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Adding *Sphagnum* to peat growing medium improves plant performance under water restricting conditions

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SUMMARY

The addition of *Sphagnum* to peat-based growing media (‘*Sphagnum* replacement’) influences plant performance. The primary physical effect of *Sphagnum* addition appears to be enhanced water retention. Good performance of plants cultivated in *Sphagnum* seems partly explainable in terms of its water retention properties. The large body of nutrient solution retained in *Sphagnum* can delay disadvantageous changes in its concentration during cultivation. The physical quantity of *Sphagnum* per unit volume, i.e. its bulk density, governs the volume of retained water and thus determines the strength of effects contributing to plant performance. When subjected to severe drought, plants cultivated in *Sphagnum* did not show clear signs of water deficit up to at least 1,572 hPa of matric suction, which is the estimated wilting point for plants grown in light peat. Using *Sphagnum* to replace peat in the growing medium appears advantageous to plants not only during drought but also during ordinary greenhouse cultivation.

KEY WORDS: bog biomass, peat substitute, renewable substrate, *Sphagnum* fibre, wilting point

INTRODUCTION

Existing research recognises the critical role played by bogs as efficient sinks for atmospheric carbon (Cleary *et al.* 2005, Vasander & Kettunen 2006). Thus, the issue of peat extraction continues to receive considerable criticism (Robertson 1993) and attention is increasingly drawn to the remaining horticultural challenge of finding an abundant and sustainable alternative for peat (e.g. Ceglie *et al.* 2015, Álvarez *et al*. 2017). Studies over the past two decades have provided important information about the farming and harvesting of *Sphagnum* moss, and on its use as a growing media constituent (Gaudig *et al.* 2018). *Sphagnum* biomass appears to meet all of the physical, chemical and biological requirements (Aubé *et al*. 2015, Kumar 2017) for high quality soil-less growing media (Raviv & Lieth 2008), and may be renewable when harvested from the wild in Finland (Silvan *et al.* 2017).

The water retention capacity (volumetric moisture θ vs. pressure head ψ) of *Sphagnum* has been reported to be high by Boelter (1969), Hayward & Clymo (1982) and Thompson & Waddington (2013) among others. Hayward & Clymo (1982) focused on *Sphagnum capillifolium* and *Sphagnum papillosum* and discussed the respective roles of the outer (later termed ‘secondary’) and inner (‘primary’) pore matrices in moving and storing water. Kämäräinen *et al.* (2018) discussed the role of bulk density in *Sphagnum* growing media, describing the spatial relations between the primary and secondary pore matrices. These intra- and extrafibrillar pore spaces form an integrated whole that determines the total water retention capacity of *Sphagnum* growing media.

Understanding water availability for plants growing in *Sphagnum* requires consideration of the specific growing media properties of *Sphagnum* biomass, which render one of the fundamental principles of soil science inappropriate. Briggs & Shantz (1911) introduced the method for determining the wilting point (wilting coefficient) and presented relative values for different plant species. According to the studies of Kramer (1949), plant wilting (Cassel & Nielsen 1986) takes place at a soil matric suction of approximately 15,000 hPa. The key drawback of adopting the same matric potential (approximated for soils with often narrow and unimodal pore-size distributions) for *Sphagnum* growing media is that it does not take account of multimodality in the pore-size distribution of the medium (see Heiskanen 1993, Durner 1994, Caron *et al.* 1998). The unsaturated hydraulic conductivity of *Sphagnum* biomass has been reported to decrease rapidly during drying (Price *et al.* 2008). Water flow in hummocks (*Sphagnum rubellum* Wils.) was studied by Price & Whittington (2010), who concluded that the physical structure of *Sphagnum* results in a swift transition from saturation to a low but stable water content when the water table falls. In combination with the substrate water itself (θ) and its chemical characteristics (Ψ_t), hydraulic conductivity is a major physical determinant of the amount of water available to plants (Raviv & Lieth 2008). Although a plant thriving in *Sphagnum* creates low water potential around its roots, similarly to a plant growing in any other soil-less media, the unique anatomy of *Sphagnum* with its highly regular pore structure creates a novel root–medium interface governing water availability.

Thompson & Waddington (2013) presented water retention (drying) curves for living *Sphagnum fuscum* and pointed out the important role of bulk density in determining the capacity of peat to retain water. They further concluded that the humification of *Sphagnum* caused less water to be retained per unit dry mass. In an earlier paper we proposed that, as *Sphagnum* biomass dries to a matric suction of 100 hPa, a significant proportion of its original water content remains stored in hyaline cells, i.e. in the primary pore matrix (see Kämäräinen *et al*. 2018, Figure 10). This is in line with the findings of Hayward & Clymo (1982) and further supported by Price & Whittington (2010), who found that the hydraulic conductivity of living *Sphagnum* dropped by several orders of magnitude with reducing water content. In other words, as the *Sphagnum* structure dries, its high water conductivity at saturation (Price *et al*. 2008, Kämäräinen *et al*. 2018) can be assumed to turn rapidly into a dramatically slower flow, first through corners and second on the surfaces of the secondary pore space (Tuller *et al*. 1999, Tuller & Or 2001).

Gaudig *et al*. (2018) reviewed plant growing trials conducted in *Sphagnum*. It appears that, depending on the species cultivated and the composition of the *Sphagnum* biomass used, at least 50 % of the horticultural peat in growing media mixtures can safely be replaced with *Sphagnum*. The proportion of *Sphagnum* biomass may be greater than 50 % for many crops (Blievernicht *et al*. 2013). Reinikainen *et al*. (2012) grew seedlings of tomato, cucumber and lettuce in *Sphagnum* and recorded that they achieved significantly greater fresh weight than in controls (white peat or mineral wool). So far, however, very little attention has been paid to the causal connections between *Sphagnum* water retention and plant growth.

The aim of this study was to examine plant performance in peat-based growing media containing *Sphagnum*. We further aimed to determine matric potentials at wilting point in *Sphagnum*-containing growing media (i.e. the moisture content at which the force adhering water to growing media particles exceeds the force exerted by plant roots, resulting in wilting). We hypothesised that plant performance is affected by the addition of *Sphagnum*, both in general and under water deficit conditions, and this led to two further questions:

1. Is there a systematic increase in water retention by light peat when *Sphagnum* is added?
2. Do the tortuous routes for corner and surface flow (see Kämäräinen *et al*. 2018, Figure 10) in drying *Sphagnum* result in plants wilting at higher water content than they would in light peat?

This study argues that *Sphagnum* growing media can be advantageous to plants not only during drought but also during ordinary greenhouse cultivation.

METHODS

Growing media materials

Two different types of *Sphagnum* biomass were used. *Sphagnum fuscum* (Schimp.) Klinggr. dominated material was collected as parallelogram-shaped bales (approximate height 30 cm, width 25 cm, depth 25 cm) in September 2013 by cutting with a chainsaw. The biomass was then air-dried on greenhouse tables and stored for later use. The collection site was a sparsely drained and almost natural raised bog in Neva-Lyly, Karvia, central Finland (62° 19.13′ N, 22° 84.26′ E). More details on the harvesting site and physical characteristics of the collected material are given in Kämäräinen *et al*. (2018). Hydraulic conductivity (K_s) was 2671, 1584 and 1024 cm h^{-1} in *Sphagnum* samples with natural structure, 40 mm fibre length and 5 mm fibre length, respectively, and total porosity ranged from 97.4 % to 97.8 % with no significant differences. Compacting the *Sphagnum* from a bulk density (BD) of 40 kg m^{-3} to 80 kg m^{-3} increased the plant-available water in the growing medium and reduced its total porosity. The saturated hydraulic conductivity (K_s) decreased steadily from 634 cm h^{-1} to 93 cm h^{-1} as the bulk density increased from 40 kg m^{-3} to 80 kg m^{-3}.

