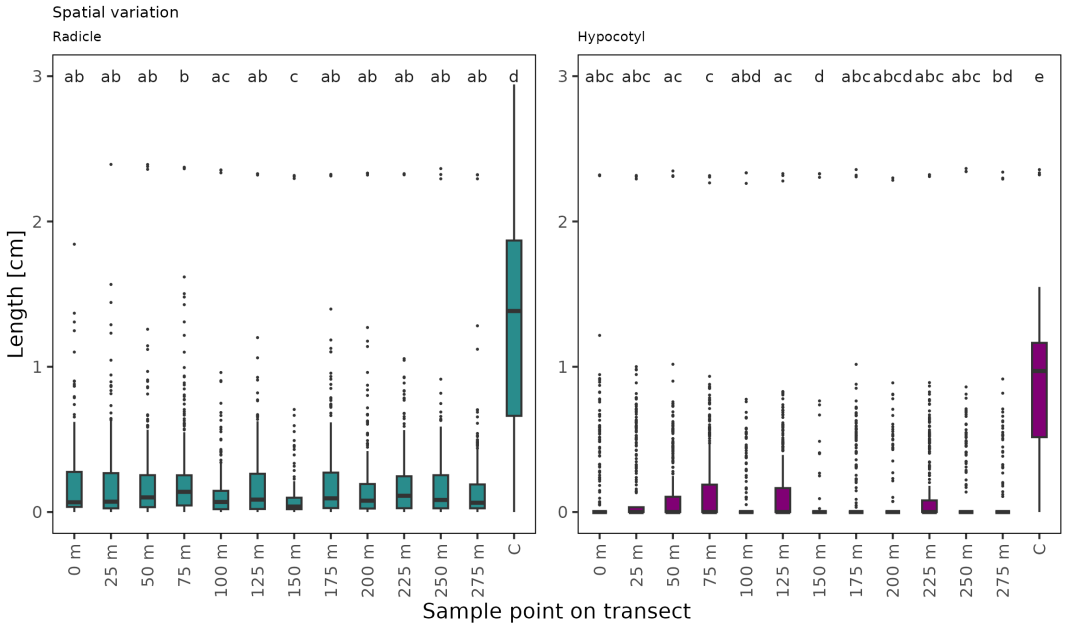


FIGURE 3
Median, distribution, and interquartile range of radicle and hypocotyl length (cm) of LsC treated with extracts prepared from SBM sampled at the Hankhausen Sphagnum farming site (Lower Saxony, Germany) in April 2018. Each distance step represents a pooled sample of three subsamples taken along the transect line and 50 cm to the left and right at the given distance. Control treatment (C). Different letters indicate statistically significant differences ($P < 0.05$) between means, as determined by Dunn's test as a *post hoc* test following the Kruskal–Wallis Test ($n_{treatment} = 96$, $n_{control} = 480$).

10.3389/fhort.2025.1725946

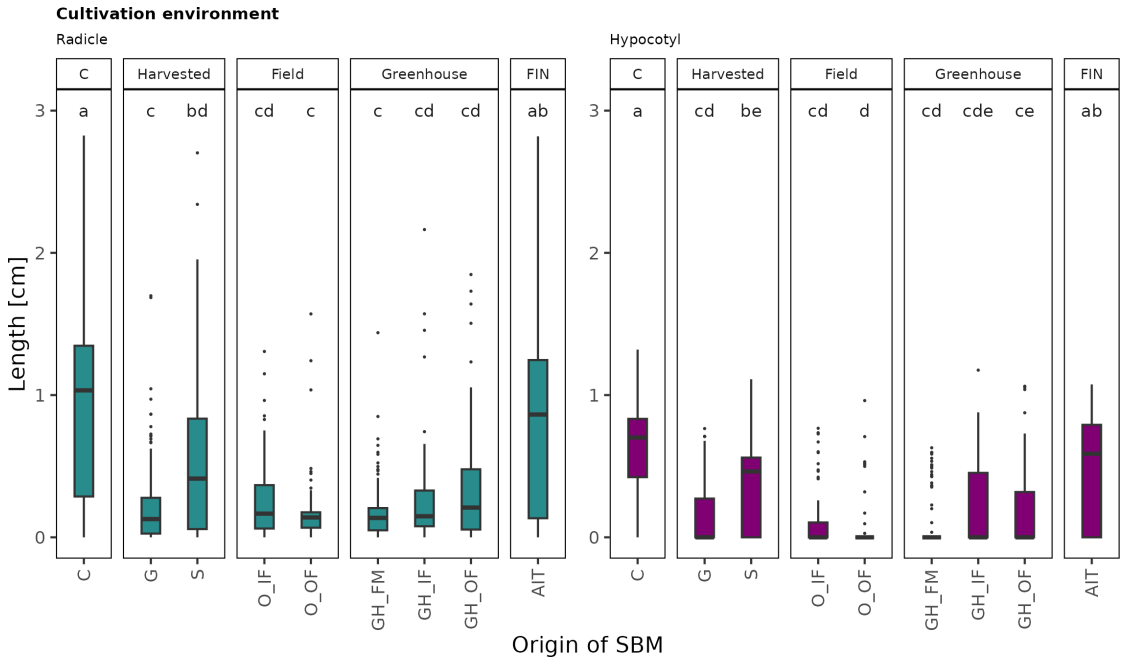


FIGURE 4
Median, distribution, and interquartile range of radicle and hypocotyl length (cm) of LsC treated with extracts prepared from SBM harvested at or transferred from the Hankhausen Sphagnum farming site (Lower Saxony, Germany). Harvested SBM: gravitational water removed (G) or firmly squeezed at harvest (S). Field samples taken near inflow (O-IF) or outflow (O-OF) of the ditch system. Greenhouse-cultivated SBM (12 months) originally taken from inflow (GH-IF), outflow (GH-OF), and field margin (GH-FM). SBM from the municipality of Aitoneva, Finland (dried and sieved). Control treatment (C). Different letters indicate statistically significant differences ($P < 0.05$) between means, as determined by Dunn's test as a *post hoc* test following the Kruskal–Wallis Test ($n_{treatment} = 96$, $n_{control} = 480$).

