

Seasonal indicators as key descriptors of water deficit in *Sphagnum* farming systems

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SUMMARY

Paludiculture, in the form of *Sphagnum* farming, is a renewable and cyclical way to produce *Sphagnum* moss fibres. The duration and frequency of water deficit due to the positioning of the water table level in the peat profile is a key driver for biomass accumulation rates in *Sphagnum* farming. For optimal outcomes, it is necessary to establish the threshold water table depth beyond which *Sphagnum* productivity decreases. In this article the daily water deficit (WD), the sum of daily water deficit (SWD) and the seasonal average water table (\bar{h}) are examined to quantify water deficit. The compilation of data from five years of experimental *Sphagnum* farming, in both managed peatlands and greenhouse mesocosms, was used to build a dataset covering a wide variation of water table levels. This study strengthens the idea that the higher the water deficit, the lower the productivity of the *Sphagnum* species. Among the water deficit indicators analysed, WD and SWD have stronger correlation with *Sphagnum* productivity than \bar{h} . The threshold water table depth determined for each subgenus is as follows: Acutifolia at 13.8 ± 1.9 cm, Sphagnum at 12.5 ± 1.4 cm, and Cuspidata at 3.1 ± 1.8 cm. These values correspond to a water table closer to the surface than reported in the literature for *Sphagnum* peatland recolonisation, which is 40 cm, and this is because the aim in *Sphagnum* farming is to maximise productivity.

KEY WORDS: capillarity, *Sphagnum* productivity, threshold water table, water management

INTRODUCTION

Sphagnum farming is defined as the sustainable production of *Sphagnum* biomass which often takes place in rewetted peatlands (Gaudig *et al.* 2018, Gutierrez Pacheco *et al.* 2021). This moss fibre production is made on a renewable and cyclical basis, with the timespan of each cycle currently between five and six years (Pouliot *et al.* 2015, Gaudig *et al.* 2018). Cultivated moss fibres from *Sphagnum* farming could be used as a sustainable alternative to partly diminish the need for extracted peat as a constituent of growing media (Jobin *et al.* 2014, Aubé *et al.* 2015). Moreover, *Sphagnum* farming can also be used to provide plant material to restore degraded peatlands (Money 1994, Glatzel & Rochefort 2017). Paludiculture, in the form of *Sphagnum* farming, is proposed as a nature-based solution for climate change mitigation by transforming disturbed peatlands and even agricultural pastures into carbon sinks (Pouliot *et al.* 2015, Gaudig *et al.* 2017, Ludwig 2019).

Several experiments aimed at developing methods to grow *Sphagnum* mosses in farming basins have established that better control of the hydrological conditions (e.g., soil water tension, water table level) is a key factor for achieving optimal biomass accumulation rates (Price *et al.* 2002, Pouliot *et al.* 2015, Brown *et al.* 2017). The goal of controlling the hydrological conditions is to ensure sufficient capillary water flow to the capitula of the *Sphagnum* (where most of the photosynthetic activity occurs) to support its establishment and growth (Clymo & Hayward 1982). Sufficient water flow to the *Sphagnum* capitula is achieved when the water table level is sufficiently high. A water table close to the *Sphagnum* capitula increases the number of water-filled pores, thereby enhancing the hydraulic conductivity of both the *Sphagnum* and the peat (Golubev & Whittington 2018).

However, maintaining a uniformly shallow and stable water table in large-scale field basins is challenging for two main reasons. The first reason is the natural variability of the basin. For example, peat

porosity changes both spatially and temporally due to biological processes, such as microbial decomposition (Siegel & Glaser 2006), or the specific botanical composition of the peat at different locations (Graf & Rochefort 2009), affecting groundwater flow. The second reason is the parabolic profile of the water table created by the irrigation channels. Even if the drainage network is adapted with wooden dams to retain water over summer (Pouliot *et al.* 2015, Guéné-Nanchen *et al.* 2017), it has been shown that the water table level is not uniform due to the hydraulic gradient, which causes the water table level to be higher near the channel than in the centre of the basin (Price & Whitehead 2001). Water table levels measured simultaneously at two different points in a single *Sphagnum* farming field can differ by up to 30 cm, affecting *Sphagnum* moss cover and productivity (Brown *et al.* 2017, Kim *et al.* 2021).

The seasonal mean of the water table level as water deficit indicator

A realistic criterion for determining soil water availability for plants is the soil matric potential, also known as soil water tension (Singh *et al.* 2014). It has been shown that *Sphagnum* growth is gradually reduced when matric potential falls below -100 mbar (-100 cm) (Price & Whitehead 2001). Soil water tension constitutes the force by which water is retained in the soil matrix and is measured by a tensiometer. However, tensiometers are inadequate for predicting water deficit in porous media like *Sphagnum* moss and peat, which can have over 90 % porosity (Boelter 1969, Cornejo *et al.* 2005). This is due to poor contact with the ceramic tip, making them unsuitable for measuring suction in *Sphagnum* moss (Kennedy & van Geel 2000). Besides, the water table level has been shown to strongly control soil water tension and, thus, the water deficit for *Sphagnum* (Moore & Waddington 2015). This relationship is significant for the first 40 cm of water table lowering below capitulum level, while beyond that depth the relationship weakens (Price & Whitehead 2001).

In the context of *Sphagnum* farming, the water table level is the standard indicator for water management and stress assessment. Water table measurements are affordable, easy to implement, and can be recorded automatically when personnel are unavailable. In the similar context of restoration of drained peatlands, many studies have used the mean annual water table level to assess rewetting success (LaRose *et al.* 1997, Landry & Rochefort 2012) and to assist in the interpretation of surface vegetation development (Andersen *et al.* 2010, González *et al.* 2014). Evaluating the water table position relative to

the *Sphagnum* capitula or the peat surface is an effective method for estimation of the water available for *Sphagnum* mosses because they are non-vascular and thus rely primarily on capillary rise (Clymo 1973, Clymo & Hayward 1982). Several researchers have shown that *Sphagnum* growth is optimal when the water table is located just below the capitula, regardless of the preferred hydrological niche of the species (Hayward & Clymo 1983, Campbell & Rochefort 2001, Robroek *et al.* 2009, Kim *et al.* 2021).

Associating annual *Sphagnum* growth with the average annual water table position does not account for the amplitude of water table variation or the frequency at which the water table remains at critical depths for *Sphagnum* productivity, leading to water deficit. Brown *et al.* (2017) suggest that the range of seasonal water table level oscillations is more important than the average water table position for CO₂ uptake by *Sphagnum* mosses. Repetitive dry conditions generally resulted in lower aboveground net primary production (Weltzin *et al.* 2000). Mechanistically, Kim *et al.* (2021) have shown that water table fluctuations inhibit *Sphagnum* growth due to fungal infection. While a single drought event can impact plant productivity, the cumulative effect of prolonged drying events could be far more significant (Schouwenaars & Gosen 2007, Taylor *et al.* 2016). Figure 1 illustrates two cases with different water management systems, demonstrating this situation. Both cases were recorded in the third growing season at an experimental *Sphagnum* farming system in Eastern Canada, focusing on the species *Sphagnum rubellum*. There are no significant differences (p-value = 0.18) in the average water table depth between cases: 14.4 cm below the surface for Case A and 16.5 cm for Case B. Figure 1 shows greater variation in water table levels for Case B, with depths dropping several times to 30 cm, which is detrimental to *Sphagnum* growth (Price 1997, Górecki *et al.* 2021). As a result, there was a difference in the *Sphagnum* biomass harvested, with Case A yielding 366 g m⁻² and Case B 175 g m⁻². This example demonstrates that the seasonal average water table position overlooks the magnitude and duration of drought events affecting *Sphagnum* growth, highlighting the need for complementary information on water deficiency.

Seasonal water deficit indicators based on daily water deficit

In the absence of extreme conditions, such as drought or flooding, plants grow in a cumulative, staggered manner. However, their growth is strongly influenced by environmental conditions, particularly by the

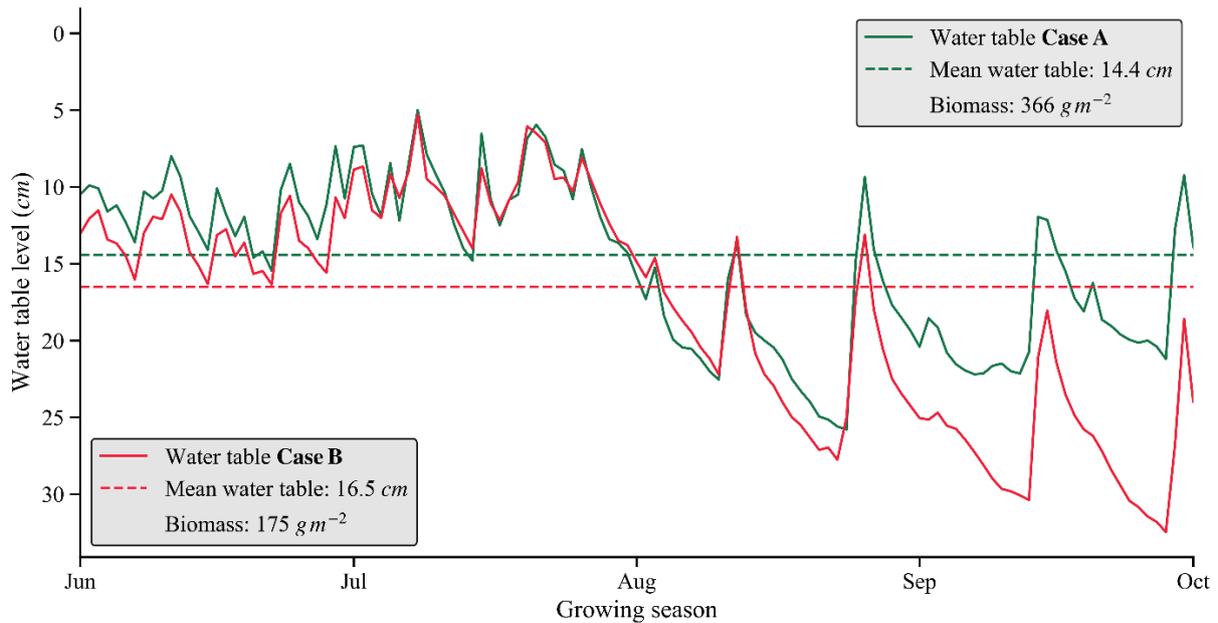


Figure 1. Examples of recorded water table levels for two water management systems in a *Sphagnum* farming system in eastern Canada during the third growing season and associated cumulative *Sphagnum* biomass accumulation. The solid lines represent the daily water table position recorded, and the dotted lines represent the average water table level for each case.

duration and frequency of drought periods. A drought period is represented by high temperatures and/or significantly low water levels belowground. While the effect of environmental temperature on the growth of *Sphagnum* has been widely studied under the concept of heat accumulation, related to physiological development (Thormann & Bayley 1997, Breeuwer *et al.* 2008, Flanagan & Syed 2011, Gerdol & Vicentini 2011, Campbell & Rydin 2019, Mironov *et al.* 2019), little attention has been paid to the duration and frequency of water deficits due to deep water table levels and their effects on *Sphagnum* growth. Although excess water (inundation) is another cause of water stress (Schipperges & Rydin 1998, Tuittila *et al.* 2004), this phenomenon occurs less frequently than water deficit in the experimental sites analysed. Therefore, excess water in *Sphagnum* farming will not be studied in this article.