The second type of *Sphagnum* biomass was collected in September 2016 from a sparsely drained *S. fuscum* pine swamp in Nivusneva, Parkano, central Finland (62° 09.12′ N, 22° 98.25′ E). Here the surface layer comprised common *Sphagnum* species, namely *S. fuscum* (hummocks), *S. medium* Limpr. (lawns) (formerly identified as *S. magellanicum*, see Laine *et al*. 2009) and *S. rubellum* (hollows). In addition to mosses, the ground vegetation was mainly composed of vascular plant species common in bogs (i.e. *Eriophorum vaginatum* L., *Carex pauciflora* Lightf., *Empetrum nigrum* L., *Calluna vulgaris* L. and *Ledum palustre* L.). At Nivusneva the biomass was collected with a machine-operated bucket grapple by cutting out the uppermost layer (30 cm thick), then mixing it and reducing its water content by pressing *in situ*. This method for collecting and handling *Sphagnum* biomass from the wild in Finland is briefly reviewed by Gaudig *et al*. (2018). The machine-collected material was stored (until April 2017) in a covered outdoor stack before use.

In the growing media mixtures tested, light *Sphagnum* peat (H2–H3) of Finnish origin with no liming, nutrients or wetting agents was combined with *S. fuscum* dominated or machine-harvested *Sphagnum* moss. Figure 1 shows the appearance of these three experimental materials. The amount of liming agent (Puutarhurin kalkki, Nordkalk Oy, Kokkola, Finland) needed to reach the target pH of 6 was determined by preparing a gradually rising liming series for each growing media mixture. pH was determined (Inolab pH 720 WTW, Mexico) in a suspension of 1 part by weight of experimental growing media mixture to 4 parts water after a 12-day neutralising period (data not shown).

The chemical properties of the growing media materials were evaluated by standardised testing with three replicates. Three mixed samples (3 dm^3) were constructed from each experimental material (3 × 3). The analyses were conducted at Eurofins (Viljavuuspalvelu Oy, Mikkeli, Finland), which is a T096 (EN ISO/IEC 17025) accredited laboratory. The content of soluble N was determined in a 1:5 water suspension using the Kjeldahl method as described in SFS-EN 13652. Soluble P, K, Mg, Cu, Fe, Mn, Na, S, Zn and B were extracted with calcium chloride and analysed using inductively coupled plasma atomic emission spectroscopy (ICP-AES) following the standard SFS-EN 13651. pH was measured as in SFS-EN 13037. The potential cation exchange capacity (CEC) was determined with a NH4OAc (pH 7) solution following the procedures presented by Hesse (1971) and Tan (1995). Loss on ignition was determined by dry combustion following the standard SFS-EN 13039. Finally, total mineral nutrient contents were determined with ICP-AES plant material analyses following the standards SFS-EN ISO 5983-2 for N and SFS-EN ISO 5516 for P, K, B and Mn. A note of caution about making comparisons is necessary here, as a newer standard (SFS-EN 15510) was followed in determining P, K, B and Mn for the machine-harvested *Sphagnum*. Tables 1 and 2 summarise the soluble mineral nutrient contents and the total mineral nutrient contents of the three experimental materials.

Experimental growing media treatments

The *S. fuscum* fibres from Neva-Lyly were cut to ~ 2 cm length before use. The shorter-cut machine-collected *Sphagnum* was used as it was. To construct the experimental growing media mixtures, *Sphagnum*

Figure 1. Left: the machine-harvested *Sphagnum* biomass appeared short-cut and processed without further treatment. Right: samples of the three experimental materials on metal trays - light peat (top), machine-harvested *Sphagnum* biomass (middle), and *S. fuscum* dominated biomass (bottom).

Table 1. Soluble mineral nutrient contents and chemical properties for the dry matter of *Sphagnum* biomass dominated by *S. fuscum*, machine-harvested *Sphagnum* and light *Sphagnum* peat. Standard deviation is given in brackets.

Elements and properties	Units	*S. fuscum* dominated biomass	Machine-harvested biomass	Light peat
N	g kg^{-1}	0.42 (0.23)	0.10 (0.06)	0.16 (0.05)
P	g kg^{-1}	0.08 (0.04)	0.01 (0.004)	0.01 (0.02)
K	g kg^{-1}	1.53 (0.12)	0.58 (0.04)	0.09 (0.01)
Mg	g kg^{-1}	0.46 (0.02)	0.54 (0.05)	0.90 (0.05)
Cu	mg kg^{-1}	3.86 (3.31)	3.83 (1.29)	1.96 (1.43)
Fe	mg kg^{-1}	130 (10.0)	240 (36.45)	270 (10.0)
Mn	mg kg^{-1}	133 (5.77)	91.6 (16.5)	33.7 (1.53)
Na	mg kg^{-1}	233 (155)	216 (15.27)	79 (1.00)
S	mg kg^{-1}	92.0 (9.90)	26 (0.01)	17.3 (7.57)
Zn	mg kg^{-1}	24.3 (0.58)	30.5 (2.12)	4.63 (0.06)
B	mg kg^{-1}	< 0.10	0.56 (0.36)	0.33 (0.23)
pH (1:5)		4.10 (0.06)	4.7 (0.1)	4.30 (0.11)
EC	mS cm^{-1}	0.05 (0.002)	0.01 (0.005)	0.02 (0.004)
CEC	meq/100 g	221 (29.6)	196 (12.43)	230 (6.43)
LOI	%	98.83 (0.11)	95.73 (0.51)	99.06 (0.11)

CEC = cation exchange capacity; EC = electrical conductivity; LOI = loss on ignition. n = 3.

Table 2. Mineral nutrient contents in dry matter of *Sphagnum* biomass dominated by *S. fuscum*, machine-harvested *Sphagnum* and light *Sphagnum* peat. Standard deviation is given in brackets. For machine-harvested biomass, SFS-EN 15510:2008 was followed; in other cases the previous ISO 5516:1978 method was followed. n = 3.

Element	Units	*S. fuscum* dominated biomass	Machine-harvested biomass	Light peat
N	g kg^{-1}	4.70 (0.20)	24.6 (3.7)	7.47 (0.12)
P	g kg^{-1}	0.25 (0.01)	1.4 (0.264)	0.21 (0.02)
K	g kg^{-1}	1.6 (0.10)	2.76 (0.37)	< 0.7
Mn	mg kg^{-1}	240 (11.5)	353 (49.5)	59 (1.00)
S	mg kg^{-1}	6.21 (0.01)	2.63 (0.02)	8.27 (0.02)
B	mg kg^{-1}	< 2	9.64 (0.47)	< 2

was added to peat in proportions of 0, 25, 50, 75 and 100 % (dry mass basis). The required dry mass quantities were weighed and put into resealable plastic bags, one replicate at a time. The material for each replicate was then gently mixed in the bag until evenly blended and hand compacted into the pot. Sieve cloths were added to the bottoms of the pots (12 × 10 cm for basil in the greenhouse, 5.5 × 7 cm for basil in the growth chamber and 7 × 7 cm for verbenas) as they were assembled.

Plant performance

To study the effects of *Sphagnum* on plant performance under optimal and water-restricting conditions, three separate experiments were conducted, two using sweet basil (*Ocimum basilicum* L.) and one with verbena (*Verbena x hybrida* Groenl. and Rumpler) as the test plant. Verbenas were grown in both machine-harvested and *S. fuscum* dominated biomass, whereas the two experiments with sweet basil employed *S. fuscum* dominated biomass only. A commercial peat-based mixture served as a point of comparison in Experiments 1 and 3. An overview of the three experiments is given in Table 3.