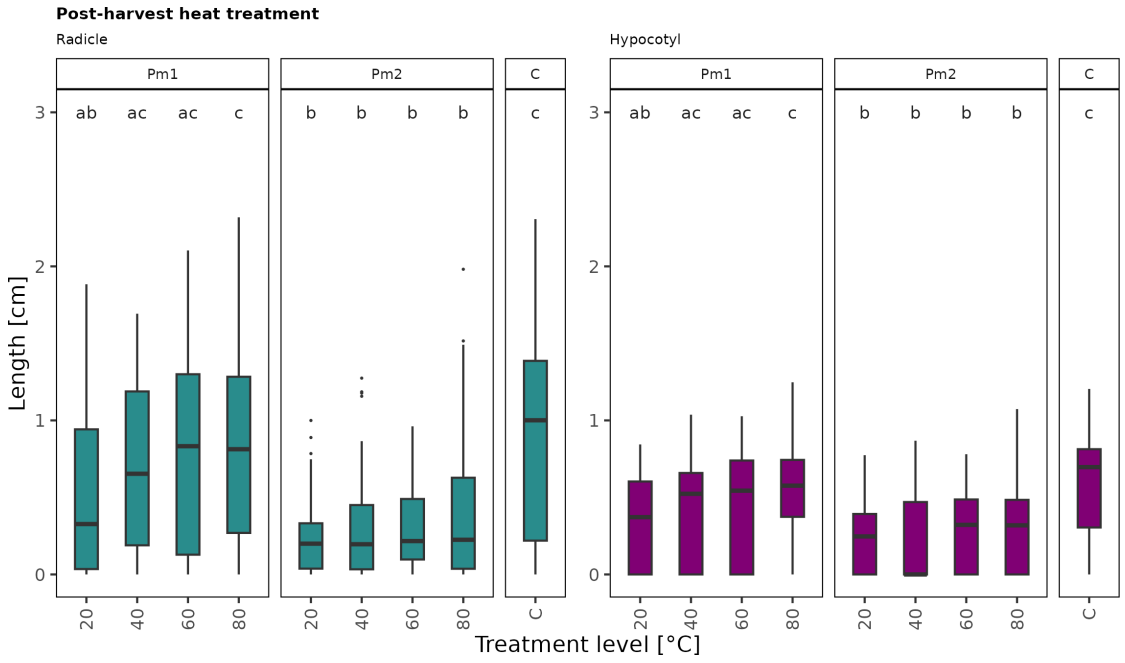


FIGURE 5
Median, distribution, and interquartile range of radicle and hypocotyl length (cm) of LsC treated with extracts prepared from heat-treated SBM (20, 40, 60, and 80 °C) for two mono-specific samples of *S. palustre* (Pm1 and Pm2). Control treatment (C). Different letters indicate statistically significant differences ($P < 0.05$) between means, as determined by Dunn's test as a *post hoc* test following the Kruskal–Wallis Test ($n_{treatment} = 96$, $n_{control} = 480$).

10.3389/fhort.2025.1725946

TABLE 2 Major peaks detected by HPLC–MS (negative ionization).

Peak	MS negative (m/z)	*mz*1	*mz*2	*mz*3	*mz*4	S1	S2	S3	S4	Core	Group
PK01	311	135	93	–	–	–	x	–	–	–	–
PK02	395	353	191	–	–	–	x	–	–	–	C
PK03	209	165	121/93	–	–	x	x	x	–	–	–
PK04	491	–	–	–	–	–	x	–	–	–	–
PK05	397	353	177	133	–	x	x	x	x	o	A
PK06	267	133 (233)	–	–	–	–	x	–	–	–	A
PK07	383	177	133	–	–	x	x	x	–	–	A
PK08	577	531	–	–	–	–	x	–	–	–	–
PK09	207	163	119	–	–	x	x	x	x	o	B
PK10	339	163	119	–	–	x	x	x	x	o	B
PK11	371	325	163	119	–	–	x	–	–	–	B
PK12	369	206	191	–	–	–	x	–	–	–	C
PK13	533	357	–	–	–	–	x	–	–	–	–
PK14	533	357	–	–	–	–	x	–	–	–	–
PK15	NMD	–	–	–	–	x	x	x	x	o	–
PK16	585	187	125	97	–	–	x	–	–	–	–
PK17	221	177	133	–	–	x	x	x	x	o	A
PK18	535	313	137	93	–	–	x	–	–	–	–
PK19	545	339	163	119	–	x	x	x	x	o	B
PK20	243	225	207	163	97	–	x	–	–	–	B
PK21	545	339	163	119	–	x	x	x	–	–	B

Peaks are labeled in order of appearance throughout the run. S1, monthly samples; S2, transect samples; S3, cultivation environment samples; S4, heat-treated samples. Presence in the respective subset (at least one sample) is marked with x. Members of the core peak group (present in all subsets) are denoted with o. Letters in the "Group" column assign peaks to groups A (sphagnum acid group), B (*cis-p*-coumaric acid glucuronide group), and C (191 group). NMD, no mass detected by MS.

amounts, *cp*CouAG represented the third most abundant compound in nine of the twelve extracts.

Cultivation environment—The reference material from Aitoneva (Finland; AIT-FI) showed the lowest TPC_{core} within this sample set. It contained approximately 30-fold less TPC_{core} than the highest greenhouse-cultivated sample (GH-FM). Nevertheless, the most prominent compounds from the other sample sets, *t*SphA and PK15, were also present. All fresh samples, whether taken directly from the SFS or after 12 months of greenhouse cultivation, contained high amounts of core phenolics. In the fresh plant material samples from June 2016, *t*SphA and PK15 also dominated the profiles. In greenhouse-cultivated SBM from GH-FM and GH-IF, PK05 occurred very prominently. The two samples from June 2016 (G and S) contained markedly lower TPC_{core} compared with the respective fresh samples from the same month and SFS. In these samples, *t*SphA was not the prevailing peak.