To analyse the effect of water deficit caused by a deep water table level on *Sphagnum* growth, the first step is to define a methodology for the quantification of seasonal water deficit. The concept of seasonal stress by detrimental water table levels is used in corn production (Kanwar *et al.* 1988, Haan & Skaggs 2003, Kuang *et al.* 2012), wheat production (Malik *et al.* 2001) and soybean production (Evans *et al.* 1990, 1991). The results on agricultural crops consider that the response to water stress varies according to the species and phenological stage. Phenological stages

are not obviously apparent in mosses, so in *Sphagnum* farming the term growing seasons is used instead of phenological stage (Pouliot *et al.* 2015).

The principal indicator used is the sum of daily exceedances from a 30 cm depth (SEW₃₀; Smedema 1988). SEW₃₀ is a measure of cumulative daily stress caused by excessive soil saturation conditions within the root zone, assumed to be the first 30 cm of the soil profile. The SEW₃₀ is calculated during the period of interest, usually the growing season (Hiler 1969, Hardjoamidjojo & Skaggs 1982). This indicator assumes that a water table above 30 cm reduces crop productivity due to lack oxygenation in the root zone. The SEW₃₀ indicator is a measure of the stress degree imposed on the crop and reflects both the intensity and duration of excess water. Mathematically, the SEW₃₀ value (in cm-day) during the entire monitoring period (n days) can be calculated as:

$$SEW_{30} = \sum_{i=1}^n (30 - h_i) \quad [1]$$

where h_i (in cm) is the daily registered water table below the *Sphagnum capitula*. Negative values of summation are neglected.

Based on this concept, two other seasonal water stress indicators based on water table depth (h_i , in cm) have been developed.

1. Sum of daily water deficit (SWD; in cm-day), calculated (following Smedema 1988) as:

$$SWD_x = \sum_{i=1}^n (h_i - h_{DT}) \quad [2]$$

where h_{DT} (in cm) is the threshold of water table depth at which water deficit is detrimental to *Sphagnum* productivity. Both h_i and h_{DT} are measured as distances below the ground surface. Negative values of summation are neglected.

2. Daily water deficit (WD, in days), calculated (again following Smedema 1988) as:

$$WD = \sum_{i=1}^n \begin{cases} \text{if } h_i > h_{DT} \text{ then value} = 1 \\ \text{if } h_i \leq h_{DT} \text{ then value} = 0 \end{cases} \quad [3]$$

Howie *et al.* (2020) report an initial exploration of SWD in the context of peatland vegetation occurrence. In their work, they use the sum of levels deeper than 0 cm ($h_{DT} = 0$). However, selection of the threshold depth at which water table is detrimental to plant productivity must be consistent with the physiology of the *Sphagnum* moss crop. Threshold water table depths correlated with water stress are related to preferential ecological ranges for water table depth per species (Campbell & Rochefort 2001). For example, *Sphagnum* mosses colonising depressions, mostly species of the subgenus *Cuspidata* in bogs, are adapted to grow in a very humid environment, sometimes forming floating mats. On the other hand, typical hummock species such as *Sphagnum fuscum* or lawn species such as *Sphagnum rubellum* can tolerate deeper water tables. Threshold water table depths could also be determined based on the response of *Sphagnum* photosynthetic activity in relation to water table depth (Harley *et al.* 1989, Murray *et al.* 1989, Schipperges & Rydin 1998). However, there is currently no clear methodology for determining thresholds related to seasonal water deficit indicators for *Sphagnum* farming.

The primary objective of this article is to establish a methodology for quantifying water stress caused by water table level fluctuations within the peat profile, particularly when the water table drops to depths known to affect *Sphagnum* productivity. A secondary objective of the study was to identify the critical water table depth at which the productivity of each *Sphagnum* species starts to decrease.

METHODS

Description of experimental systems

To quantify water stress and compute indicators, extensive data covering a wide range of water table levels are needed. We used data from five years of experimental *Sphagnum* cultivation in three systems at various locations in eastern Canada, where water table levels and *Sphagnum* productivity were recorded.

The first experimental site was the *Sphagnum* farming system located in Saint-Modeste (Quebec, 47° 49' 55" N, 69° 27' 55" W), established in 2012 (Gutierrez Pacheco *et al.* 2021) and hereafter named the Hemiboreal site based on the Köppen-Geiger climate classification (Kottek *et al.* 2006). The average air temperature and cumulative precipitation between May and October were 12.9 °C and 494 mm, respectively (Environment Canada 2021). A system of six basins (50 m × 10 m) that covered about 3000 m² were built within the natural margin of a vacuum-extracted bog on moderately well-decomposed peat (H3–H5 on the von Post scale, mean peat depth 1.6 m). Four of the six basins were irrigated with two different types of channel configuration (Table 1), and the other two basins were not irrigated. The irrigated basins were supplied with water (pH = 5.6 ± 0.4, EC = 267 ± 163 μS cm⁻¹) collected from the industrial bog's drainage system. The water table regimes (Table 1) were controlled through an automated irrigating installation. The water level in basin channels was monitored by ultrasonic sensors installed at the dams (water outlet of each basin). Thus, when the water level was lower than the targeted level, the pumping system was activated to irrigate the channels. The species cultivated in the Hemiboreal system were *S. medium* (Hassel *et al.* 2018), *S. papillosum* and *S. rubellum*, and they were manually reintroduced using an area ratio of 1:10.

The second *Sphagnum* farming system was in Shippagan (New Brunswick, 47° 41' 35" N, 64° 45' 47" W) and was established in 2013 on a formerly block-cut peatland (Brown *et al.* 2017, Goulet 2019). This *Sphagnum* farming system is hereafter identified as the Atlantic maritime system. The mean air temperature from May to October was 14.0 °C, with a mean cumulative annual precipitation of 511 mm (dataset from 2000 to 2020; Environment Canada 2021). From 1940 to 1970, peat was extracted using the manual block-cut method, leaving a topography characterised by alternating baulks and trenches. In 2013, six cultivation basins (50 m × 20 m) were established over an area of 6000 m², on slightly to

Table 1. Description of the three experimental systems for *Sphagnum* production based on drain and channel configuration, target water table depth, and associated *Sphagnum* survey methodology (Figures A1 and A2 in the Appendix).

Experimental system	Mesocosm or basin ID	Drain or channel configuration	Target water table depth (cm)	<i>Sphagnum</i> survey
Hemiboreal	PC-20	Peripheral	20	The number of <i>Sphagnum</i> samples varies over the five-year experiment. Between 63 and 143 samples of <i>Sphagnum</i> biomass and 360 samples of <i>Sphagnum</i> carpet thickness were collected along 12 transects systematically disposed.
	PC-10		10	
	PC-NI		Non-irrigated	
	CC-20	Central	20	
	CC-10		10	
	NC-NI		No channel	
Atlantic maritime	PC-20	Peripheral	20	The number of <i>Sphagnum</i> samples varies over the four-year experiment. About 228 to 239 samples of <i>Sphagnum</i> biomass and 600 samples of <i>Sphagnum</i> carpet thickness were collected in 25 × 25 cm quadrats along 10 transects that were systematically disposed across the length of basins.
	PC-10		10	
	CD-20	Central drain linked to an irrigation channel on the shorter side of the basin	20	
	CD-10		10	
	LC-20	Four drains linked to an irrigation channel located on the longer side of the basin	20	
	LC-10		10	
Greenhouse	SF	Water table in the mesocosms was controlled by an inverted siphon	Slow fluctuation. Fluctuating water table between 5 and 35 cm over a 30-day period	All the <i>Sphagnum</i> biomass in the mesocosms was collected at the end of the 12-month long experiment. The thickness of the <i>Sphagnum</i> carpet was measured five times per mesocosm at the end of the experiment. In total there were 20 mesocosms (three experimental units with three different species per mesocosm).
	FF		Fast fluctuation. Fluctuating water table between 5 and 35 cm over a 10-day period	
	SWT:0–5		Stable water table between 0 and 5 cm	
	SWT:10–15		Stable water table between 10 and 15 cm	
	SWT:20–25		Stable water table between 20 and 25 cm	

moderately decomposed peat (von Post H2–H5, mean peat depth 1.5 m). Each basin had a different channel configuration, detailed in Table 1. The basins were irrigated with water sourced from a nearby peatland lake (water supply source: pH = 4.9 ± 0.5 , EC = $104 \pm 19 \mu\text{S cm}^{-1}$). The water table regime was controlled by an automated irrigation system, with each basin assigned a different regime (Table 1). In essence, the basins were divided into two groups, with the target water table level set at 10 cm or 20 cm below the surface. Excess water in the channels was evacuated by a check valve controlled by a linear actuator (Goulet 2019). The *Sphagnum* species cultivated were *S. flavicomans* and *S. medium* (Hassel *et al.* 2018), manually reintroduced at a ratio of 1:10.