Experiment 1: Sweet basil, greenhouse

The pots containing the experimental growing media mixtures were first saturated with nutrient solution (Taimi superex NPK 19-4-20 1 mS cm^{-1} Kekkilä Oy, Vantaa, Finland) for a ten-day period. The level of the nutrient solution was raised gradually during the first two days and later maintained at a height of 3 cm above the upper edges of the pots. Swelling and floating was controlled by placing frames with nylon gauzes on top of the pots. On the ninth day of the saturation period the surfaces of the experimental mixtures in the pots were levelled to correspond to a substrate volume of 0.97 dm^3. With compacting we aimed for bulk densities of ~72 kg m^{-3} in all replicates. One day after levelling the surfaces, the pots were lifted onto the growing table without bottom trays (added at planting) to equilibrate. The pots were weighed the following morning.

Sweet basil (*Ocimum basilicum* L. 'Mariam') seeds were planted using a circular cardboard jig with three holes to standardise the distance between seeds. Two seeds were planted in each hole and the planting holes were thinly covered with a mixture of fine vermiculite and perlite. There were five extra replicates with plants on the growing table, which were used to monitor pH and electrical conductivity (EC). A total of 80 additional pots were filled with a commercial substrate mixture of light peat, sand, clay and mineral nutrients (Karkea ruukutusseos W R8014, pH 5.9, Kekkilä Oy, Vantaa, Finland). These were planted similarly to the experimental pots and placed around the experimental set-up to eliminate edge effects. Eight of the pots with commercial substrate served as standard points of comparison. Due to the presence of mineral fractions in the commercial substrate, its bulk density was not adjusted.

After a week of growing, the weaker of the two seedlings was pinched from each planting hole, leaving three seedlings to grow in each pot. Once every three days the plants were irrigated from above with nutrient solution, to the point where some of the solution trickled through to the bottom tray. The watering regime was designed to offer abundant water and nutrients and to achieve an average matric potential of approximately -5 hPa in the growing media. The plants were not topped. A four-week growth trial with destructive measurements at the end was undertaken using a completely randomised design with four replicates and three plants per replicate (a total of 12 plants per treatment). At the end, plants were assessed for shoot length and leaf area, and for the fresh and dry weights of their above-ground parts. At this point the formation of roots through the experimental mixtures was visually confirmed. Atmospheric conditions in the greenhouse (temperature and relative humidity, RH) were set to 25 °C and 60 %, respectively. A light period of 14 hours per day was provided, using high pressure sodium (HPS) lamps. when an irradiation level lower than 250 μmol m^{-2} was detected. Soil water for EC and pH measurements was obtained prior to each irrigation by vertically pressing the surface of the growing medium until approximately 30 ml had dripped on the bottom tray.

At the beginning of this experiment we had 13 replicates (pots with three plants). Four of these were taken for destructive measurements after four weeks, and seven pots per treatment continued into water deficit. The remaining pots were arranged on the growing table in a randomised block design. Altogether, there were 21 plants in seven pots representing each experimental treatment.

At the beginning of the drought period, all pots were irrigated sufficiently to raise the level of the nutrient solution to the upper edge of the bottom tray (+20 mm from the bottom of the pot). The growing media were allowed to absorb the solution for one hour. After this wetting period, the bottom trays were removed and the pots were left on the growing table overnight (12 hours) before weighing. The pots were irrigated no more, and were weighed daily from then on.

Our pre-trial revealed that wilting of a sweet basil plant proceeds upward from the lowest sun leaves to

Table 3. Summary of the three experiments with plants.

Experiment	Treatments (% *Sphagnum*, dry weight basis)	Plant species tested	Environment	Biomass harvesting method	Biomass composition in replacements	Fixed bulk density (kg m^{-3})	Response variables	Number of replicates
1	0, 25, 50, 75 and 100	*Ocimum basilicum* L. ‘Mariam’	Greenhouse	Hand picked	Mainly *S. fuscum*	72	Growth and wilting tolerance	4 and 7 (drought)
2	0, 25, 50, 75 and 100	*Ocimum basilicum* L. ‘Mariam’	Growth chamber	Hand picked	Mainly *S. fuscum*	65	Leaf temperature	4
3	0, 25, 50, 75 and 100	*Verbena x hybrida* ‘Lanai® Up Purple’	Greenhouse	1) Hand picked 2) Machine with bucket grapple	1) Mainly *S. fuscum* 2) Mixture of *S. fuscum*, *S. medium, S. rubellum*	67	Growth and wilting tolerance	8

the upper plant parts. When the apical sun leaves were beginning to change their appearance, the lower sun leaves had already wilted. Applying the early principles presented by Kramer (1949) for assessing soil moisture at the permanent wilting point (PWP) for sunflowers, a sweet basil plant was deemed wilted when the uppermost pair of leaves on the main stem had significantly changed in appearance. Plants were observed for their condition once every 3 hours during the light period. When the wilting time of each plant was documented the plant was cut, weighed and oven dried. When the last of the three plants in a pot had wilted, the PWP for that experimental unit was reached. As a basis for more reliable discussions, laboratory measurements of water retention (see Figure 9) were undertaken at bulk densities similar to those used in the pots with plants (~ 72 kg m^{-3}). This seemed essential because the dominant role of bulk density in determining the water retention properties of both *Sphagnum* and peat has been widely recognised (e.g. Thompson & Waddington 2013). Matric potentials (ψ) at PWP were approximated for *Sphagnum* and peat using the averaged media water content at wilting. Seven replicates produced the average θ that was used to solve individually parametrised double van Genuchten equations (water content θ against ψ) for theoretical ψ.

Experiment 2: Sweet basil, growth chamber

The drought stress responses of sweet basil were studied further by undertaking leaf temperature measurements on plants cultivated in the 0, 25, 50, 75 and 100 % mixtures of light peat and *S. fuscum* dominated moss, which were subjected to three weeks of drought in a growth chamber (FytoScope, PSI, Czech Republic). The growing medium in each pot was hand-pressed to a bulk density of 65 kg m^{-3} so that a single pot contained 11.7 g of dry matter in a volume of 0.18 dm^3. The total number of plants was 20 (five treatments with four replicates). Each plant had its own rectangular (5.5 × 7 cm) pot, integrated into a special tray for the phenotyping platform. Two seeds were sown in each pot and the weaker seedling was pinched out after one week. Growth conditions in the chamber were 16 hours light / 8 hours darkness and 22 °C, the target RH was 60 % and the light intensity was 130 μE (MS6610, Mastech, China). The plants were watered by immersing the tray (20 pots with bottom openings) in a receptacle containing nutrient solution (Taimi Superex 1 mS cm^{-1}) for 15 minutes at intervals of 3 days until noon on Day 23. The level of the nutrient solution was targeted to the middle of the pots to give Ψ = -0 hPa at watering. At the end of the experiment, the dry weights of the wilted plants were recorded.

The National Plant Phenotyping Infrastructure facility at the University of Helsinki (https://www.helsinki.fi/en/infrastructures/national-plant-phenotyping) was used once a week for infrared imaging and weighing of the pots with plants. For this analysis a camera was positioned in a PlantScreenTM chamber with automated transportation of plants between the weighing and imaging stations. Images of all 20 plants were used for automatic online calculation of leaf temperatures (PlantScreenTM analyser, PSI, Czech Republic).