Post-harvest heat treatment—Extracts from post-harvest heat-treated samples showed profiles distinct from those of seasonal and transect samples. PK05 from the SphA group (A) was considerably more prominent and often represented the dominant peak. PK15 occurred at much lower proportions than in profiles from the SFS. In addition, PK19 from the CouA group (B) was present in higher amounts in profiles from heat-treated samples. Overall, the composition more closely resembled that of greenhouse-derived samples originating from the SFS. TPC_{core} did not increase consistently with rising temperature but showed a clear tendency toward higher values. In particular, *t*SphA in Pm2 increased more than twofold at 60 and 80 °C compared with 20 °C.

3.3 Cause-effect-relationship

Forward feature selection—The identified compounds were available only as mixtures in AE_{SBM}. *A* distinct assignment of the observed inhibitory effects to individual substances would have required fractionation of AE_{SBM} or identification of the core peak

10.3389/fhort.2025.1725946

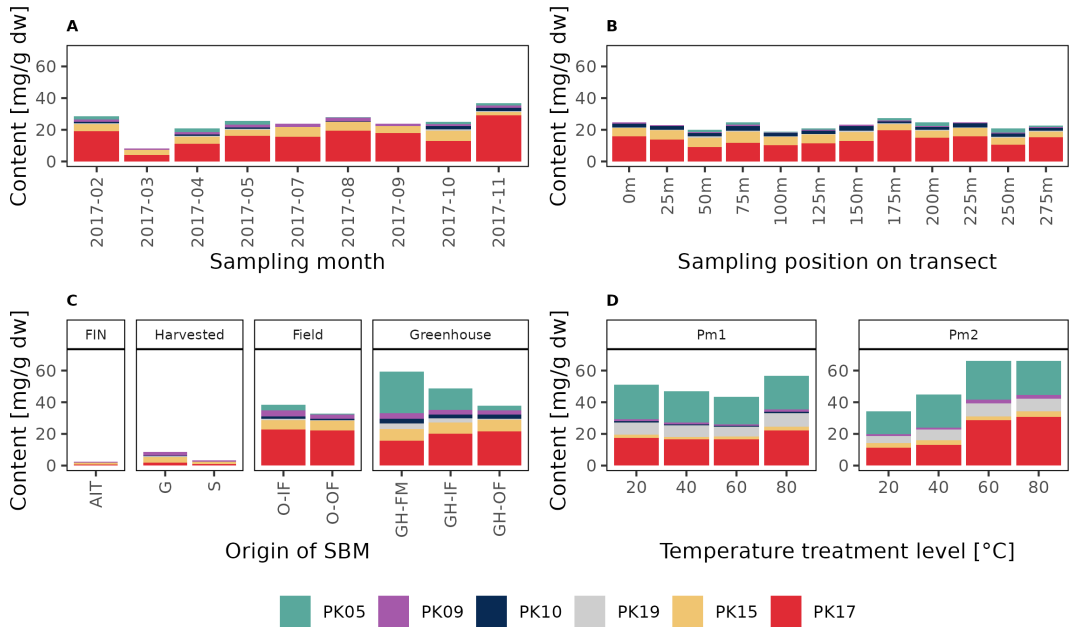


FIGURE 6
Content of core group peaks (mg/g dry weight) for **(A)** monthly samples, **(B)** transect samples, **(C)** cultivation environment and harvest-type samples (harvested G = gravitational water removed; harvested S = water squeezed out after harvest; field O-IF = field sample taken near inflow; field O-OF = field sample taken near outflow; greenhouse = SBM transferred and cultivated for 12 months in a greenhouse from field margin [GH-FM], inflow [GH-IF], and outflow [GH-OF]; harvesting, field sampling, and transfer in June 2016; AIT = SBM from Aitoneva, Finland), and **(D)** heat-treated samples (20, 40, 60, and 80 °C).

group members to conduct single-substance assays. Assuming that radicle and hypocotyl length serve as proxies for the inhibitory effects of AE_{SBM}, these variables may correlate with the contents of the detected peaks. However, possible interdependencies among peaks within the dataset did not yield an interpretable correlation analysis (data not shown). Therefore, random forest regression was used to train two models—one for radicle length and one for hypocotyl length—to identify peaks with the strongest influence using forward feature selection. Model training was performed using the core peaks listed in Table 2, as these were present in all samples. For the target variable radicle length, the model identified *cp*CouAG, PK15, and *t*SphA as predictive features on the test data. For hypocotyl length, peaks PK05 and PK19 were selected as the most relevant predictors. In both models, PK15—an unknown peak without MS detection—was identified as an important feature for predicting the target variables.

Feature importance—In the radicle model, only three of the six included peaks yielded a measurable importance score (Figure 7). PK15 showed the highest importance for splits in the random forest when predicting radicle length. PK19 and PK17 exhibited approximately threefold lower importance scores. As shown in Figure 7, the highest importance score in the hypocotyl model was again assigned to PK15, followed by PK19 and PK17 with markedly lower scores. In the hypocotyl model, PK05 and PK10 contributed to splits in the random forest but only to a minor extent. In both models, PK15 showed a distinctly higher importance score, indicating a prevailing influence of this peak on the observed inhibitory effects.

4 Discussion

4.1 Assays

Symptoms—The growth inhibition observed in the experiments confirms that AE_{SBM} can negatively affect germination and early plant growth of LsC. In contrast, a minor proportion of plants within individual wells appeared to be only weakly affected or almost unaffected. No clear pattern in the variable response of seeds within the well plates was observed. Potenially LsC seeds are differently susceptable to the allelopathic agents present in AE_{SBM}. Although the use of a selected cultivar should have minimized such variation, seeds were not entirely uniform. For example, variation in testa thickness or testa composition may have influenced the rate of extract uptake. A second possible explanation approach would be a different content of the allelopathic agent between the wells of the plate. In principle, allelopathic agents could have been degraded by photolysis (Herrera et al., 1998) in the solution before exerting effects on seeds. Such differential degradation would require non-uniform light exposure or reflection conditions across the plate.