Finally, an indoor *Sphagnum* culture system was established within the Université Laval greenhouses complex (Quebec, 46° 46' 32" N, 71° 16' 58" W) using mesocosms (Kim *et al.* 2021). This *Sphagnum* farming system is hereafter referred to as the Greenhouse system. The data used in this article were collected from April 2016 to April 2017. The mesocosms consisted of plastic containers measuring 110 cm × 72 cm × 100 cm (length × width × height) which were filled with horticultural peat (von Post H3). The mesocosm profile consisted of 35 cm of peat and a base layer of 15 cm of sand. The air conditions in the greenhouse were set at 22 °C and 50 % relative humidity during the day, and 18 °C and 85 % relative humidity overnight. The species introduced for the experiment were *S. rubellum*, *S. medium* (Hassel *et al.* 2018) and *S. fallax*, at a ratio of 1:5. There were 20 mesocosms, each with three experimental units. Each experimental unit had one different *Sphagnum* species. The water level in each mesocosm was maintained independently, between 0 cm and 25 cm below the peat surface, by inverted siphons which controlled the respective water table regimes (Table 1). Twice a week, the mesocosms were watered with rainwater until the excess water escaped via the inverted siphons.

For all *Sphagnum* farming systems, the start of each production cycle was established using an adaptation of the Moss Layer Transfer Technique (Pouliot *et al.* 2015, Guêné-Nanchen & St-Hilaire 2022).

***Sphagnum* survey**

Sphagnum carpet thicknesses were measured annually. For outdoor experimental systems, the value per sampling point was the average of five measurements, one in each corner of the 25 × 25 cm quadrat and one more in the centre of the quadrat. Sample points for *Sphagnum* carpet thickness were chosen according to a systematic *Sphagnum* survey,

which varied among the systems (Table 1). For the Greenhouse system, five measurements were taken per experimental unit. The measurements reflected the cumulative change of the *Sphagnum* carpet thickness but not the annual *Sphagnum* elongation.

Samples for accumulated *Sphagnum* biomass measurements were collected at the end of each growing season, generally between September and October for the outdoor experimental systems and in April for the Greenhouse system (at the end of the experiment). For the Greenhouse system, all of the *Sphagnum* biomass in the mesocosms was collected. For outdoor sites, biomass samples were collected along transects perpendicular to the length of the basin, and the number of samples per transect varied for each system (Table 1). Biomass sampling points were relocated each year to avoid repeatedly affecting the same area. Biomass samples were collected in 25 × 25 cm quadrats where all the vegetation newly formed on the residual peat was harvested. Then, different *Sphagnum* species, other mosses, vascular plants and straw mulch were separated, dried at 70 °C and weighed (error of about 1 mg). *Sphagnum* biomass accumulation was calculated as the ratio of dry biomass (g) and the sample area (0.0625 m²). Since the *Sphagnum* biomass sampling points moved each year, the measure is expressed as *Sphagnum* biomass accumulation and not as annual *Sphagnum* productivity. For the purposes of this five-year study, decomposition of *Sphagnum* fibre was considered minimal, although it is known to influence biomass accumulation (Bengtsson *et al.* 2016).

Water table monitoring and estimation

Observation wells were made of 2-inch diameter PVC and were covered with nylon stockings to prevent solids from entering. They were installed to a depth of approximately 70 cm using an auger. Water table levels in the wells were observed relative to the growing surface of the moss. Some wells were equipped with pressure transducers and others were monitored manually at weekly or bimonthly intervals. The number of wells was different for each experimental system (Table A1 in the Appendix). For instrumented wells, water table depth was recorded every hour by pressure transducers (U20 HOBO, Onset Computer Corporation, Bourne MA, USA, accuracy: ±0.5 cm; and Levelogger Edge 3001, Solinst, Georgetown ON, Canada, accuracy: ±0.75 cm). The barometric compensation method was used to obtain the corrected hourly readings of the water table, and field-installed barometers were used for this purpose (U20-001-04 HOBO, Onset Computer Corporation, Bourne MA, USA, accuracy:

± 0.3 cm and Barologger Gold—Model 3001, Solinst Canada Ltd., Georgetown ON, Canada, accuracy: ± 0.75 cm).

The daily value of water table depth (h_i , cm) was estimated from hourly measurements as the average of the maximum ($h_{max,i}$) and minimum ($h_{min,i}$) values recorded during each day of the growing season (Equation 4).

$$h_i = \frac{h_{max,i} + h_{min,i}}{2} \quad [4]$$

The time series decomposition method (TSD; Gutierrez Pacheco *et al.* 2021) was used to estimate missing daily water table values in wells with infrequent measurements. TSD is a novel approach for estimating daily water table levels from infrequent measurements in restored ombrotrophic peatlands. It decomposes water table fluctuations into a local trend (λ) from infrequent measurements and a daily fluctuation component (ρ) from a nearby reference well with continuous monitoring. TSD provides accurate daily estimates without model training or parameter calibration, with an error of about ± 2.5 cm compared to actual measurements. It outperforms six alternative methods, including machine learning models, and ensures reliable estimates without generating artificial data. TSD is robust, easy to implement, and applicable across different sites, making it an optimal tool for hydrological monitoring in peatland restoration and management.

Correspondence between biomass samples and well locations

Since the original data collection did not include a water table observation well next to each *Sphagnum* sampling point, only sample locations near an observation well were retained. For systematically distributed biomass and carpet thickness samples, a correspondence criterion based on proximity to the observation well was defined.

Field observations show that the water table in a *Sphagnum* experimental basin follows a parabolic profile due to the irrigation canals. Cross-sectional variation in water table levels is more significant than longitudinal variation. Within 5 m longitudinally, the water table can vary by 4 cm, while the same variation occurs within 1.5 m cross-sectionally. Therefore, assigning the nearest observation well based on a circular zone of influence is not advisable. Instead, wells were assigned to sample points using a rectangular zone of influence (3×10 m; Figure A3). Each zone had one observation well, and if multiple sampling points fell within a zone, the well information was duplicated for each point.

The correspondence between samples and well locations was established for outdoor *Sphagnum* farming systems, as the Greenhouse system's water table measurement represents the entire mesocosm. Information on the cultivated *Sphagnum* species was also retained for each sampling location. This rigorous correspondence methodology retained 25 % of the collected *Sphagnum* biomass data and 27 % of the carpet thickness data. Rejected data were generally near basin edges or lacked an observation well within a 3×10 m zone of influence. At the Hemiboreal system, 13–22 % of biomass data and 16–18 % of carpet thickness data were preserved. For the Atlantic maritime system, 3–6 % of data were retained, except for the second growing season, which retained 21–25 % (Table A2).

Water stress indicators and estimation of threshold water table depth

After the correspondence stage, water stress indicators were computed for the retained *Sphagnum* data. Three water stress indicators based on daily water table measurements were used, explicitly, the sum of daily water deficit (SWD; Equation 2), the daily water deficit (WD; Equation 3), and the seasonal average water table (\bar{h}). These indicators serve to quantify water deficit in relation to productivity reduction of the *Sphagnum* species introduced.

For WD and SWD computation, the values used for threshold water table depth (h_{DT} , Equations 2 and 3) were established between 0 and 40 cm, spaced 0.5 cm apart. In total, 161 indicators were computed for each *Sphagnum* sampling location, namely 80 SWD indicators, 80 WD indicators and a single indicator containing the seasonal average water table (\bar{h}). The computation of each water stress indicator for each growth season was made considering the duration of the water table log (Table A3). For the calculation of threshold water table depth from the second year for outdoor systems, the total value of the stress indicator since the establishment of *Sphagnum* cultivation was considered.

For each h_{DT} value of the SWD and WD indicators, and for the seasonal average water table level (\bar{h}), a linear regression model was obtained (Figure 2). For each case, the Pearson correlation coefficient (r) for a sample paired data was calculated as:

$$r = \frac{\sum_{i=1}^m (x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum_{i=1}^m (x_i - \bar{x})^2} \cdot \sqrt{\sum_{i=1}^m (y_i - \bar{y})^2}} \quad [5]$$

where m is the number of observations in the paired dataset after correspondence between water stress

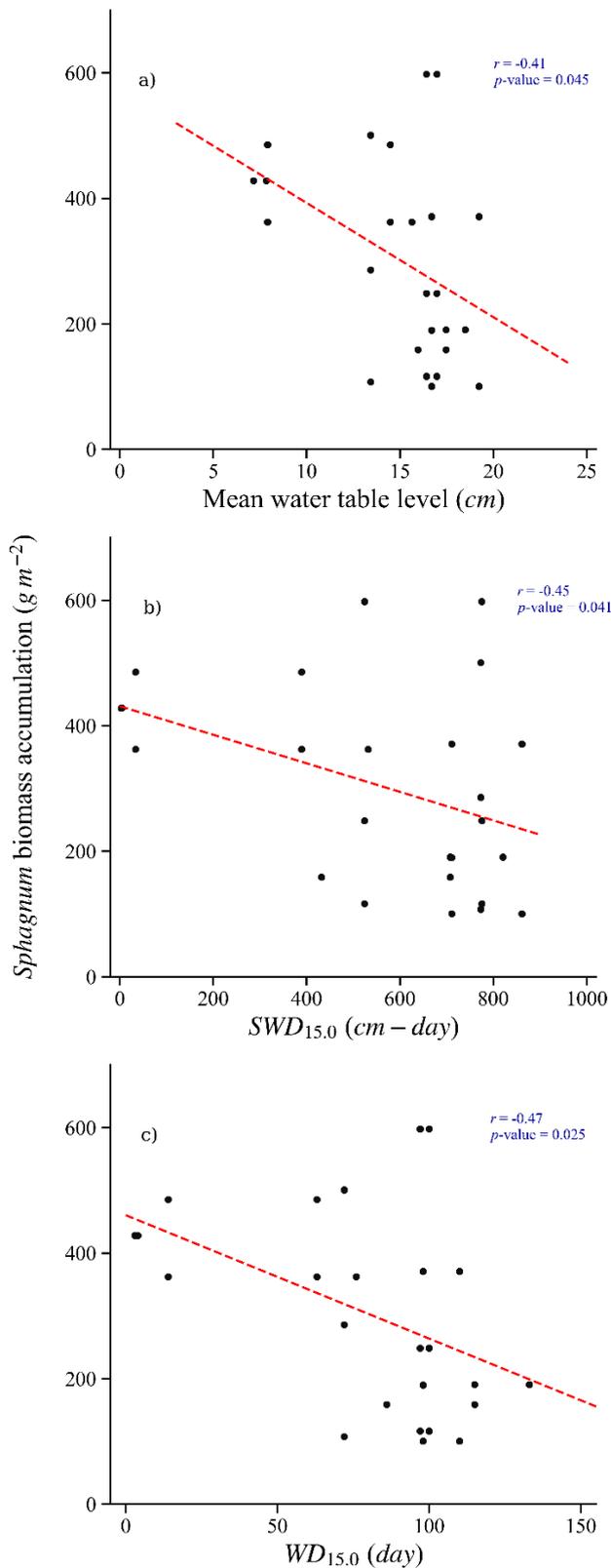


Figure 2. Example of the computation of the water stress threshold for each indicator. Linear regression model between *Sphagnum* biomass accumulation and a) seasonal average depth of the water table level, b) SWD₁₅ ($h_{DT} = 15$ cm), and c) WD₁₅ ($h_{DT} = 15$ cm).

indicators and the information from *Sphagnum* survey, x_i is the water stress indicator and y_i is the biological variable (either *Sphagnum* biomass accumulation or *Sphagnum* carpet thickness).