Experiment 3: Verbena, greenhouse

Mass-based mixtures of growing media constructed similarly to those reported for sweet basil were assembled in pots (10 × 8 cm) in eight replicates. Here we used both the machine-harvested and the *S. fuscum* dominated biomass ($2 \times 5_{treat.} \times 8_{reps}$) with a commercial growing media mixture (Karkea ruukutusseos W R8014, pH 5.9, Kekkilä Oy, Vantaa, Finland) as the point of comparison. Bulk densities in the pots were standardised to 67 kg m^{-3}. Hence, a single pot contained 20.1 g of experimental dry matter pressed to a volume of 0.33 dm^3. We used rooted cuttings (height ~ 2.5 cm) of verbena (*Verbena x hybrida* 'Lanai® Up Purple'). These were received growing in a mixture of light peat, fine sand and clay in a plug tray from a commercial plant supplier (Schetelig Oy, Vantaa, Finland) and immediately planted in the treatment mixtures. The experiment followed a randomised block design with environmental and light conditions similar to those in Experiment 1.

The plants were grown for four weeks and were hand irrigated from above with nutrient solution (Taimi superex, NPK 19-4-20 1.5 mS/cm Kekkilä Oy, Vantaa, Finland) every two days. Pots were weighed before and after irrigation. The method for determining pH and EC was modified from Experiment 1. To avoid physical interference with the mixtures, the first run-off solution was extracted by carefully adding fresh nutrient solution to the top surface of the experimental mixture. As soon as the changing hydrostatic pressure had caused sufficient (approx. 20 ml) of the old solution to filter into the bottom tray, it was collected for measurement. The method was chosen to reflect the chemical situation in the most easily available water (assuming that the water possessing the highest matric potential would be the first to run off); compressing the growing media would have mixed the water stored in the secondary and primary pore matrices. To promote flowering, the fertiliser was changed to Kukka superex (NPK 19-4-20 Kekkilä Oy, Vantaa, Finland) in the third week. The nutrient concentration of the irrigation water was increased gradually so that EC rose by 0.25 mS cm^{-1} per week, reaching 2.25 mS cm^{-1} in the last week of the growing phase. The drought was initiated at the beginning of the fifth week, by ceasing irrigation entirely.

The wilting of verbenas proceeded very rapidly, starting from the flower buds and continuing downward through the rosette. A plant (one per pot) was deemed to be wilted when all of its flower buds had lost their turgor, i.e. had flattened. At this stage, wilting time from the beginning of the drought was documented, together with the fresh and dry weights of the plant. The growing medium was weighed at PWP and oven dried for water content. It was not possible to further investigate the prevailing matric potential at wilting because the planting mixture originally used for the plugs contained mineral particles (sand), making our dry weight based approach less trustworthy.

Water retention in laboratory

To better understand how the addition of *Sphagnum* affects the water regime of peat, water retention measurements were performed for the experimental growing media with 0, 25, 50, 75 or 100 % (w/w) of *S. fuscum* dominated biomass mixed with peat. Testing of the water retention properties (drying curves) of the experimental mixtures was conducted at a standardised bulk density of ~72 kg m^{-3} with three replicates. The target bulk density was attained by applying the three steps given in Kämäräinen *et al*. (2018), namely:

1) weighing and gently mixing the appropriate proportions of *Sphagnum* and peat in re-sealable plastic bags and equilibrating this mixture to a mass-based water content of one part dry mass to two parts water;

2) using a rubber collar for pouring and a handheld piston for compacting the experimental material into soil sample cylinders; and

3) saturating compacted samples in a sandbox with a plastic tray on top to prevent volume changes.

The bulk densities (kg m^{-3} ± standard deviation (SD)) of the samples tested for water retention were, from 100 % *Sphagnum* to 100 % light peat in 25 % increments: 72.02 (0.22), 72.01 (0.18), 71.88 (0.13), 71.92 (0.09) and 72.10 (0.24), respectively. Water retention measurements were conducted with pressure head values of 0, -2.5, -10, -31.6, -63.1, -100, -1,000 and -15,000 hPa, resulting in a total of 120 measurements (3 × 5 × 8). A sandbox and porous plates in pressure kettles were used for matric potentials (Ψ) of -2.5 to -100 hPa and -1,000 hPa, respectively. The water content at Ψ = -15,000 hPa was determined by placing 1 g of air-dried sample material in a desiccator containing a saturated solution of the salt $(NH_4)_2C_2O_4$ (RH 99.0 %) and weighed after eight weeks (when equilibrium was assumed). The theoretical approach and methodology for determination of the water retention curve (WRC) are extensively summarised by Dane & Topp (2002).

Water retention equation, fitting and modelling

To approximate the relationship between water content θ and matric potential ψ_m in each substrate mixture, the values of volumetric water content for each sample at the eight levels of ψ_m were fitted to the double van Genuchten equation:

$$\theta_\Psi = \left(\theta_{r_1} + \frac{\theta_{s_1}-\theta_{r_1}}{(1+|\alpha_1\Psi|^{n_1})^{m_1}}\right) + \left(\theta_{r_2} + \frac{\theta_{s_2}-\theta_{r_2}}{(1+|\alpha_1\Psi|^{n_2})^{m_2}}\right) \quad [1]$$

where θ_ψ is the WRC, ψ is suction, θ_s is saturated water content, θ_r is residual water content, α is related to the inverse of the air entry suction and n is a measure of the pore-size distribution (van Genuchten 1980). The double van Genuchten equation was used with the Mualem (1976) constrainer, $m = 1-1/n$, and setting the residual water content to zero.

Statistics

To evaluate the effects of *Sphagnum* addition on plant growth in Experiment 1, the data from the destructive measurements at the end of the 4-week growing period were compared using analysis of variance (ANOVA). To satisfy the ANOVA assumption of independency, the results of Experiment 1 (with three sweet basil plants per pot) were analysed using the averages obtained per pot. The same approach was applied to pH and EC measurements during the growth phase of Experiment 1. ANOVA was also used to compare the laboratory measurements of water retention, as well as all measurements of substrate water content and plant growth. To test the effect of *Sphagnum* addition on plant performance under water deficit conditions, sense-perceptional datasets of time elapsed before the plants wilted were created for Experiments 1 and 3; and these data, now reflecting tolerance against wilting in hours, were examined using ANOVA. The p-value required for a significant difference was set to < 0.05. Multiple comparisons of means were carried out using Tukey's HSD tests. SPSS 25 statistical software was used for the analyses (SPSS Inc., IL, USA).

Higher order equations (Equation 1) were fitted using the Excel Solver function, by varying a group of parametric cells so that the sum of the squared deviations of the equations from the measured values at ψ_m was at a minimum. The goodness of fit was quantified in terms of root mean square error (RMSE), defined as:

$$RMSE = \sqrt{\frac{1}{N}\sum\left(\theta_{measured} - \theta_{fitted}\right)^2} \qquad [2]$$

RESULTS

Plant performance

Experiment 1: Sweet basil, greenhouse

Sweet basil plants gained more dry weight ($p < 0.05$) in the mixtures of *Sphagnum* and peat than in the pure materials. Similar differences were detected in the other plant growth variables (dry and fresh weight, leaf area and main shoot length) (Figure 2). *Sphagnum* addition (≥ 50 %) increased the average pH value of pore water between watering, while at the same time EC seemed to decrease (Figure 3).