Monthly variation—The pronounced variation in effects observed among monthly SBM samples suggests a strong dependence on one or more external environmental factor(s). These factors cannot be specified, as the necessary multifactorial ecological monitoring of the production site was beyond the scope of this study. A link to metabolic processes within the surrounding microbiome is likely, given the strong association between *Sphagnum* sp. to its surrounding microorganisms. For example,

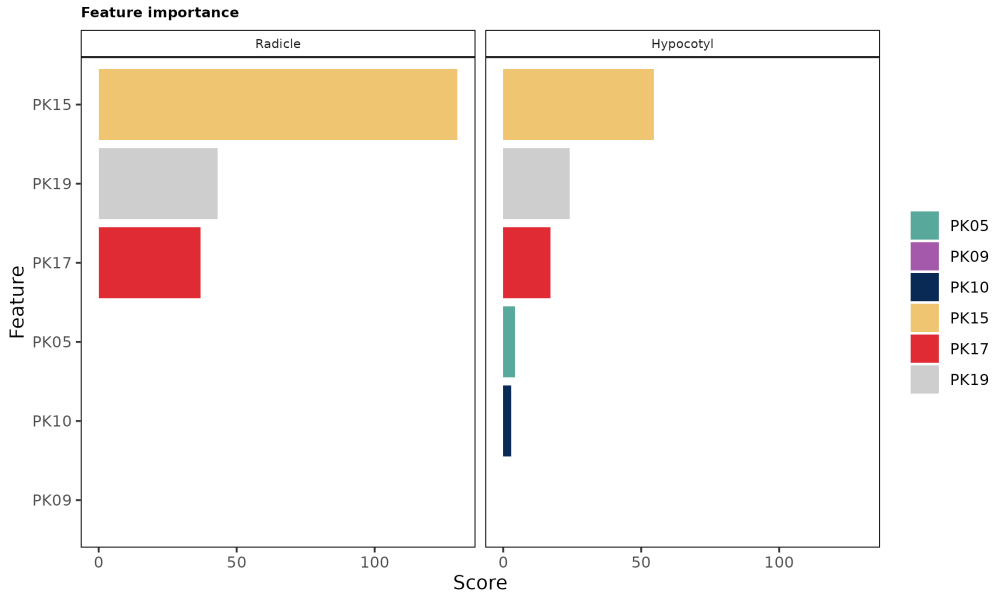


FIGURE 7
Feature importance of peaks included in the core group for prediction of radicle and hypocotyl length (R package mlr3, learner = regr.rpart).

the seasonal shift of available nutrients through water inflow might influence the surrounding microbial communities (van den Elzen et al., 2017). Comparable intra-annual variation in phenolic profiles has been reported previously (Jassey et al. (2010); Liu et al. (2023)) and suggests that SBM should preferably be harvested during periods of low phenolic (acid) content. These periods must be determined on a site-specific basis, as seasonal and weather conditions vary locally.

Transect samples—Extracts prepared from transect samples collected in April 2018 showed overall strong inhibitory effects on germination and early seedling development. This finding is consistent with the pronounced effects observed for the sample collected in April 2017. The effects observed along the transect imply a potential influence of micro-topography within the production field. As the transect crossed two minor ditches, the content of allelopathic agents may be related to local water saturation conditions of *Sphagnum* at the sampling points. Individual *Sphagnum* plants in wetter zones are likely to exhibit higher tissue water content as well as different oxygen and CO_2 levels, resulting in altered reaction conditions compared with drier areas of the field. These differences may affect the synthesis or degradation of secondary metabolites.

Cultivation environment—The AIT-FI sample was included as a positive control representing non-inhibitory SBM. This material has been used in extensive growing media trials with various woody species and has demonstrated suitability as a horticultural growing medium (Irrgang et al., 2018). This was confirmed in the present assays, as extracts from AIT-FI did not significantly inhibit germination or early growth. The species composition of this SBM differs from that of the other samples and consists mainly of *S. fuscum* and *S. rubellum*. This indicates that species selection may be relevant for the use of SBM in growing media. This interpretation is further supported by the greenhouse-cultivated samples in this subset. Material originating from the same SFS as the monthly (Figure 2) and transect samples (Figure 3) did not lose its allelopathic potential after 12 months of greenhouse cultivation (Figure 4). Therefore, site-specific effects on the development of allelopathic properties appear less likely than species-specific characteristics or differences in microbiome composition.

Heat treatment—Application of elevated temperatures for 24 h clearly reduced the allelopathic potential of treated material in Pm1 and confirms earlier observations by Tsubota et al. (2006). Therefore, thermal treatment could be suggested as a processing step when preparing growing media out of SBM. Since application of heat needs a relevant energy and consequently also financial input, a targeted use of this treatment should be implemented. This clearly needs an understanding of the processes behind the observed effects. If growth inhibition derived from one of the identified core peaks, the observed effects in the temperature subset is counter intuitive. Peak contents increased with temperature. If none of the core peaks is directly responsible for growth inhibition, a possible protective effect of these compounds may increase with higher availability. Another probable explanation would be a heat induced decrease of enzymes, which are contained in the SBM. Such enzymes may be involved in the degradation of detected peak substances. If degradation products are responsible for inhibitory effects, inactivation of the relevant enzymes would reduce allelopathic potential despite increased concentrations of precursor compounds. Tutschek (1979) reported decreasing peroxidase activity in *S. magellanicum* at temperatures above 52 °C, which aligns with the present findings, as the most pronounced effects were observed above 60 °C. Wilschke (1989) identified *p*-hydroxybenzoic acid as one of two *in vitro* degradation products of sphagnum acid, a

compound that may exert strong allelopathic effects (Liu et al., 2019; Huang et al., 2020; Yan et al., 2022).