After finding all the Pearson correlation coefficient values for each threshold water table, these were plotted against threshold curves (Figure 3) to find the optimum point. The water table threshold (h_{DT}) value chosen for SWD and WD corresponded to the optimum value of the curve. Thus, the defined threshold water table depth is the value for which the highest Pearson's correlation coefficient was obtained, indicated under the shaded area in the example shown in Figure 3. For the same case, i.e., same species, same system and same growing season, the threshold for SWD and WD may differ, as in the example shown in the Figure 3. Finally, due to the differences between systems, the estimation of water stress threshold was conducted for each system individually.

To calculate a confidence interval for the threshold water table (h_{DT} ; mean \pm SE), the bootstrapping test was used (Efron 1979). The bootstrapping test was done 100 times over the original dataset and the confidence interval was calculated from the 100 optimum threshold values found. The size of the resample set was equal to the size of the original dataset. The resampling algorithm was implemented in Python 3 (version 3.7.9, Van Rossum & Drake 2009) using the utilities of the scikit-learn package (Pedregosa *et al.* 2011).

Hydrophysical properties of peat and acrotelm

Measuring hydrophysical properties of peat and a part of the acrotelm (living material, mainly *Sphagnum* moss) in the different systems helps to better understand and explain the expected differences in threshold water table depth (h_{DT}). To determine the peat bulk density (ρ_b) and degree of humification (H, von Post scale; Bastien 2002), three samples for each differentiated peat layer were taken from each experimental system. Each system had a different peat layer profile: two layers in the Greenhouse system (0–40 cm and 40–55 cm), three in the Atlantic maritime system (0–30 cm, 30–60 cm and 60–100 cm), and four in the Hemiboreal system (0–20 cm, 20–40 cm, 40–70 cm and 70–100 cm). For the outdoor systems, the depths 0–20 cm or 0–30 cm include part of the acrotelm. For all *Sphagnum* farming systems, the auger hole method (Van Beers 1958) was used for in-situ measurement of saturated hydraulic conductivity (K_{sat}). For all *Sphagnum* farming systems, the alignment of *Sphagnum* biomass and thickness measurements within the same quadrat enabled the estimation of bulk density

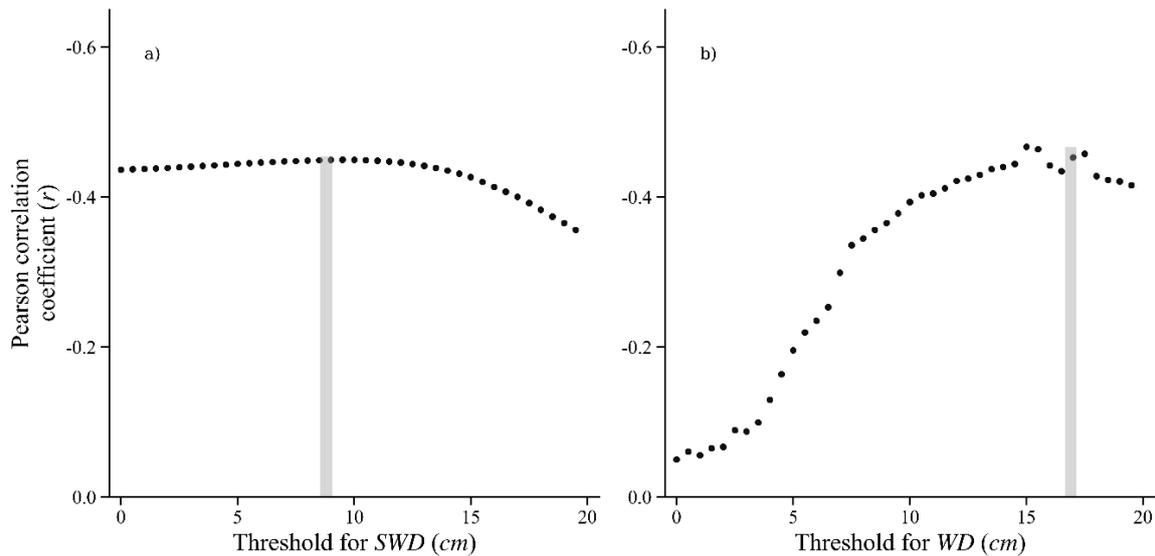


Figure 3. Optimum value of the curve between the Pearson correlation coefficient obtained and the water stress threshold water table depth values for the computation of a) SWD and b) WD.

(kg m^{-3}) of the newly formed *Sphagnum* carpet. Only quadrats with *Sphagnum* cover equal to 100 % were retained for this estimation. This was reported for both sites during the fourth growing season and categorised by reintroduced species.

RESULTS

Performance of water stress indicators

The water stress indicators show a moderately significant correlation coefficient ($-0.50 > r > 0.75$) for the second and third growing seasons in the outdoor systems, and a very strong correlation coefficient ($-0.75 > r > 1.0$) in the 12-month-long experiment at the Greenhouse system (Figure 4). There is a trend of decreasing performance of water stress indicators in the following order: number of daily deficits of water (WD) is better than the sum of daily water deficit (SWD), which is better than the seasonal average water table (\bar{h}). This trend is especially visible for the correlation with *Sphagnum* biomass (Figure 4a). In addition, it is worth clarifying that the results for each water stress indicator were calculated using the threshold water table depth value (h_{DT}) that offered the highest correlation coefficient.

Closer inspection of the relationship with accumulated *Sphagnum* biomass in Figure 4a shows negligible and positive Pearson correlation coefficient values. These cases occur where \bar{h} is used for *S. papillosum* and *S. medium* at the Hemiboreal experimental system after one growth season, and for *S. flavicomans* at the Atlantic maritime experimental system after four growing seasons. This result is

somewhat counterintuitive, as it suggests that higher water deficits lead to higher *Sphagnum* productivity. Regarding the relationship with *Sphagnum* carpet thickness (Figure 4b), the correlation coefficient is high and similar for all the indicators in the Greenhouse system. For outdoor systems there is only one contradictory result, which is for *S. flavicomans* at the Atlantic maritime system after four growing seasons.

Strong association for the threshold water table depth calculated in Greenhouse

The threshold water table depth (h_{DT}) is essential for computing water stress indicators (Equations 2 and 3). Given the differences between systems, these thresholds were estimated separately for each system, based on both *Sphagnum* biomass accumulation and carpet thickness. In general, the highest correlation coefficient values were found for the Greenhouse system, which is why the results are primarily focused on that system. However, the detailed breakdown of each h_{DT} value for outdoor sites is shown in the Tables A4 to A7. These threshold water table depth values must be interpreted with caution due to the lack of an exact association between *Sphagnum* biomass and water table levels. A significant portion of the data was discarded, leaving cases such as the first year of the Hemiboreal system and the third year of the Atlantic maritime system with only 43 % and 8 % of the original data retained, respectively.

When biomass was considered as a biological variable, absolute values of the Pearson correlation coefficient were greater than 0.6 (Table 2). The