The 50 % substitution of peat with *Sphagnum* increased the water retention capacity of the experimental media (Figure 4). At the wilting point of sweet basil, the average moisture contents of *Sphagnum* and light peat were, respectively, 0.95 and 0.96 g of water per g of dry growing medium. When the wilting point was reached, there were no differences in water content between the growing media mixes ($p = 0.198$) or between the wilted plants ($p = 0.09$). Figure 5 presents the rather interesting finding that a significant increase in wilting tolerance was obtained following the addition of at least 50 % *Sphagnum* to the growing medium. Referring to the averages obtained from the growth experiment, the dry mass of plants grown in pure *Sphagnum* increased most during the drought when compared with plants grown in substrates containing peat. The increases in dry mass (g) during the drought were 0.98 (SD = 0.08) for 100 % *Sphagnum*, 0.95 (0.06), 0.88 (0.07), 0.76 (0.07), and 0.65 (0.08) for 100 % peat. When parametrised double van Genuchten (1980) equations for pure *Sphagnum* and peat were solved using obtained values for θ_w, the matric potential values were -1,876 and -1,572 hPa, respectively.

Experiment 2: Sweet basil, growth chamber

During the drought period, the leaf temperatures of sweet basil were lower for plants grown in *Sphagnum* than for plants rooted in light peat (Figure 6, top). Furthermore, the plants grew larger ($p < 0.05$) in peat to which *Sphagnum* had been added. At the end of

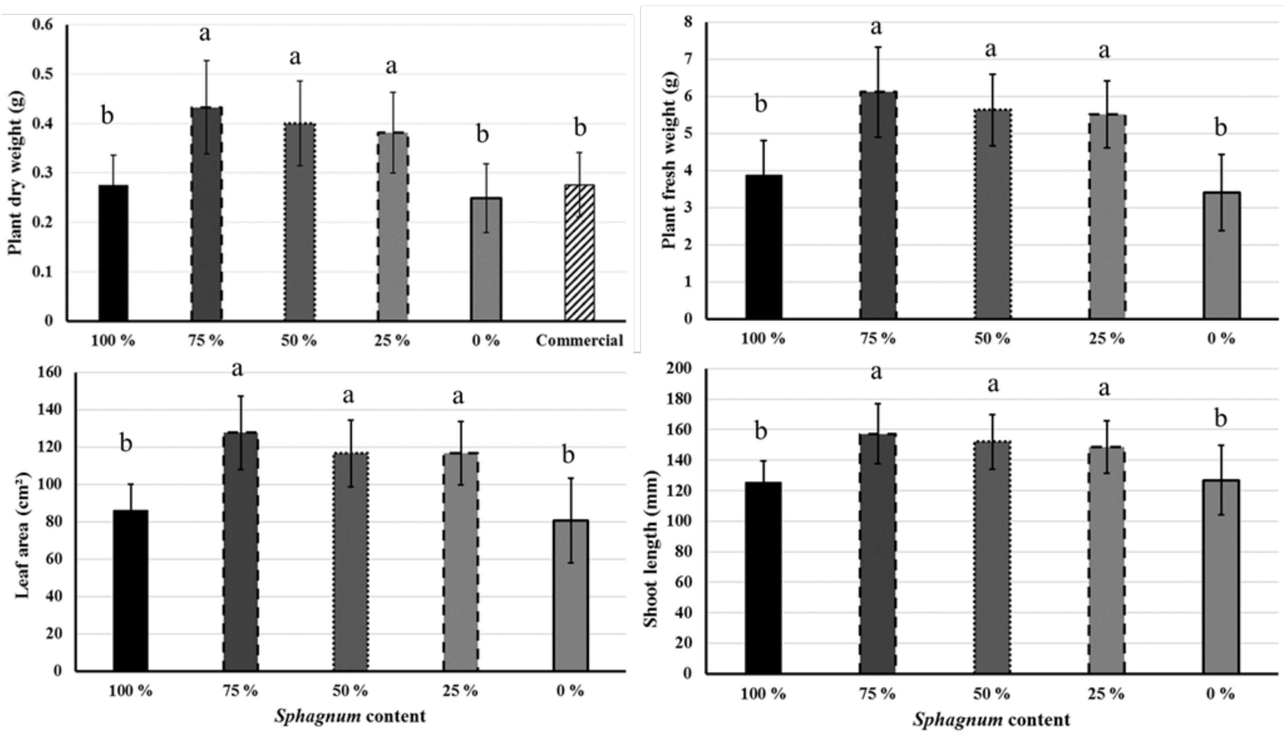

Figure 2. Assessed indicators for the growth of sweet basil in various mixtures of *Sphagnum* and peat. Dry weights of plants grown in commercial growing media were assessed for reference (top left). Letters (a, b) denote significant differences between groups (p < 0.05) for measurements (n = 12) and analyses (n = 4).

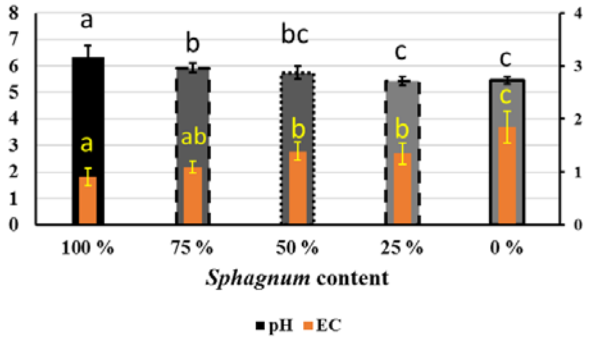

Figure 3. Average pH (left-hand axis) and electrical conductivity (EC) (mS cm^{-1}) (right-hand axis). Values obtained from pore water prior to irrigation with nutrient solution (EC 1 mS cm^{-1}, pH 6.5). Letters denote the detected differences between groups ($p < 0.05$). Bars denote ± SD. n = 12.

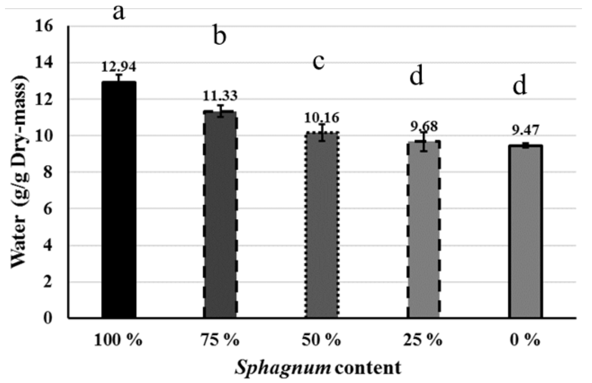

Figure 4. Water retention of sweet basil experimental mixtures (*S. fuscum* dominated) after a 10-day saturation period and a 24-hour equilibration period without bottom trays. The dry matter in each pot was standardised to 70 g, resulting in bulk densities of ~72 kg m^{-3}. Letters indicate significant differences between groups ($p < 0.05$). Bars denote ± SD. n = 16.

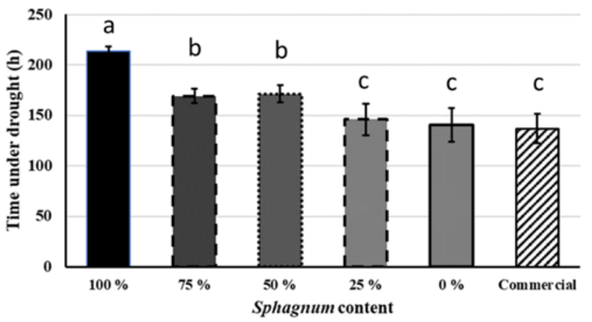

Figure 5. The average time elapsed between the beginning of the drought experiment and the wilting of sweet basil plants. Y-axis denotes elapsed time from the beginning of the drought period. Letters indicate significant differences between groups ($p < 0.05$). Bars denote ± SD. n = 21.

the experiment, the average dry weights (± SD) of basil plants grown in mixtures with *Sphagnum* content ranging from 100 % to 0 % were 0.32 g (0.04), 0.41 g (0.02), 0.36 g (0.01), 0.34 g (0.01) and 0.25 g (0.01), respectively. Although a dataset for wilting time was not created here, wilting seemed to occur later in high-*Sphagnum* mixtures despite the larger sizes of the plants. The weights of all pots increased until the beginning of the drought (Day 23; Figure 6, bottom). The largest difference in weight (approximately 50 g, between the 100 % and 0 % *Sphagnum* treatments) was detected at the beginning of the drought period. This difference remained fairly constant until the second week of the drought.