4.2 Chemical composition of AE_{SBM}

Plant material of *Sphagnum* spp. typically contains various phenolic compounds, of which sphagnum acid is considered the signature compound of the genus. In AE_{SBM}, only the *trans*-configuration was detected. Previously described degradation products of sphagnum acid, such as hydroxybutenolide (Wilschke (1989)) or (-)-2,5-dihydro-S-hydroxy-4-[4'-hydroxyphenyl]-furan-2-one, or *p*-hydroxybenzoic acid (Rasmussen et al. (1996)) were not detected. Peaks PK02 and PK12, which constitute group C, may represent derivatives of hydroxybutenolide due to the presence of a fragment with identical molecular weight. In addition, the coumaric acid conjugate 4'-O-beta-D-glucosyl-*cis*-*p*-coumaric acid, previously described for *S. fallax* (Rasmussen et al., 1996), was not part of the detected profile. As reported in other studies using water as solvent (Chiapusio et al., 2018), large parts of the phenolic profile remained unidentified. With the exception of PK15, for which no fragmentation pattern was detected, all compounds of the core peak group are likely derivatives of sphagnum acid or coumaric acid.

Monthly variation—The pronounced variation in *t*SphA content among monthly samples indicates dynamic processes of synthesis, storage, consumption, or breakdown. The particularly low values observed in March 2017 may be explained by increased enzymatic breakdown during early spring without concomitant synthesis by *Sphagnum* plants. There seems to be no interaction between *t*SphA and PK15, since a decrease of *t*SphA did not lead to an increase of PK15. If *t*SphA serves as a precursor for allelopathic substances, SBM should ideally be harvested during periods of minimal *t*SphA content. For the year 2017, March would therefore represent the most favorable harvesting period.

Transect—Despite the relatively small size of the sampled field (0.68 ha), variation in peak profiles and content is clearly observed among individual sampling points. This variability may be attributed to microtopography within the field. The two sub-ditches provide equal water distribution. Areas closer to these sub-ditches may receive freshwater more frequently, resulting in increased nutrient availability. This may influence species composition within the sphagnosphere and, consequently, the profile of specific phenolic compounds. Phenolic composition can be influenced by temperature (Carrell et al. (2019)), season (Dahl et al. (2020)), and habitat-specific conditions (Tian et al. (2019). As *Sphagnum* plants interact closely with their surrounding microbiome, it is likely that phenolic profiles are influenced—or even determined—by the entire sphagnosphere (Singer et al. (2019)).

Cultivation environment—The extremely low content of core peaks in AIT-FI is consistent with its minimal inhibitory effects in LsC assays. In contrast, heat-treated samples—particularly those treated at 80 °C—exhibited markedly higher contents of nearly all core peaks (except PK10) while displaying low inhibitory potential. Similarly, the sample in which water was squeezed out after harvest (S) showed a low but still significant inhibitory effect, despite a generally low TPC_{core} content dominated by PK15 and PK09. Samples taken directly from the field as well as those cultivated in the greenhouse exhibited significant inhibitory effects on LsC and contained a substantially higher number of individual peaks compared with the harvested sample G. Despite large differences in TPC_{core}, inhibitory effects on seeds and seedlings did not differ substantially. This observation further underscores the potential importance of PK15, which was present in sample G as well as in field and greenhouse samples.

Temperature treatment increases peak content—The observed increase in core compound content with increasing heat treatment temperature was unexpected. Heat treatment was applied to lyophilized material with minimal water content, making biological processes such as *de novo* synthesis highly unlikely. A more plausible explanation is that elevated temperatures inactivated enzymes (e.g., phenol oxidases and peroxidases) responsible for the degradation of peak compounds during subsequent aqueous extraction. Taking into account the decreasing allelopathic potential of the heat treated extracts, this would lead to the assumption that enzymatic degradation breakdown products of the defined core group could be involved in the allelopathic effects from the AE_{SBM}. The extraction period of 24 h would allow enzymatic degradation to occur. Increasing treatment temperatures may progressively inactivate these enzymes. Rudolph and Samland (1985) described enzymatic degradation of sphagnum acid mediated by specific oxidases and peroxidases. Reported degradation products include hydroxybutenolide (Rasmussen et al., 1996) and *p*-hydroxybenzoic acid (Wilschke et al., 1989). Neither compound was detected by HPLC–MS in the present study, which may have several explanations. Both substances may have been masked by conjugation to adducts such as glucosides, rendering them undetectable. Additionally, the low solubility of *p*-hydroxybenzoic acid in water (Nordström and Rasmuson, 2006), combined with microcrystallization, may have hindered detection. Furthermore, the activity of different isoenzymes of Sphagnum peroxidase can result in varying proportions of sphagnum acid degradation products (Wilschke, 1989). Assuming the simultaneous presence of these isoenzymes in AE_{SBM} and competition for available substrate, this may explain the variable symptom severity observed among individual wells within treatments.

4.3 Attribution of compounds

Sphagnum is a bryophyte that cannot be examined in isolation from its environment. This applies to natural, semi-natural (paludiculture/Sphagnum farming), and even artificial cultivation conditions (greenhouse or vertical farming). Even when occurring as mono-specific patches, *Sphagnum* grows and persists within a complex framework of diverse microorganisms, collectively referred to as the sphagnosphere (Singer et al., 2019). In most cases, other mosses, bacteria, fungi, and vascular plants are also present in the microhabitat and, consequently, in SBM. The sponge-like micro- and macroscopic properties of *Sphagnum* tissue provide an optimal

matrix for the absorption of organic chemical compounds. This complicates reliable attribution of compounds detected in SBM to *Sphagnum* itself, with the exception of *trans*- and *cis*-sphagnum acid. Macroscopically visible non-*Sphagnum* plant material can be removed, but smaller organic residues remain within the analyzed samples and contribute to peak profiles and compound contents.

From a practical perspective—particularly regarding the use of SBM as a growing media constituent—it is more important to identify which substances are responsible for growth-inhibitory effects than to attribute them to a specific biological source. Nevertheless, a mechanistic understanding of allelopathic effects in SBM is essential and can only be achieved by identifying the origin of the relevant chemicals. Otherwise it would not be possible to conduct targeted chemical analysis prior to the use of SBM in growing media production. Hence, it would also be beneficial to influence the cultivation conditions in Sphagnum Farming or to include the occurrence of relevant compounds in the process of genotype selection (or even breeding).