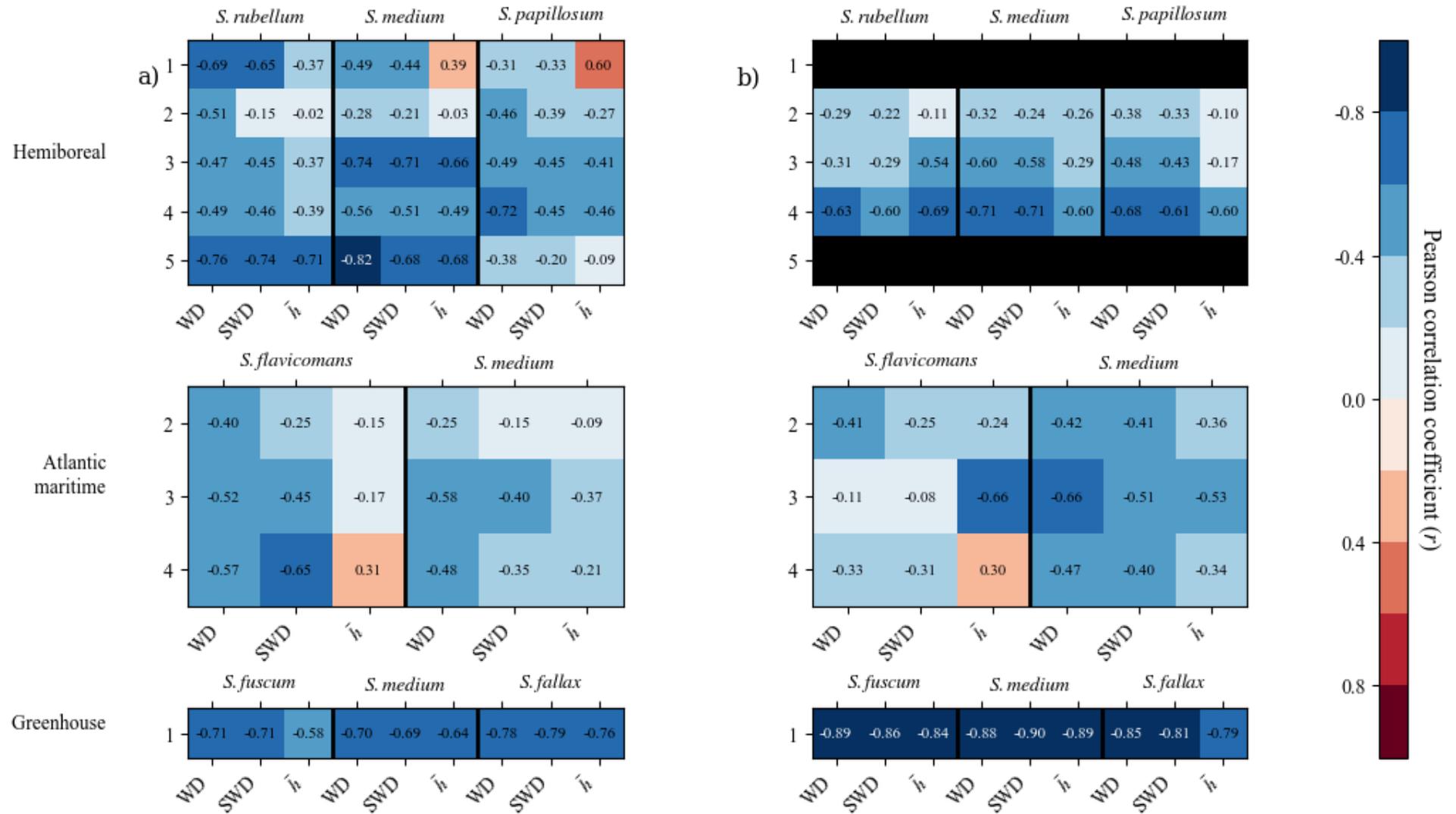


Figure 4. Correlation analysis between each water stress indicator with its optimal threshold depth value (h_{DT}) and the *Sphagnum* biological variables a) accumulated biomass and b) carpet thickness. Each block represents one experimental system of *Sphagnum* cultivation, discriminated according to growing seasons (per row) and *Sphagnum* species (per group of three columns). Black cells reflect missing values for *Sphagnum* carpet thickness.

Table 2. Estimated threshold water table depth values (h_{DT} , mean \pm SE) for the computation of daily water deficits (WD) and sum of daily water deficit (SWD), and Pearson correlation coefficients (r) between water stress indicators and the biological variable for introduced *Sphagnum* species in the Greenhouse system. In Greenhouse, the number of paired data is $n = 19$ for all *Sphagnum* species.

Biological variable	Water stress indicators	<i>S. fuscum</i>		<i>S. medium</i>		<i>S. fallax</i>	
		Threshold h_{DT} (cm)	r	Threshold h_{DT} (cm)	r	Threshold h_{DT} (cm)	r
Biomass	WD	20.1 \pm 1.9	-0.71	16.4 \pm 1.7	-0.70	6.0 \pm 1.6	-0.78
	SWD	13.6 \pm 1.8	-0.71	7.2 \pm 1.4	-0.69	1.5 \pm 1.2	-0.79
	h	-	-0.58	-	-0.64	-	-0.76
Carpet thickness	WD	4.3 \pm 0.7	-0.89	8.9 \pm 0.8	-0.88	3.8 \pm 1.2	-0.85
	SWD	0.2 \pm 0.4	-0.86	0.1 \pm 0.1	-0.90	0.9 \pm 0.9	-0.81
	h	-	-0.84	-	-0.89	-	-0.79

highest threshold water table depth h_{DT} values were found for *S. fuscum*, followed by *S. medium* and finally *S. fallax*. Also, the threshold water table depth values for WD were deeper than for SWD (Table 2). A similar result was found when the *Sphagnum* carpet thickness was considered as a biological variable. Absolute values of the Pearson correlation coefficient were greater than 0.79 and, in general, threshold water table depths were closer to the surface than thresholds estimated based on biomass. However, the threshold water table values (h_{DT}) do not follow the same trend as those calculated for biomass. Using WD, the higher threshold water table depth was for *S. fallax* (3.8 \pm 1.2 cm) and the deeper threshold depth value was for *S. medium* (8.9 \pm 0.8 cm). Using SWD, on the other hand, the values for the three *Sphagnum* species were almost identical (0.2 \pm 0.4 cm for *S. fuscum*, 0.1 \pm 0.1 cm for *S. medium*, and 0.9 \pm 0.9 cm for *S. fallax*). Lastly, the lower performance of the water stress indicators based on *Sphagnum* carpet thickness ($r = -0.79$ for *S. fallax* using h; Table 2) was equal to the highest performance based on biomass accumulation ($r = -0.79$ for *S. fallax* using SWD; Table 2).

Hydrophysical properties of peat and acrotelm

Peat properties showed slight variations between the experimental cultivation systems (Table 3). The peat at the Hemiboreal site was somewhat more decomposed compared to the Atlantic maritime site and the Greenhouse, where horticultural blonde peat was used. These differences are reflected in the slightly lower K_{sat} and porosity (higher bulk density), particularly noticeable at greater depths. As expected,

K_{sat} decreased with peat depth in outdoor systems, ranging from 1.40 \pm 0.43 to 2.01 \pm 0.97 m day⁻¹ at the surface (0–15 cm) to 0.0008 \pm 0.0002 to 0.14 \pm 0.11 m day⁻¹ at greater depths (60–100 cm). In the Greenhouse system, the hydrophysical properties of the mesocosm profile including the underlying 15-cm layer of sand with high K_{sat} (5.04 \pm 4.26 m day⁻¹; Table 7) likely facilitated faster water movement, which may have influenced *Sphagnum* growth. Based on the estimation of bulk density during the fourth growing season (Table A8), the newly formed *Sphagnum* carpet was approximately twice as dense in the Atlantic maritime *Sphagnum* farming system (for all species: 25.41 \pm 5.03 kg m⁻³) compared to the Hemiboreal system (11.61 \pm 2.72 kg m⁻³).

DISCUSSION

Relationship of water stress with *Sphagnum* growth

We found a negative correlation between *Sphagnum* productivity (biomass accumulation, carpet thickness) and the three water stress indicators (daily water deficit WD, sum of daily water deficit SWD, seasonal average water table h). Pearson correlation coefficients reached -0.82 for biomass accumulation and -0.90 for carpet thickness in the case of *S. medium*, in both Hemiboreal and Greenhouse systems. The negative relationship between *Sphagnum* biomass accumulation, carpet thickness and water stress indicators aligns with previous studies that demonstrate a decrease in *Sphagnum* productivity with increased water deficits (Schipperges & Rydin 1998, Stokes *et al.* 1999, McNeil & Waddington

Table 3. Hydrophysical properties (von Post degree of humification, saturated hydraulic conductivity (K_{sat}), bulk density (ρ_b); mean \pm SE) of identified peat layers in *Sphagnum* experimental cultivation systems.

Depth (cm)	Hemiboreal			Atlantic maritime			Greenhouse		
	von Post	K_{sat} (m day ⁻¹)	ρ_b (g cm ⁻³)	von Post	K_{sat} (m day ⁻¹)	ρ_b (g cm ⁻³)	von Post	K_{sat} (m day ⁻¹)	ρ_b (g cm ⁻³)
0									
5									
10	H3	1.40 \pm 0.43	0.13 \pm 0.05						
15				H2–H3	2.01 \pm 0.97	0.11 \pm 0.01			
20							H3	1.33 \pm 0.07	0.12 \pm 0.09
25									
30	H3–H4	0.24 \pm 0.12	0.12 \pm 0.03						
35									
40									
45				H3	0.72 \pm 0.19	0.11 \pm 0.04	Sand	5.04 \pm 4.26	1.63 \pm 0.05
50									
55	H4	0.07 \pm 0.02	0.14 \pm 0.04						
60									
65									
70									
75				H3–H4					
80					0.14 \pm 0.11	0.12 \pm 0.04			
85	H5	0.0008 \pm 0.0002	0.18 \pm 0.03						
90									
95				H5					
100									

2003, Tuittila *et al.* 2004). While previous research in *Sphagnum* farming and restoration has measured water stress (Price *et al.* 2003, Petrone *et al.* 2004, Pouliot *et al.* 2015, Brown *et al.* 2017), it has not provided a method for quantifying seasonal water deficit or defined a specific threshold water table depth (h_{DT}), essential for computing water stress indicators (Equations 2 and 3).

This inverse relationship can be explained by the increase in peat water tension that *Sphagnum* species must overcome to maintain flows to the capitulum. Higher water tension reduces the availability of free water in the peat matrix, increasing resistance to water movement and leading to capitulum desiccation (Price & Ketcheson 2009, McCarter & Price 2014). Additionally, as water content declines, vertical hydraulic conductivity in *Sphagnum* peat decreases, further restricting water transport (Price & Whittington 2010). In parallel, vertical hydraulic conductivity decreases rapidly as peat moisture content decreases, so fewer saturated pores are available for water transport (Golubev & Whittington

2018). As a result, insufficient water flux to the *Sphagnum* capitulum reduces photosynthesis and growth (Rydin 1993, Gerdol *et al.* 1996, Sagot & Rochefort 1996).

The seasonal average water table does not allow the estimation of a fixed h_{DT} value associated with each *Sphagnum* species, which is satisfied for the other two indicators WD and SWD. Consequently, WD and SWD could be used to quantify water stress related to *Sphagnum* productivity. Among the *Sphagnum* systems analysed, WD and SWD show a stronger correlation with productivity than h . The h index has a regular performance ($0.6 > r > -0.76$), and even positive Pearson correlation coefficient values which are not consistent from a biological point of view. Although h is a usual indicator for water management and water stress assessment, the average value of the water table level does not consider either the duration or the magnitude of the water deficit.

The threshold water table depth values found, for the computation of either SWD or WD, generally

fluctuate between 7 and 20 cm. Those threshold depth values correspond to shallower water tables than the 40 cm threshold documented by Price *et al.* (2003) and Ketcheson & Price (2011). For *Sphagnum* farming, the priority is to maintain a high rate of photosynthesis to maximise productivity (Rydin 1993, Sagot & Rochefort 1996, Schipperges & Rydin 1998). Consequently, the threshold water table depth is shallower than the value of 40 cm which is the maximum depth suitable for *Sphagnum* recolonisation in ecological restoration of bogs.

There are still many unanswered questions about the differences in threshold water table values (h_{DT}) between species, systems and growing seasons. Part of these differences can be explained by the variation in residual peat and local climatic conditions, which are discussed in the next section. When comparing the weighted averages of water table depth thresholds (Table 4), the species of subgenus Acutifolia (*S. flavicomans*, *S. fuscum* and *S. rubellum*) and Sphagnum (*S. medium* and *S. papillosum*) have deeper thresholds than species of subgenus Cuspidata (*S. fallax*). However, no clear trend of these values over time is found. Further research should investigate the differences in threshold water table depth between the establishment and biomass accumulation stages. *Sphagnum* coverage of 90 % marks the transition between these stages (Gaudig *et al.* 2017). Future work should aim to establish a better association between biological variables and water stress based on daily water table values.