Experiment 3: Verbena, greenhouse

The dry weights of the verbena plants were found to be similar in all growing media mixes (p = 0.592). However, a significant increase in tolerance against wilting seemed to occur with the addition of 50 % or more of *S. fuscum* dominated biomass to the peat. A corresponding effect was achieved with machine-harvested biomass only when peat was substituted entirely by *Sphagnum* (Figure 7). The water content (g water per g of dry growing medium, including the weight of the transplanting plugs) at which wilting of verbenas grown in 100 % *Sphagnum* occurred was slightly higher than the water content at which sweet basil wilted in Experiment 1, here averaging 1.07 for the machine-harvested and 1.14 for the *S. fuscum* dominated biomass. For light peat the corresponding value was 1.04. However, the differences in substrate water content at wilting point between the growing media mixes were found to be insignificant (p = 0.188). No significant differences (p = 0.09) in the water content of wilted plants at the moment of cutting were found between the groups. The greater water retention capacity of *Sphagnum* when compared with peat was clearly demonstrated by weighing the irrigated pots (Figure 8). The experimental mixtures constructed using *S. fuscum* dominated biomass seemed to retain more water than those constructed using machine-harvested biomass, whose physical structure had been more drastically altered during collection.

Our method for pH and EC determination was designed to reflect the situation in the substrate water prior to irrigation. In parallel with Experiment 1 (sweet basil), the pH of the water in pure peat was consistently lower than that of the water in *Sphagnum*-intensive mixtures. However, the absolute values of chemical properties (pH, EC) are not further presented or analysed here due to the changes in fertiliser regime during the growth period.

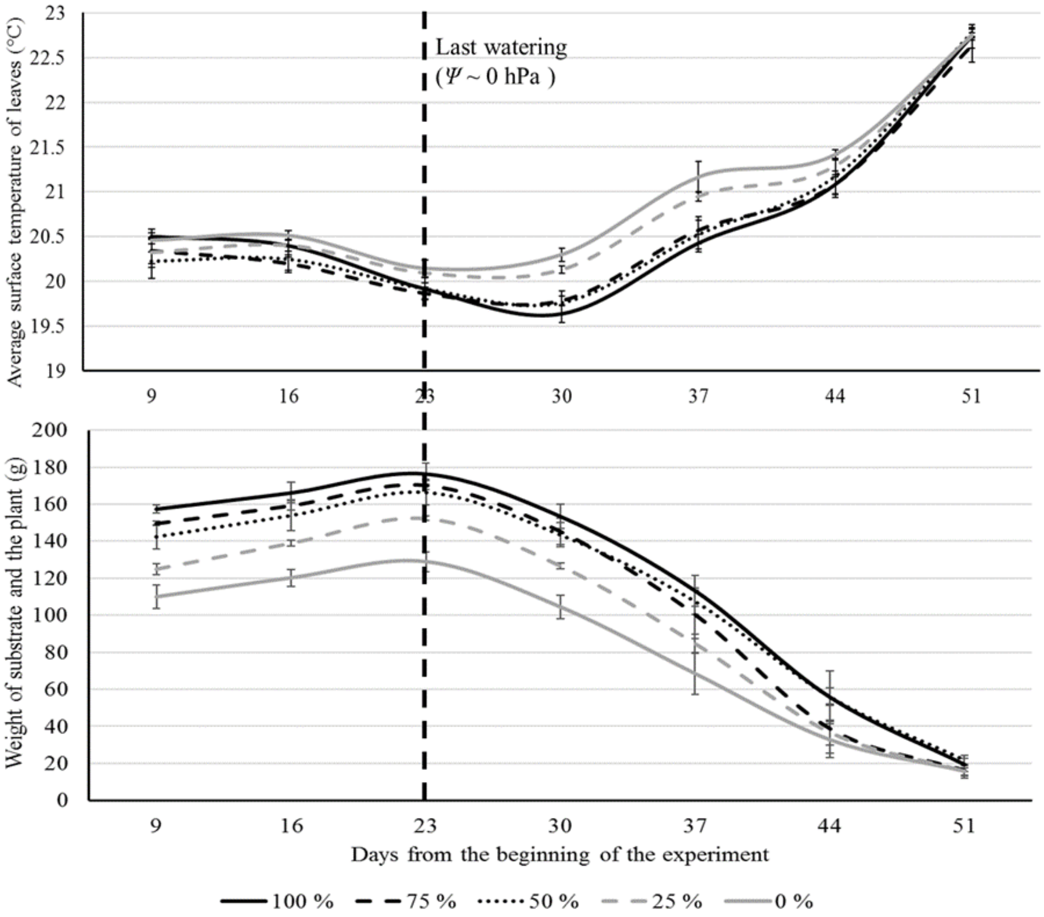

Figure 6. Results of Experiment 2 (sweet basil plants grown in the experimental mixtures of 0–100 % *Sphagnum* with peat, inside a growth chamber; severe drought was imposed on Day 23). Above: average leaf temperature derived by infrared (IR) imaging; below: pot weights. As a rule, the experimental replicates were weighed prior to the IR measurements, hence the pot weights illustrate the time course of drying. Error bars denote ± SD. n = 4.

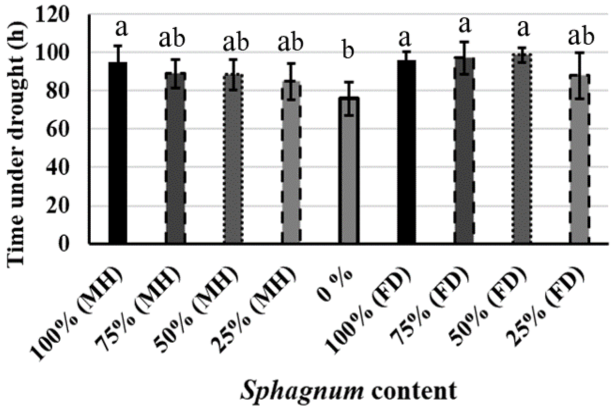

Figure 7. Average time elapsed between the beginning of the drought experiment and wilting of the verbena plants. FD = *S. fuscum* dominated biomass, MH = machine-harvested biomass. Differences between means ($p < 0.05$) are indicated by different letters (a, b). Error bars denote ± SD. n = 8.

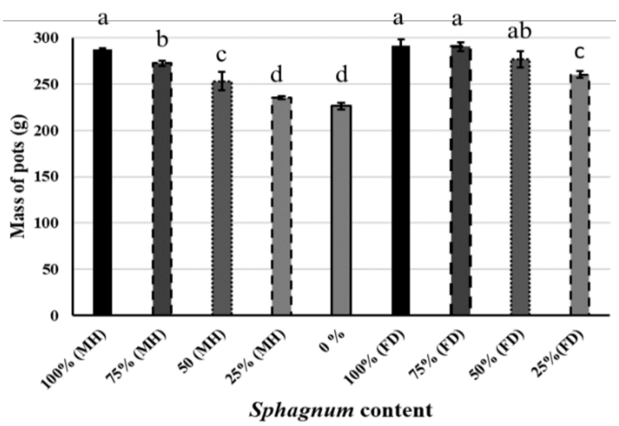

Figure 8. Pot mass at the beginning of the verbena experiment. FD = *S. fuscum* dominated biomass, MH = machine-harvested biomass. Target bulk density in all treatments was 67 kg m^{-3}. Differences between means ($p < 0.05$) are indicated by different letters (a, b, c, d). Error bars denote ± SD. n = 8.