The results of the machine learning–based analysis cannot be used to infer causality between the presence of individual compounds and growth inhibition. However, a tendency toward involvement of certain peaks is evident. PK15 was selected as a relevant feature for prediction in both the radicle and hypocotyl models and exhibited the highest feature importance scores. Consequently, detection and fractionation of this compound would be of high interest, either to confirm or exclude its relevance. All other selected peaks are derivatives of sphagnum acid or coumaric acid, suggesting that these compounds may also contribute to mechanisms underlying germination and growth inhibition. *p*-Coumaric acid has been shown to significantly reduce germination and seedling growth in barnyardgrass (Chung et al., 2002), indicating that structurally related derivatives may exert comparable effects, particularly if solubility or membrane transportability is enhanced by conjugation.

Methodological considerations—The applied extraction system yielded relatively low amounts of phenolic compounds but was designed to approximate conditions within a root–substrate system during horticultural cultivation. The underlying scenario represents a freshly potted and watered plant, with growing media saturated with water and composed solely of SBM, without additional nutrient input. This setup approximates mild extraction of water-soluble phenolics in a system where microorganisms and enzymes originating from SBM remain active. Under these conditions, potential allelochemicals are diluted, become available to plant roots, and may influence growth. Monthly and transect samples were collected to represent harvested biomass. Variation in *Sphagnum* species composition among samples may therefore have influenced phenolic compound concentrations.

The selected analytical equipment and methods represent a targeted approach, assuming that responsible compounds belong to secondary plant metabolites, specifically phenolic acids. This assumption is supported by the documented allelopathic activity of numerous phenolic acids. A non-targeted analytical approach, such as MALDI-TOF, would likely have detected a broader range of compounds (cf. Fudyma et al., 2019). In addition, it cannot be excluded that growth inhibition was caused by volatile organic compounds (VOCs). For instance, caryophyllene has been detected in *S. fimbriatum* (Joshi et al., 2023), and β-caryophyllene has demonstrated phytotoxic effects against *Avena fatua* and *Melilotus indicus* (Akbar et al., 2023). On the other hand, Vicherova et al. (2020) showed a growth promoting effect of VOCs from *S. flexosum* on the Varnished Hook-moss (*Hamatocaulis vernicosus*).

5 Conclusions

The extended use of SBM in growing media is currently limited mainly by the low availability of standardized, high-quality material. Availability of SBM can be improved by expanding production across different farming systems. At the same time, SBM quality must be ensured through detailed knowledge of its chemical properties and the underlying metabolic mechanisms. It is not advisable to use the scattered allelopathic effects of SBM—or more specifically, its aqueous extracts—as justification to exclude SBM as a highly promising growing media constituent for professional horticulture. Since SBM batches without allelopathic effects clearly exist, the primary task is to further elucidate the biological processes responsible for inhibitory effects. In addition, *Sphagnum* species and genotypes with no or reduced detrimental effects are evidently present. Thermal treatment was shown to reduce allelopathic effects. However, before providing general recommendations for implementing thermal treatment in SGM production, further experiments are required to determine the minimum effective treatment duration and appropriate water content are necessary. Nonetheless, heat treatment of 80 °C lowered the risk of growth inhibition. To provide an unequivocal attribution of the observed inhibitory effects, further analytical work is necessary. First, currently unidentified peaks—particularly PK15—should be fractionated and structurally identified using NMR spectroscopy. Second, the contribution of sphagnum acid degradation products to growth inhibition should be confirmed or excluded. Once this information is available, threshold values for the responsible compounds should be incorporated into official quality specifications for SBM. Given that the development of SBM as a growing media constituent is still at an early stage, it would be advisable to include the allelopathic potential of *Sphagnum* species or genotypes in selection or breeding criteria. Furthermore, a detailed understanding of *Sphagnum*-specific enzymes and their post-harvest dynamics could facilitate material processing by enabling targeted strategies for enzyme inactivation.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

SI: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. AB: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – review & editing. TS: Investigation, Methodology, Resources, Writing – review & editing. CU: Supervision, Writing – review & editing, Funding acquisition, Project administration. NF: Investigation, Methodology, Resources, Supervision, Validation, Writing – review & editing.

Funding

The author(s) declared that financial support was received for this work and/or its publication. Project "EVA - Entwicklung eines Multi-Ebenen-Verfahrens zur nachhaltigen Produktion und Standardisierung der physikochemischen Eigenschaften von Sphagnum-Biomasse für die Herstellung von Standard-Kultursubstraten im Erwerbsgartenbau" was funded by Agency for Renewable Resources (FNR) on behalf of the Federal Ministry of Agriculture (2219 NR 222). The work, but not the publication, was financed by FNR. The article processing charge was funded by the Open Access Publication Fund of Humboldt-Universität zu Berlin.

Acknowledgments

We would like to thank the company "Torfwerk Moorkultur Ramsloh" (MOKURA) for the opportunity to acquire samples from the Hankhausen Sphagnum farming site. We would especially like to thank Silke Kumar (MOKURA), who did part of the sampling with great effort. We would also like to thank Susanne Meier for her contribution to the laboratory analysis as well as Ivy Wichmann for supporting the preparation of plant assays.

Conflict of interest

The authors declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that generative AI was not used in the creation of this manuscript.

Any alternative text (alt text) provided alongside figures in this article has been generated by Frontiers with the support of artificial intelligence and reasonable efforts have been made to ensure accuracy, including review by the authors wherever possible. If you identify any issues, please contact us.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fhort.2025.1725946/full#supplementary-material

References

Akbar, M., Raza, A., Khalil, T., Yasin, N. A., Nazir, Y., and Ahmad, A. (2023). Isolation of herbicidal compounds, quercetin and β-caryophyllene, from *Digera muricata*. *Arabian J. Chem.* 16, 104653. doi: 10.1016/j.arabjc.2023.104653

Blievernicht, A., Irrgang, S., Zander, M., and Ulrichs, C. (2012). "The youngest peat - sustainable production of *Sphagnum* ssp. and its use as a growing media in professional horticulture," in *Abstracts of the 14th International Peat Congress*, Stockholm, Schweden.