Factors related to threshold water table depths

Understanding the factors that influence threshold water table depths is essential for interpreting species-specific differences and their implications for *Sphagnum* productivity. These factors include species morphology, ecological preferences, and responses to hydrological changes. Threshold water table depths vary depending on species morphology (Goetz & Price 2015, Taylor & Price 2015, Golubev & Whittington 2018, Elliott & Price 2020), and can significantly affect *Sphagnum* productivity under changing water and climate conditions. This variation aligns with the preferential ecological positioning of *Sphagnum* species relative to the water table (Lindholm & Vasander 1990, Campbell & Rochefort 2001) and the ability of hummock/lawn species to resist water loss more effectively (Campeau & Rochefort 1996, Sagot & Rochefort 1996, Grosvernier *et al.* 1997, McCarter & Price 2014).

In the Greenhouse system, where conditions were more controlled due to the size of experimental units, these species-specific differences in threshold water

table depth were more pronounced. A stronger correlation was observed between *Sphagnum* productivity (in terms of biomass accumulation and carpet thickness) and water stress indicators compared to the outdoor systems. The threshold water table depths based on biomass accumulation, derived via the WD and SWD computation, follow the sequence of ecological preferences *S. fuscum* > *S. medium* > *S. fallax* (Table 4). This outcome complements the findings of Kim *et al.* (2021), who reported that the responses of these three *Sphagnum* species in the Greenhouse system were influenced by different water table regimes.

Across the *Sphagnum* farming systems, variations in peat properties also contributed to differences in threshold water table depths. Considering the estimated threshold water table depth (h_{DT}) for *S. medium* - the only species present in all systems (Table 4) - the WD and SWD threshold values based on biomass were deeper in the Hemiboreal system (20.3 ± 1.0 and 12.6 ± 1.5 cm, respectively) than in the Atlantic maritime (9.7 ± 1.3 and 11.2 ± 1.6 cm, respectively) and Greenhouse systems (12.6 ± 1.9 and 3.6 ± 1.4 cm, respectively). One explanation for this pattern lies in the hydrophysical properties of the upper peat layers. Peat in the Hemiboreal system is slightly denser and has a lower K_{sat} compared to the Atlantic maritime and Greenhouse peats. This indicates a smaller pore size, resulting in higher water retention when unsaturated (Price *et al.* 2003, Verry *et al.* 2011, Caron *et al.* 2015). As a result, the water table can drop further without causing water deficit for the same *Sphagnum* species. This suggests that the peat structure in the Hemiboreal system may provide a greater water reserve for *Sphagnum*, potentially explaining the deeper threshold water table depths calculated. However, above a certain value, denser peat layers can have the opposite effect, while increasing water holding capacity, the retained water becomes inaccessible to *Sphagnum* (Taylor & Price 2015). This relationship between peat density and water availability is complex and not linear, resembling a curve with an optimal peak; beyond this point, increased density becomes detrimental. A critical bulk density (ρ_b) of 0.2 g cm^{-3} has been identified, above which hydraulic properties change dramatically (Liu & Lennartz 2018). Additionally, as mentioned above, variations in species morphology influence the ability of *Sphagnum* to tolerate water table fluctuations, with certain species maintaining hydration more effectively through capillary transport (McCarter & Price 2014, Golubev & Whittington 2018).

Another important factor is the weather conditions. Between May and October, The Atlantic

Table 4. Weighted average of estimated threshold water table depth values (h_{DT} ; mean \pm SE) for the computation of daily water deficits (WD) and sum of daily water deficit (SWD), calculated for all *Sphagnum* species of the system analysed.

Indicator	Subgenus: Acutifolia			Sphagnum		Cuspidata	
	Site	<i>S. rubellum</i>	<i>S. fuscum</i>	<i>S. flavicomans</i>	<i>S. medium</i>	<i>S. papillosum</i>	<i>S. fallax</i>
WD	Hemiboreal	19.2 \pm 1.4			20.3 \pm 1.0	18.6 \pm 1.0	
	Atlantic maritime			12.5 \pm 2.0	9.7 \pm 1.3		
	Greenhouse		12.2 \pm 2.0		12.6 \pm 1.9		4.9 \pm 2.0
SWD	Hemiboreal	14.6 \pm 1.6			12.6 \pm 1.5	11.0 \pm 1.5	
	Atlantic maritime			17.4 \pm 2.3	11.2 \pm 1.6		
	Greenhouse		6.9 \pm 1.8		3.6 \pm 1.4		1.2 \pm 1.5

maritime system experienced slightly higher average and maximum temperatures than the Hemiboreal system (Table A9). Higher temperatures increase evaporative demand for *Sphagnum* (Goetz & Price 2015, Moore & Waddington 2015), requiring greater upward water transport from the water table to maintain surface moisture. Since *Sphagnum* relies on capillary transport to sustain physiological functions, a higher evaporative demand leads to a shallower threshold water table depth for ensuring sufficient water flow to the *Sphagnum* capitulum. These differences may explain why the h_{DT} value for *S. medium* was closer to the surface in the Atlantic maritime system compared to the Hemiboreal system. Otherwise, in response to increased evaporative demand, *Sphagnum* mosses may alter their growth structure, developing a denser carpet that enhances water retention and reduces water stress (Turetsky *et al.* 2008, Elumeeva *et al.* 2011, McCarter & Price 2014, Golubev & Whittington 2018, Gauthier *et al.* 2018). Although *Sphagnum* in the Atlantic Maritime system exhibited a denser structure, this adaptation was insufficient to significantly lower the threshold water table depth.

Importance of site-specific conditions

Another part of *Sphagnum* productivity variation is due to the intrinsic variability of the biosystem (Chirino *et al.* 2006). Factors such as microclimatic and microtopographical conditions, peat layer thickness, field preparation, and interaction with companion plants (Rochefort *et al.* 2003, Pouliot *et al.* 2015, Gu  n  -Nanchen *et al.* 2017, Grobe *et al.* 2021, Moore *et al.* 2021) play a role in the accumulation of *Sphagnum* biomass. These factors

influence the correlation coefficients obtained, especially for outdoor sites, where most of these factors are difficult to control. Therefore, certain points within the same basin do not generate the expected productivity even though the water table regime seems optimal for *Sphagnum* growth. A site-specific approach can be used to identify basin clusters that share similar water stress conditions and comparable hydrophysical and chemical properties. Additionally, for outdoor systems, the association method between biomass samples and well locations is not 100 % direct, and there could have been more subtlety in the variability of the water table level.

Considerations for a future reliable predictive model

For the correct calculation of water deficit indicators, knowledge of the specific water table depth threshold for *Sphagnum* species is required. Currently, no clear methodology for the estimation of these threshold depths is reported, and this study shows the procedure and results using the correspondence with the highest Pearson correlation coefficient value for a given growing season.

The water stress indicators for outdoor systems have a weak to acceptable correlation (Tables A4 to A7). However, the results suggest that the threshold water table depth is influenced not only by climate conditions and the hydrophysical conditions of the peat but also by the structural adaptations of *Sphagnum*, which may modify its response to water stress over time. Thus, this value is highly dependent on the context of each system. To predict *Sphagnum* productivity based on water stress due to water table fluctuations, it might be possible to use stress-day-index models (Hiler 1969, Evans *et al.* 1990, 1991).

These models allow us to determine the productivity related to a water deficit, quantified by a water stress indicator, and a crop sensitivity factor. For the moment, this study has identified the indicators to quantify water deficit and possible values for the threshold. The next step is to identify the crop sensitivity factor, which could depend on *Sphagnum* cultivation age, species, and the density of the newly formed *Sphagnum* carpet. It is recommended that these tests be carried out under controlled conditions, for example using lysimeters such as those used by Evans *et al.* (1990).

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AUTHOR CONTRIBUTIONS

SGP originated and planned the work, wrote the first draft, and is the lead author; SGP, MGN and SH undertook the laboratory work; SGP, SH, SG and LR planned the compilation of data and developed the experimental protocols; RL, MGN and SH contributed to the statistical analysis, the preparation of the graphs and the revision of the first draft; RL, SG and LR reviewed and edited the final version of manuscript. All authors have read and agreed to the published version of the manuscript.

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Appendix

Table A1. Inventory of observation wells for each experiment system.

Experimental system	Year	Wells with pressure transducer*	Wells with manual measurements	Manual measurement frequency	Total number of wells
Greenhouse	1	2	17	Every 2–3 days	19
	2	6	44		
Atlantic maritime	3	2	48	Weekly	50
	4	9	41		
	1	10	49		
Hemiboreal	2	11	48	Bimonthly	59
	3	14	45		
	4	13	46		
	5	15	44		
	1	10	49		

*Number of instrumented wells varied according to the annual availability of pressure transducers.

Table A2. Inventory of retained biomass and thickness data after assignment with observation wells by species and by growth session, after sorting and assigning based on the predefined zone of influence of 3 x 10 m for outdoor experimental systems (Figure A3).

Growing season	Hemiboreal			Total harvested samples	Atlantic maritime		Total harvested samples
	<i>S. rubellum</i>	<i>S. medium</i>	<i>S. papillosum</i>		<i>S. flavicomans</i>	<i>S. medium</i>	
Biomass samples							
1	8	9	10	63	-	-	-
2	28	30	28	138	60	50	239
3	26	19	25	128	9	11	228
4	22	24	18	139	6	13	235
5	29	21	23	143	-	-	-
Carpet thickness samples							
1	-	-	-	-	-	-	-
2	59	66	66	360	161	154	600
3	60	60	62	360	23	32	600
4	59	66	66	360	23	32	598
5	-	-	-	-	-	-	-

Table A3. Duration of the water table logs for each *Sphagnum* farming experimental system.

Experimental system	Log start date	Log end date	Log duration (n)
Hemiboreal	12 May	18 October	159
Atlantic maritime	24 May	03 October	132
Greenhouse	27 April 27	10 April 2017	348

Table A4. Estimated threshold water table depth values (mean \pm SE) for the computation of daily water deficit (WD) and sum of daily water deficit (SWD), with Pearson correlation coefficients (r) between the water stress indicators and *Sphagnum* biomass accumulation for introduced species in Hemiboreal system.