Water retention in laboratory

Significant increases in water retention ($p < 0.05$) were detected in all *Sphagnum*-containing experimental mixtures at matric potentials of -2.5, -10, -31.6 and -63.1 hPa. However, the difference between the 100 % *Sphagnum* and 25 % peat treatments were lost ($p > 0.05$) at 100 hPa. Figure 9 presents the water retention (drying) curves obtained for experimental mixtures in the laboratory. The laboratory findings were in line with the differences obtained by weighing the pots. What stands out in the WRC (Figure 9) is the interaction between *Sphagnum* and peat at the matric potential of -1,000 hPa, when water content tended to be greater (although insignificantly; $p > 0.05$) for mixtures than for either of their components at the same matric potential. The double van Genuchten equation fitted the water content measurements well (Table 4).

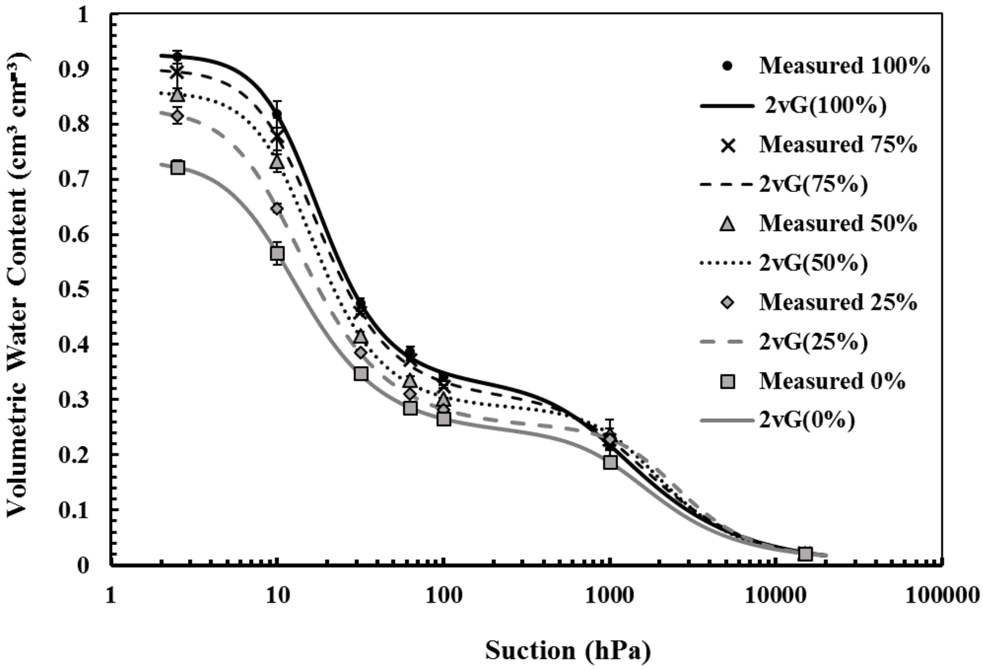

Figure 9. Measured water retention values and estimated drying curves for mixtures of *Sphagnum* and peat at matric suctions ranging from 2.5 to 15,000 hPa. The curves were obtained by fitting the double van Genuchten equation (van Genuchten 1980). The percentage (dry mass basis) of *Sphagnum fuscum* dominated biomass included in each mixture (compressed to BD ~72 kg m^{-3}) is shown in the legend. Error bars denote ± SD for measured points.

Table 4. The double van Genuchten parameters and fitting values for all experimental mixtures. Curves were fitted to average values for three replicates and seven matric potentials. RMSE = root mean square error.

Sphagnum content (%)	θ_{s1}	θ_{s2}	α_1	α_2	n_1	n_2	RMSE	r
100	0.5971	0.3288	0.0699	0.0011	2.6816	1.9256	0.0090	0.9998
75	0.5421	0.3910	0.0685	0.0021	3.0150	1.6815	0.0340	0.9993
50	0.5741	0.2846	0.0767	0.0006	2.6126	2.3426	0.0052	0.9999
25	0.5792	0.2495	0.0989	0.0005	2.2424	2.4702	0.0016	0.9999
0	0.4939	0.2405	0.1051	0.0008	2.2611	2.1640	0.0002	0.9999

DISCUSSION

Large specific surface area (~ 320 m^2 g^{-1}), together with the unique mechanical composition and cellular arrangements for water regime, give rise to high levels of water retention energy (see Iwata *et al.* 1994) in compacted *Sphagnum* moss (Kämäräinen *et al.* 2018). This study, undertaken at standardised bulk densities, confirms that the addition of *Sphagnum* to light peat (at similar bulk densities) is associated with a strong increase in plant-available water. Our results further confirm that the water retained in *Sphagnum* pore structures is available to plants up to at least the same matric potential as the water retained in light peat. The present results appear aligned with previous observations (e.g. De Boodt *et al.* 1974) indicating matric potentials for plant wilting (~ -3,000 hPa) in a soil-less culture. It is most interesting to note that in Experiments 1 and 3 we found no differences in the water content of the growing media mixes when the wilting points were reached, nor in the water content of wilted plants at the same moment. Thus, a rough rule of thumb for both *Sphagnum* and light peat could be that, during wilting, the water content of the growing medium approaches its own dry mass.

Thermal imaging is based on the principle that a plant cools itself by transpiration and plant temperature rises as the stomata close. Kaňa & Vass (2008) showed that the increased thermal signal correlated with a reduced assimilation efficiency. Thermal measurement of plant tissue has been accepted as a suitable method for the analysis of plant stress (Virlet *et al.* 2014). However, environmental variability (e.g. in temperature, light intensity and RH) affects the accuracy of these measurements. Therefore, the highest reliability for thermal measurements and their interpretation is most commonly reached in a controlled environment, i.e. on in-house integrated imaging platforms (Humplik *et al.* 2015) as used in our experiments. Our findings with the thermal camera suggest that most of the water stored inside undecomposed hyaline cells (primary matrix) is efficiently extracted by plant roots under water deficit conditions. We found that the main chemical substrate properties (CEC, EC and pH) of *Sphagnum* parallel those of light peat. Furthermore, the concentrations of soluble mineral nutrients seemed low and hence adjustable during use of the substrate (Raviv & Lieth 2008).

The very good fit of the double van Genuchten model suggests that the water retention properties of a mixture of *Sphagnum* and light peat can be described in terms of the sum of their two pore matrices. Here the terms θs_1 and θs_2 (Table 4) are considered to describe the volumes of water retained in the secondary and primary pore matrices, respectively (see Kämäräinen *et al.* 2018). This means, however, that the theoretical matric potential corresponding to the water content at wilting was different for *Sphagnum* and light peat. As the measured water content at wilting θ was substituted in the double van Genuchten model with its individually estimated parameters (see Table 4) for both, the equations yielded matric potential values of -1,876 and -1,572 hPa for *Sphagnum* and for light peat, respectively. These findings appear useful, promoting understanding of the magnitude of Ψ when the wilting point (Ψw) is approached in *Sphagnum*. When considering these lower boundaries for water availability in *Sphagnum*, our findings confirm that the amount of true 'plant available water', i.e. the volume of water retained between -10 hPa (also air-filled porosity) and the wilting point, is increased by adding *Sphagnum* to the peat.