Blum, U., and Thomas M., G. (2005). Relationships between phenolic acid concentrations, transpiration, water unilization, leaf area expansion, and uptake of phenolic acids: Nutrient culture studies. *J. Chem. Ecol.* 31, 1907. doi: 10.1007/s10886-005-5934-5

Carrell, A. A., Kolton, M., Glass, J. B., Pelletier, D. A., Warren, M. J., Kostka, J. E., et al. (2019). Experimental warming alters the community composition, diversity, and N_2 fixation activity of peat moss (*Sphagnum fallax*) microbiomes. *Global Change Biol.* 25, 2993–3004. doi: 10.1111/gcb.14715

Chiapusio, G., Jassey, V. E. J., Hussain, I. M., and Binet, P. (2013). Evidences of Bryophyte Allelochemical Interactions: The Case of *Sphagnum*. In: *Allelopathy: Current Trends and Future Applications*, Z. A. Cheema, M. Farooq and A. Wahid (eds). Berlin, Heidelberg: Springer, 39–54.

Chiapusio, G., Jassey, V. E. J., Bellvert, F., Comte, G., Weston, L. A., Delarue, F., et al. (2018). *Sphagnum* species modulate their mhenolic profiles and mycorrhizal colonization of surrounding *Andromeda polifolia* along peatland microhabitats. *J. Chem. Ecol.* 44, 1146–1157. doi: 10.1007/s10886-018-1023-4

Chung, I., Kim, K., Ahn, J., Chun, S., Kim, C., Kim, J., et al. (2002). Screening of allelochemicals on barnyardgrass (*Echinochloa crus-galli*) and identification of potentially allelopathic compounds from rice (*Oryza sativa*) variety hull extracts. *Crop Prot.* 21, 913–920. doi: 10.1016/s0261-2194(02)00063-7

Dahl, M. B., Krebs, M., Unterseher, M., Urich, T., and Gaudig, G. (2020). Temporal dynamics in the taxonomic and functional profile of the *Sphagnum*-associated fungi (mycobiomes) in a *Sphagnum* fariming filed site in northwestern Germany. *FEMS Microbiol. Ecol.* 96, 1–11. doi: 10.1093/femsec/fiaa204

Emmel, M. (2008). Growing ornamental plants in *Sphagnum* biomass. *Acta Hortic.* 779, 173–178. doi: 10.17660/actahortic.2008.779.20

Emmel, M., and Kennett, A.-K. (2007). Torfmoosarten unterschiedlich geeignet: Gemüse- und Zierpflanzen reagieren unterschiedlich auf einzelne Torfmoosarten im Vermehrungssubstrat. *Deutscher Gartenbau* 13, 34–35. Produktion und Handel.

Förster, N., Dilling, S., Ulrichs, C., and Huyskens-Keil, S. (2023). Nutritional diversity in leaves of various amaranth (*Amaranthus* spp.) genotypes and its resilience to drought stress. *J. Appl. Bot. Food Qual.* 96, 1–10. doi: 10.5073/JABFQ.2023.096.001

Fudyma, J. D., Lyon, J., AminiTabrizi, R., Gieschen, H., Chu, R. K., Hoyt, D. W., et al. (2019). Untargeted metabolomic profiling of *Sphagnum fallax* reveals novel antimicrobial metabolites. *Plant direct* 3, 1–17. doi: 10.1002/pld3.179

Hamard, S., Robroek, B. J. M., Allard, P.-M., Signarbieux, C., Zhou, S., Saesong, T., et al. (2019). Effects of *Sphagnum* leachate on competitive *Sphagnum* microbiome depend on species and time. *Front. Microbiol.* 10. doi: 10.3389/fmicb.2019.02042

He, H., and Roulet, N. T. (2023). Improved estimates of carbon dioxide emissions from drained peatlands support a reduction in emission factor. *Commun. Earth Environ.* 4, 1–6. doi: 10.1038/s43247-023-01091-y

Herrera, F., Pulgarin, C., Nadtochenko, V., and Kiwi, J. (1998). Accelerated photo-oxidation of concentrated *p*-coumaric acid in homogeneous solution. mechanistic studies, intermediates and precursors formed in the dark. *Appl. Catalysis. B Environ.* 17, 141–156. doi: 10.1016/s0926-3373(98)00008-3

Huang, C.-z., XU, L., Jin-jing, S., ZHANG, Z.-h., FU, M.-l., TENG, H.-y., et al. (2020). Allelochemical *p*-hydroxybenzoic acid inhibits root growth via regulating ros accumulation in cucumber (*Cucumis sativus* l.). *J. Integr. Agric.* 19, 518–527. doi: 10.1016/s2095-3119(19)62781-4

Hugelius, G., Loisel, J., Chadburn, S., Jackson, R. B., Jones, M., MacDonald, G., et al. (2020). Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw. *Proc. Natl. Acad. Sci.* 117, 20438–20446. doi: 10.1073/pnas.1916387117

Ingerpuu, N., and Vellak, K. (2013). Growth depends on neighbours: experiments with three *Sphagnum* l. species. *J. Bryology* 35, 27–32. doi: 10.1179/1743282012Y.0000000034

Irrgang, S., Blievernicht, A., and Kumar, S. (2018). Torfmoos-Biomasse (*Sphagnum* sp.) und Grünschnitt-Kompost aus Landschaftspflegemaßnahmen als Komponenten zur Entwicklung einer neuen Generation von nachhaltig produzierten gärtnerischen Substraten. 1–53.