Growing season	<i>S. rubellum</i>		<i>S. medium</i>		<i>S. papillosum</i>	
	Threshold ¹ (cm)	r	Threshold ¹ (cm)	r	Threshold ¹ (cm)	r
WD						
1	20.2 \pm 2.5 b	-0.69	21.5 \pm 3.0 ab	-0.49	10.2 \pm 7.3 b	-0.31
2	6.2 \pm 0.7 c	-0.51	20.7 \pm 2.1 b	-0.28	20.4 \pm 1.4 a	-0.46
3	19.3 \pm 1.1 b	-0.47	21.8 \pm 1.0 ab	-0.74	16.9 \pm 1.2 ab	-0.49
4	18.5 \pm 2.2 b	-0.49	24.3 \pm 1.7 a	-0.56	15.4 \pm 0.6 b	-0.72
5	24.6 \pm 0.8 a	-0.76	16.2 \pm 0.4 c	-0.82	14.5 \pm 3.0 b	-0.38
Weighted average	18.5 \pm 0.9	-	20.5 \pm 0.8	-	15.9 \pm 0.9	-
SWD						
1	21.8 \pm 1.5 a	-0.65	31.0 \pm 1.2 a	-0.44	19.8 \pm 0.3 a	-0.33
2	14.0 \pm 2.1 b	-0.15	22.6 \pm 2.0 b	-0.21	19.3 \pm 1.1 a	-0.39
3	13.7 \pm 1.4 b	-0.45	12.3 \pm 0.8 d	-0.71	8.8 \pm 1.6 b	-0.45
4	19.0 \pm 2.9 a	-0.46	19.4 \pm 2.5 c	-0.51	1.2 \pm 0.5 c	-0.45
5	9.6 \pm 1.0 c	-0.74	2.9 \pm 0.9 e	-0.68	13.4 \pm 3.1 b	-0.20
Weighted average	15.6 \pm 0.9	-	15.3 \pm 1.1	-	11.7 \pm 1.1	-
h						
1	-	-0.37	-	0.39	-	0.60
2	-	-0.02	-	-0.03	-	-0.27
3	-	-0.37	-	-0.66	-	-0.41
4	-	-0.39	-	-0.49	-	-0.46
5	-	-0.71	-	-0.68	-	-0.09

¹Values in the same column and same indicator, followed by different letters indicate differences according to Tukey-Kramer test ($\alpha = 0.05$). The number of paired data is specified in Table A2.

Negligible association ($R \geq -0.25$)	Weak association ($-0.25 > R \geq -0.50$)	Moderate association ($-0.50 > R \geq -0.75$)	Very strong association ($-0.75 > R \geq -1.0$)
----------------------------------------------	------------------------------------------------	----------------------------------------------------	------------------------------------------------------

Table A5. Estimated threshold water table depth values (mean \pm SE) for the computation of daily water deficits (WD) and sum of daily water deficit (SWD), with Pearson correlation coefficients (r) between the water stress indicators and *Sphagnum* carpet thickness for introduced species in Hemiboreal system.

Growing season	<i>S. rubellum</i>		<i>S. medium</i>		<i>S. papillosum</i>	
	Threshold ¹ (cm)	r	Threshold ¹ (cm)	r	Threshold ¹ (cm)	r
WD						
1	-	-	-	-	-	-
2	22.1 \pm 1.7 b	-0.29	20.1 \pm 1.5 ab	-0.32	19.9 \pm 0.7 b	-0.38
3	28.6 \pm 1.1 a	-0.31	18.9 \pm 1.1 b	-0.60	26.9 \pm 0.7 a	-0.48
4	14.6 \pm 1.2 c	-0.63	21.2 \pm 0.6 a	-0.71	18.1 \pm 0.6 c	-0.68
5	-	-	-	-	-	-
Weighted average	19.9 \pm 1.0	-	20.2 \pm 0.6	-	21.3 \pm 0.6	-
SWD						
1	-	-	-	-	-	-
2	25.8 \pm 1.9 a	-0.22	20.1 \pm 2.4 a	-0.24	17.1 \pm 1.1 a	-0.33
3	24.9 \pm 1.3 a	-0.29	10.8 \pm 0.8 b	-0.58	18.2 \pm 1.0 a	-0.43
4	3.7 \pm 0.8 b	-0.60	5.7 \pm 1.1 c	-0.71	0.9 \pm 0.4 b	-0.61
5	-	-	-	-	-	-
Weighted average	13.6 \pm 1.4	-	9.9 \pm 1.1	-	10.3 \pm 1.0	-
\bar{h}						
1	-	-	-	-	-	-
2	-	-0.11	-	-0.26	-	-0.10
3	-	-0.54	-	-0.29	-	-0.17
4	-	-0.69	-	-0.60	-	-0.60
5	-	-	-	-	-	-

Missing values of *Sphagnum* carpet thickness for the first and fifth seasons.

¹Values in the same column and same indicator, followed by different letters indicate differences according to Tukey-Kramer test ($\alpha = 0.05$). The number of paired data is specified in Table A2.

Negligible association ($R \geq -0.25$)	Weak association ($-0.25 > R \geq -0.50$)	Moderate association ($-0.50 > R \geq -0.75$)	Very strong association ($-0.75 > R \geq -1.0$)
----------------------------------------------	------------------------------------------------	----------------------------------------------------	------------------------------------------------------

Table A6. Estimated threshold water table depth values (mean \pm SE) for the computation of daily water deficits (WD) and sum of daily water deficit (SWD), with Pearson correlation coefficients (r) between water stress indicators and *Sphagnum* biomass accumulation for introduced species in Atlantic maritime system.

Growing season	<i>S. flavicomans</i>		<i>S. medium</i>	
	Threshold ¹ (cm)	r	Threshold ¹ (cm)	r
WD				
2	6.7 \pm 2.1 c	-0.40	9.4 \pm 1.6 a	-0.25
3	19.4 \pm 2.0 b	-0.52	7.0 \pm 1.6 a	-0.58
4	27.4 \pm 1.6 a	-0.57	7.4 \pm 1.1 a	-0.48
Weighted average	19.0 \pm 1.5	-	7.6 \pm 0.9	-
SWD				
2	21.6 \pm 3.0 b	-0.25	19.8 \pm 1.5 a	-0.15
3	21.4 \pm 2.1 b	-0.45	7.1 \pm 1.7 b	-0.40
4	30.4 \pm 1.8 a	-0.65	7.8 \pm 2.9 b	-0.35
Weighted average	25.8 \pm 1.5	-	9.5 \pm 1.3	-
\hat{h}				
2	-	-0.15	-	-0.09
3	-	-0.17	-	-0.37
4	-	0.31	-	-0.21

¹Values in the same column and same indicator, followed by different letters indicate differences according to Tukey-Kramer test ($\alpha = 0.05$). The number of paired data is specified in Table A2.

Negligible association
($R \geq -0.25$)

Weak association
($-0.25 > R \geq -0.50$)

Moderate association
($-0.50 > R \geq -0.75$)

Very strong association
($-0.75 > R \geq -1.0$)

Table A7. Estimated threshold water table depth values (mean \pm SE) for the computation of daily water deficits (WD) and sum of daily water deficit (SWD), with Pearson correlation coefficients (r) between water stress indicators and *Sphagnum* carpet thickness for introduced species in Atlantic maritime system.

Growing season	<i>S. flavicomans</i>		<i>S. medium</i>	
	Threshold ¹ (cm)	r	Threshold ¹ (cm)	r
WD				
2	2.4 \pm 0.2 c	-0.41	19.7 \pm 1.0 a	-0.42
3	16.2 \pm 2.8 a	-0.11	4.8 \pm 0.8 c	-0.66
4	7.3 \pm 1.8 b	-0.33	14.5 \pm 1.6 b	-0.47
Weighted average	6.1 \pm 1.3	-	11.8 \pm 1.0	-
SWD				
2	2.8 \pm 0.9 c	-0.25	16.7 \pm 1.0 a	-0.41
3	31.0 \pm 0.1 a	-0.08	7.0 \pm 0.5 b	-0.51
4	8.5 \pm 2.5 b	-0.31	16.6 \pm 2.4 a	-0.40
Weighted average	9.1 \pm 1.7	-	12.9 \pm 1.0	-
\hat{h}				
2	-	-0.24	-	-0.36
3	-	0.66	-	-0.53
4	-	-0.30	-	-0.34

¹Values in the same column and same indicator, followed by different letters, indicate differences according to Tukey-Kramer test ($\alpha = 0.05$). The number of paired data is specified in Table A2.