Under laboratory conditions, approaching the dry end of the WRC diminishes the difference in water content between *Sphagnum* and light peat and results in insignificant differences at -15,000 hPa at the latest (Kämäräinen *et al.* 2018). In organic media, however, severe yield reduction and subsequent wilting are known to happen at significantly higher matric potentials (e.g. ~ -3,000 hPa) (De Boodt *et al.* 1974, Lemay *et al.* 2012). Our preliminary findings suggest that sweet basil wilts at a lower matric potential in *Sphagnum* than in light peat. This interpretation emphasises the important roles of the two distinctive and interacting pore matrices in supporting the plants farther against the atmospheric demand (suction). In the laboratory equilibrium the water without dissolved solids was more tightly bound (lower matric potential for the same amount of retained water) to *Sphagnum* than to light peat. In contrast, our empirical experiments seemed to show that the water is at least equally available to drought stressed plants in practice. Furthermore, plant size has an effect on the rate of water uptake from the substrate (Anjum *et al.* 2011); for example, larger plants use more water. In line with this, the largest plants - in the experimental mixture of 75 % *Sphagnum* and 25 % light peat - seemed to lose water faster than plants growing in the other experimental mixtures (Figure 6). As the plants grew largest in high-*Sphagnum* mixtures, there is an evident source of error here; nevertheless, this observation underscores the detected positive effect of the *Sphagnum* water reserve: it appears that the faster water use by the larger plants growing in *Sphagnum* only levelled out the obtained differences in leaf temperature. However, we advise only cautious extrapolations because, in our drying data from the growth chamber (Figure 6), the increasing dry mass of plants was not determined separately and mass changes might otherwise reflect movements of water from the substrate and from the plant. Overall, both of the plant species grown in *Sphagnum* not only efficiently used the larger water reserve, but also seemed to withstand lower matric potentials without clear signs of wilting. Perhaps the most serious disadvantage, however, is that this method does not take into account the root mass and the water retained in it. It is nevertheless obvious that further empirical and modelling work will have to be conducted to better understand the links between the pore matrices of *Sphagnum* and its unsaturated hydraulic conductivity.

Plant cultivation is commonly undertaken in greenhouses at matric potentials of -10 to -50 hPa (for the definition of easily available water, see Raviv & Lieth 2008) and drier conditions rarely occur in practice (Lemay *et al*. 2012). In the following, however, we include the drier points and discuss the outcome of high water retention energy and its proposed sphere of influence during cultivation.

With respect to the aim of this research, plant growth was enhanced when *Sphagnum* was added to the growing medium. This outcome can be explained in terms of the inequality of water retention energy between the experimental mixtures (see Figures 4, 8 and 9); the high-*Sphagnum* mixtures offered more water and thus more water-soluble mineral nutrients. As water retention energy governs the distribution of water in porous media, the same energy simultaneously defines the dimensions of the air-filled network of pores (Raviv & Lieth 2008). It appears that the rapidly emptying secondary pore matrix (largest pores) in *Sphagnum* can create a highly continuous and evenly distributed network of air-filled pores. This regulated system is likely to be capable of sustaining more effective ventilation for roots at a higher water content than can be sustained in materials that possess lower water retention energies. However, Figure 2 shows that 100 % *Sphagnum* (with the largest energies) did not yield the highest growth rate. We attribute this to the lack of an adequate volume of air-filled pores in the high-density *Sphagnum*. In Experiment 1 with sweet basil the height of the growing media in the pots was assessed to be 10 cm, resulting in an average matric potential close to -5 hPa when watered through. Assuming a total porosity of ~97 % in 100 % *Sphagnum* (Kämäräinen *et al*. 2018), the volume of air-filled pores seemed to be as low as 5 % at watering. Glinski & Stepniewski (1985) among others suggested the recommendation of 10 % for the minimum volume of air-filled pores in plant cultivation. In our case, despite the good aeration properties of *Sphagnum*, there appeared to be too much water in treatments with 100 % *Sphagnum*. In other words, better growth in 100 % *Sphagnum* growing media could probably be achieved by adopting a similar watering regime but lowering the BD to increase air capacity. However, a reminder is needed here that we found plant growth in 100 % *Sphagnum* to be already equal with the growth in pure peat and in the commercial mixture. We also remind the reader of a need for caution in extrapolating our findings because requirements for root zone aeration are known to vary amongst plant species according to their age and phenotype (Glinski & Stepniewski 1985). As more and more *Sphagnum* material is collected from the wild (Gaudig *et al*. 2018), research is clearly needed to elucidate the physical differences between the most common *Sphagnum* species when used as growing media.

In addition to beneficially altering air–water relations as discussed above, the amendment of growing media with *Sphagnum* seemed also to promote plant growth indirectly. In the experiment with sweet basil it appeared that the larger body of water in *Sphagnum*-dominated mixtures efficiently regulated the chemical changes initiated by evapotranspiration during the intervals between watering. We hypothesise that the detected differences in basil growth are partly explained by the properties of the substrate water remaining more favourable for plant growth in *Sphagnum*-dominated mixtures (Figure 3). A similar trend (larger plant size) was not apparent in the verbena experiment because the dry mass of growing medium used (20.1 g in a volume of 0.33 dm^3) was insufficient to show the effect clearly; hence, only the effect of *Sphagnum* addition on water retention in light peat and the enhanced tolerance against wilting when plain *Sphagnum* was used were clearly demonstrated in this case. Total water potential in the growing media comprises several components including osmotic potential (see the applied energy concept of Iwata *et al*. 1994). The slower increase of salinity in high-*Sphagnum* than in peat-dominated mixtures promoted the observed differences in both growth and wilting tolerance. We conclude that this phenomenon is an indirect but significant consequence of the high levels of water retention energy that can be advantageous when growing plants in compacted *Sphagnum*.

This set of experiments has illustrated the main effects of the interacting intact pore matrices of *Sphagnum* (Hayward & Clymo 1982, Price & Whittington 2010, Kämäräinen *et al*. 2018). In line with our findings, Thompson & Waddington (2013) presented differences in mass-based water retention by bog biomass according to the depth profile. The water retention properties of the horticultural peat used in this study seemed to resemble those of the Baltic white peat cut to 10–30 mm that was investigated by Michel (2010). The substrate bulk density (72 kg m^{-3}) applied in our Experiment 1 approached that obtained for light peat when following the standard procedures of SFS-EN 13041. However, horticultural peat is rarely used at such low bulk densities. This underscores the presented differences in practice. Nevertheless, we have previously proposed that, on a dry matter basis and under equivalent environmental conditions, there is always more plant-available water (defined for the range of Ψ 0 to -1,000 hPa) in *Sphagnum* biomass than in light peat (Kämäräinen *et al*. 2018). The results presented here suggest that the replacement of peat with *Sphagnum* contributes positively to plant performance under water-restricting conditions. In the growth chamber experiment, the earlier rise of leaf temperature in plants grown in peat-dominated mixtures confirmed our observations of visible signs of drought stress in a greenhouse. On the basis of empirical approximation of the matric potential at wilting point for sweet basil plants grown in both light peat and *Sphagnum* we propose that plants cultivated in *Sphagnum*, when subjected to drought, can use substrate water to at least the same negative matric potential as can plants grown in light peat. However, more plant physiological research is needed to fully understand the interactions between *Sphagnum* growing media and plant performance.

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AUTHOR CONTRIBUTIONS

Antti Kämäräinen (AK), Leena Linden (LL) and Kari Jokinen (KJ) designed the research. AK performed the experiments, except for the verbena trial. AK analysed the data and wrote the first draft of the manuscript. AK, LL and KJ discussed the results and all contributed to the final version of the manuscript.

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