Jassey, V. E. J., Chiapusio, G., Mitchell, E. A. D., Binet, P., Toussaint, M.-L., and Gilbert, D. (2010). Fine-scale horizontal and vertical micro-distribution patterns of testate amoebae along a narrow fen/bog gradient. *Microbial Ecol.* 61, 374–385. doi: 10.1007/s00248-010-9756-9

Joshi, S., Singh, S., Sharma, R., Vats, S., and Alam, A. (2023). Gas chromatography-mass spectrometry (GC-MS) profiling of aqueous methanol fraction of *Plagiochasma appendiculatum* Lem. & Lindenb. and *Sphagnum fimbriatum* Wilson for for probable antiviral potential. *Vegetos* 36, 87–92. doi: 10.1007/s42535-022-00458-4

Li, H.-H., Inoue, M., Nishimura, H., Mizutani, J., and Tsuzuki, E. (1993). Interactions of trans-cinnamic acid, its related phenolic allelochemicals, and abscisic acid in seedling growth and seed germination of lettuce. *J. Chem. Ecol.* 19, 1775–1787. doi: 10.1007/BF00982307

Liu, C., Bu, Z.-J., Mallik, A., Rochefort, L., Hu, X.-F., and Yu, Z. (2019). Resource competition and allelopathy in two peat mosses: implication for niche differentiation. *Plant Soil* 446, 229–242. doi: 10.1007/s11104-019-04350-0

Liu, C., Chen, Y.-D., Mallik, A., Jassey, V. E.J., Rochefort, „. L., and Bu, Z.-J. (2023). Monthly dynamics of phenolic release an allelopathic affect in holliw and hummock *Sphagnum*. *Botany* 101, 532–541. doi: 10.1139/cjb-2023-0058

Michel, P., Burrit, D. J., and Lee, W. G. (2011). Bryophytes display allelopathic interactions with tree species in native forest ecosystems. *Oikos* 120, 1272–1280. doi: 10.1111/j.1600-0706.2010.19148.x

Müller, R., and Glatzel, S. (2021). *Sphagnum* farming substrate is a competitive alternative to traditional horticultural substrates for achieving desired hydro-physical properties. *Mires Peat* 27, 12pp. doi: 10.19189/MaP.2021.OMB.StA.2157

Nordström, F. L., and Rasmuson, Å.C. (2006). Phase equilibria and thermodynamics of *p*-hydroxybenzoic acid. *J. Pharm. Sci.* 95, 748–760. doi: 10.1002/jps.20569

Rasmussen, S., Wolff, C., and Rudolph, H. (1995). Compartmentalization of phenolic constituents in *Sphagnum*. *Phytochemistry* 38, 35–39. doi: 10.1016/0031-9422(94)00650-i

Rasmussen, S., Wolff, C., and Rudolph, H. (1996). 4′-o-beta-d-glucosyl-*cis*-*p*-coumaric acid—a natural constituent of *Sphagnum fallax* cultivated in bioreactors. *Phytochemistry* 42, 81–87. doi: 10.1016/0031-9422(95)00834-9

Rudolph, H., and Samland, J. (1985). Occurrence and metabolism of *Sphagnum* acid in the cell walls of bryophytes. *Phytochemistry* 24, 745–749. doi: 10.1016/S0031-9422(00)84888-8

Singer, D., Metz, S., Unrein, F., Shimano, S., Mazei, Y., Mitchell, E. A. D., et al. (2019). Contrasted micro-eukaryotic diversity associated with *Sphagnum* mosses in tropical, subtropical and temperate climatic zones. *Microbial Ecol.* 78, 714–724. doi: 10.1007/s00248-019-01325-7

Tian, W., Wang, H., Xiang, X., Wang, R., and Xu, Y. (2019). Structural variations of bacterial community driven by *Sphagnum* microhabitat differentiation in a subalpine peatland. *Front. Microbiol.* 10. doi: 10.3389/fmicb.2019.01661

Tommila, T., Kämäräinen, A., Kokko, H., and Palonen, P. (2022). *Sphagnum* moss is promising growth substrate in arctic bramble container cultivation. *Acta Agriculturae Scandinavica Section B - Soil Plant Sci.* 72, 997–1008. doi: 10.1080/09064710.2022.2138778

Tsubota, H., Kuoda, A., Maszuaki, H., Nakahara, M., and Deguchi, H. (2006). A preliminary study on allelopathic activity of bryophytes under laboratory conditions using the sandwich method. *J. Hattori Bot. Lab.* 100, 517–525. doi: 10.18968/jhbl.100.0_517

Tutschek, R. (1979). Characterization of a peroxidase from *Sphagnum magellanicum*. *Phytochemistry* 18, 1437–1439. doi: 10.1016/S0031-9422(00)98471-1

van Breemen, N. (1995). How *Sphagnum* bogs down other plants. *Trends Ecol. Evol.* 10, 270–275. doi: 10.1016/0169-5347(95)90007-1

van den Elzen, E., Kox, M. A. R., Harpenslager, S. F., Hensgens, G., Fritz, C., Jetten, M.S.M., et al. (2017). Symbiosis revisited: phosphorus and acid buffering stimulate N_2 fixation but not *Sphagnum* growth. *Biogeosciences Discuss* 14, 1111–1122. doi: 10.5194/bg-14-1111-2017

Vicherova, E., Glinwood, R., Hajek, T., Smilauer, P., and Ninkovic, V. (2020). Bryophytes can recognize their neighbours through volatile organic compounds. *Sci. Rep.* 10, 1–11. doi: 10.1038/s41598-020-64108-y

Wilschke, J. (1989). Untersuchungen zur Biosynthese und zum enzymatischen Abbau der Sphagnumsäure. 1–126.

Wilschke, J., Sprengel, B., Wolff, C., and Rudolph, H. (1989). A hydroxybutenolide from *Sphagnum* species. *Phytochemistry* 28, 1725–1727. doi: 10.1002/prac.199633801139

Yan, W., Cao, S., Liu, X., Yao, G., Yu, J., Zhang, J., et al. (2022). Combined physiological and transcriptome analysis revealed the response mechanism of *Pogostemon cablin* roots to *p*-hydroxybenzoic acid. *Front. Plant Sci.* 13. doi: 10.3389/fpls.2022.980745