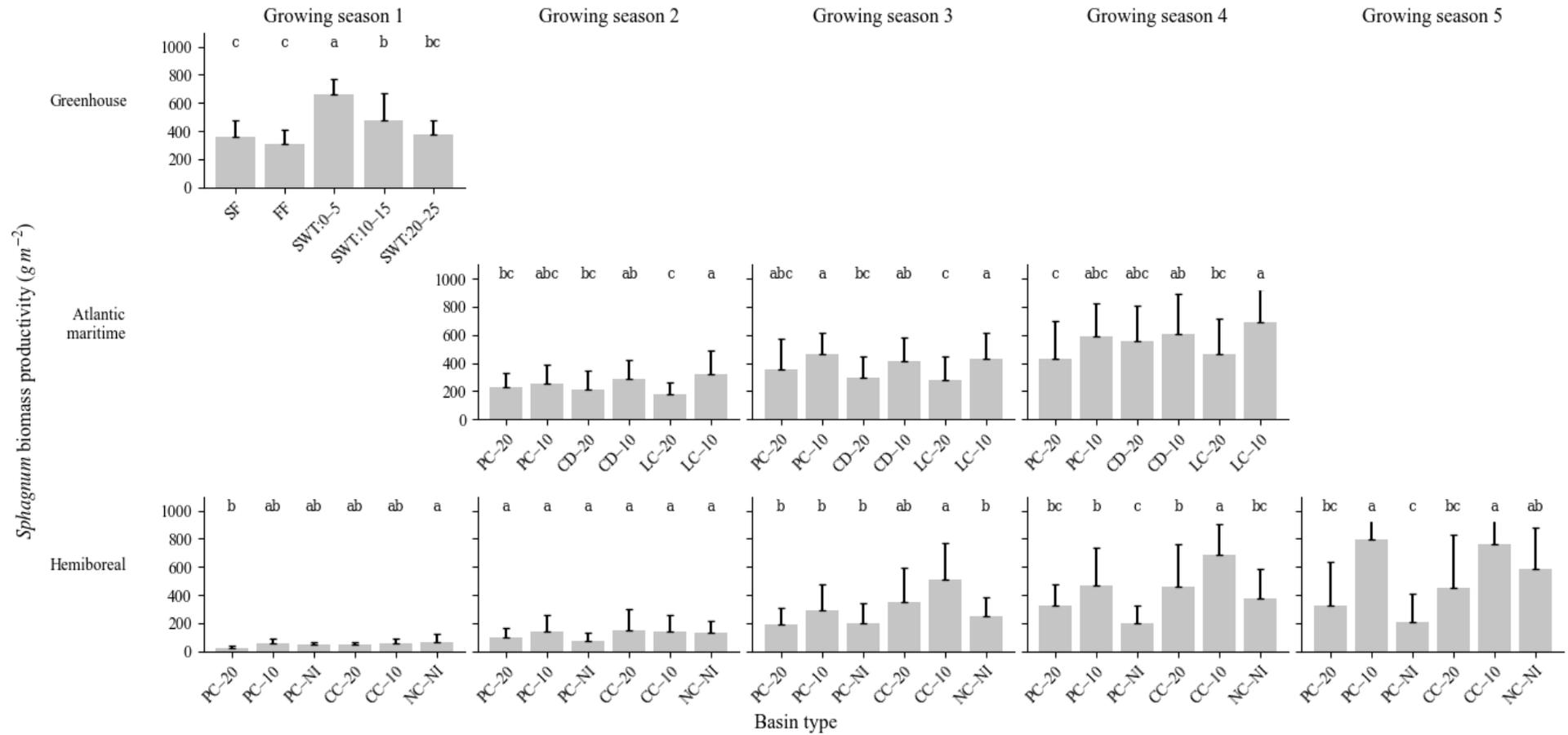


Figure A1. Annual comparison of harvested *Sphagnum* biomass by system and basin type. Means within the same system and year that share the same letter do not show statistically significant differences (Tukey HSD as multiple comparison test, $\alpha = 0.05$).



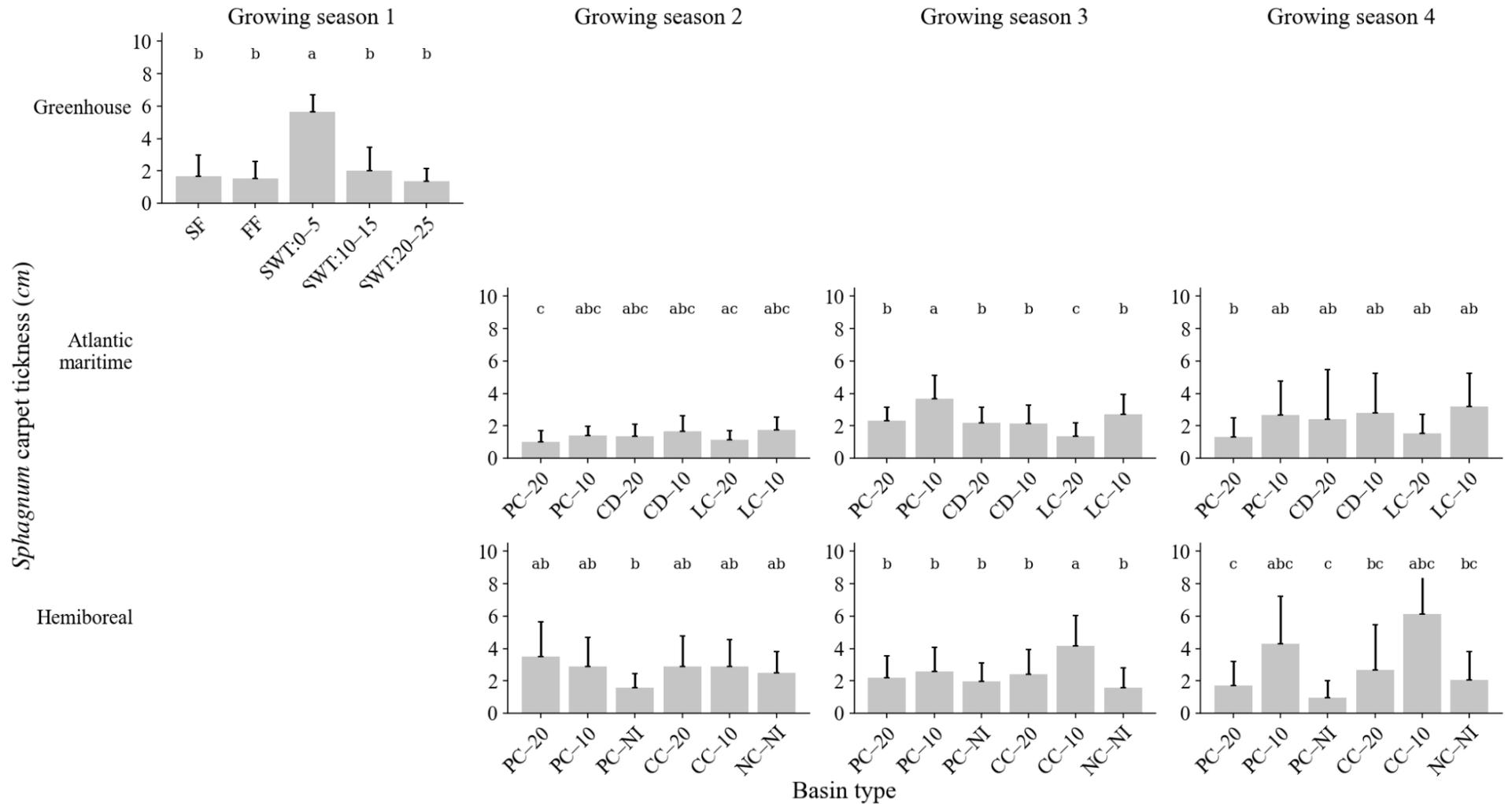


Figure A2. *Sphagnum* carpet thickness by system and basin type. Means within the same system and year that share the same letter do not show statistically significant differences (Tukey HSD as multiple comparison test, $\alpha = 0.05$).



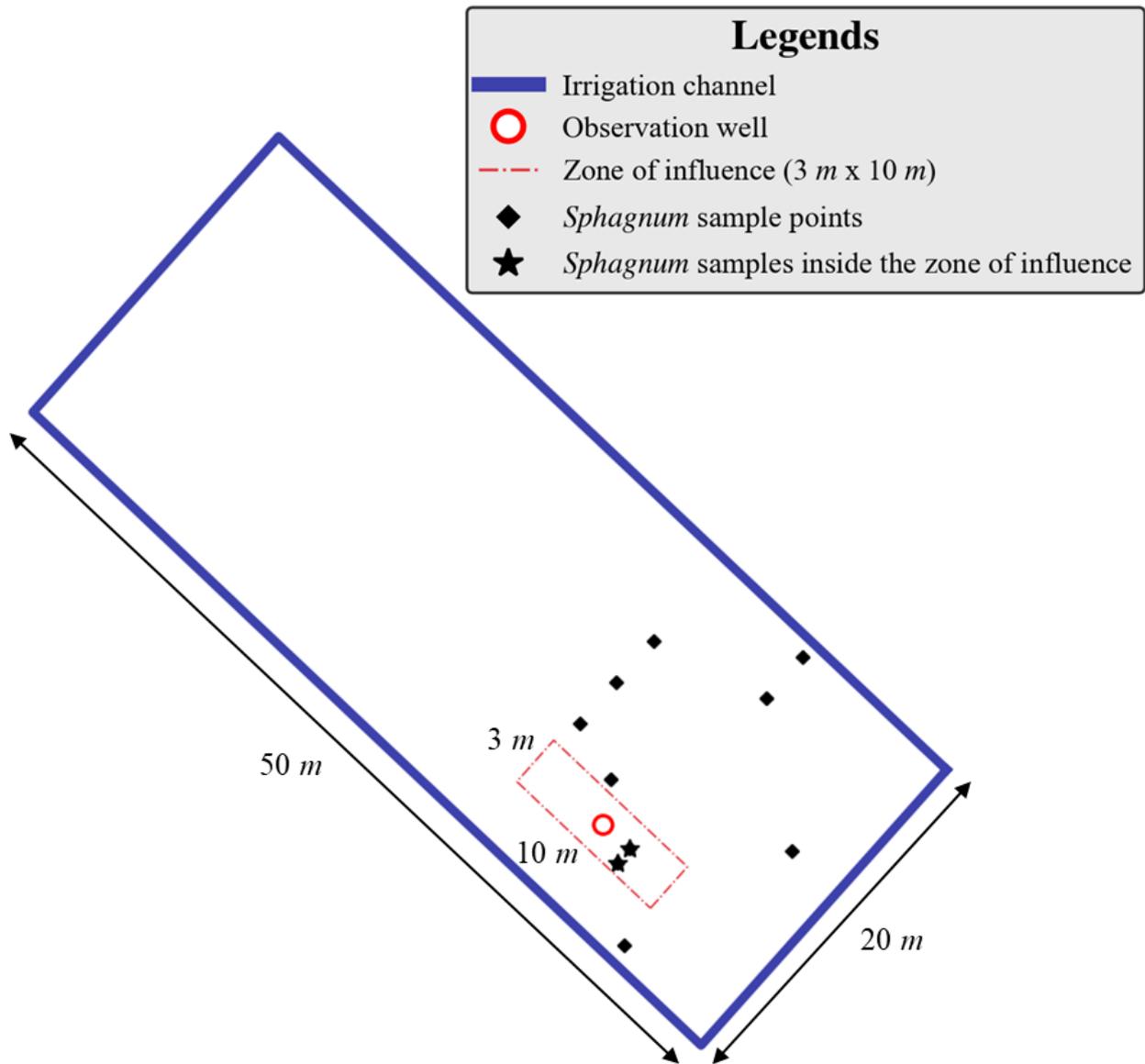


Figure A3. Example of the distribution of *Sphagnum* sample locations and the delineation of a 3 × 10 m zone of influence around an observation well, for assigning and retaining biomass and thickness data.