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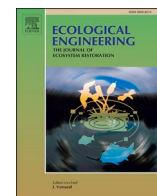
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Growing moss on bioreceptive concrete using a novel two-step approach: The effects of light, water, and species selection

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ABSTRACT

Bioreceptive concrete supports biological growth on its surface, but natural colonisation takes years, and indoor cultivation followed by outdoor translocation often results in poor long-term survival. This research aimed to develop a method for rapidly establishing a moss layer on bioreceptive concrete while ensuring long-term persistence and survival. The developed method comprised a two-step approach. First is the rapid establishment of moss on bioreceptive concrete indoors. Then, it is hardened and translocated outdoors. Findings indicate that the most effective method for growing moss on concrete indoors is to grow them at low light intensity ($70 \mu\text{mol m}^{-2} \text{s}^{-1}$ full-spectrum), while watering daily for the first six weeks. Subsequently, watering can be gradually reduced to once every 4 days, inducing drought hardening. This resulted in significant coverage and growth for both acrocarp ($M_{\text{coverage}} = 15.1\%$; $M_{\text{growth}} = 11.2 \text{ mm}$) and pleurocarp species ($M_{\text{coverage}} = 51.7\%$; $M_{\text{growth}} = 15.5 \text{ mm}$). Finally, after outdoor translocation, the moss should be covered with a light-blocking cloth for a 3-month period to allow for adaptation to UV and high light intensity conditions. When applying this method to moss species (mixtures), it was found that *T. muralis* showed slow indoor growth but the best adaptation to outdoor conditions on both north- and south-facing surfaces. Contrarily, both *P. capillare* and *B. rutabulum* displayed faster growth under indoor conditions but showed poor surface adhesion when translocated outdoors, which can, in some cases, be improved by using species mixtures. This research is a first step towards identifying the factors influencing moss growth and survival on bioreceptive concrete in the built environment.

1. Introduction

Vertical green structures (VGS) — including direct and indirect green façades, where climbing plants grow on or near building surfaces, and *Living Wall Systems* (LWS), which incorporate a substrate layer attached to a wall to support plant growth — provide an effective means of introducing greenery into urban areas where ground space is limited. (Medl et al., 2017). These vertical green structures have been linked to several local and urban-scale benefits, including – but not limited to – reductions in heat stress, noise and air pollution, stormwater run-off, and building energy consumption (Manso et al., 2021; Radić et al., 2019). However, whilst they provide many benefits, green vertical structures also have higher associated construction and maintenance costs than traditional building solutions, hindering their adoption (Manso et al., 2021). Additionally, they are sometimes limited in the locations where they can be applied due to their maintenance requirements. For example, the need for irrigation limits living wall

systems to places where such amenities are available.

There is an alternative to contemporary vertical green structures in the form of bioreceptive materials, which allow for biological growth to occur directly on the construction material. Using bioreceptive materials could, therefore, lower construction costs as they do not require an additional technical structure (Veeger et al., 2021b). Additionally, when using cryptogams, such as mosses, the need for irrigation is also removed, as they can survive water loss and extended droughts due to their poikilohydric nature (Glime, 2017b). This could allow them to be used across a broader range of applications, including infrastructure. Finally, mosses have already been linked to several benefits, such as thermal and acoustic insulation, as well as air filtration (Blok et al., 2011; Perini et al., 2025; Veeger et al., 2025a), similar to other vertical green structures.

In the past decade, several successful formulations of bioreceptive cementitious materials have been developed, which showed moderate to significant biological growth when subjected to inoculation with

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cryptogams and kept under optimal growing conditions indoors (Hayek et al., 2021; Manso et al., 2014; Snoeck et al., 2022; Tzortzi et al., 2024; Veeger et al., 2021a, 2021b). However, when these samples are subsequently placed outdoors, survivability is often poor, likely due to a lack of environmental hardening (Veeger et al., 2021b). At the same time, relying on the natural colonisation of bioreceptive materials is a very slow process (Lubelli et al., 2021; Manso et al., 2017). Usually, surfaces are first colonised by fungi, algae, and cyanobacteria, which fix nitrogen and allow for the eventual establishment of rootless plants, such as mosses (Cuzzolino et al., 2022). Furthermore, mosses have a much lower photosynthetic ability than vascular plants, and growth occurs mainly during extended wet periods (Martin and Adamson, 2001; Proctor et al., 2007b). This means it could take years for a bioreceptive surface to become covered with moss through natural colonisation. The gap in the current state-of-the-art is therefore a methodology that would facilitate rapid coverage of a bioreceptive concrete surface with a dense layer of moss that has good long-term outdoor survival.

The first challenge in the development of such a method is that the rapid establishment of a dense layer of moss on concrete requires an effective watering regime. Most mosses that are common colonisers of urban concrete surfaces (i.e. known 'concrete compatible species'), such as *Tortula muralis*, *Grimmia pulvinata*, *Ptychostomum capillare*, *Brachythecium rutabulum*, and *Hypnum cupressiforme* (Veeger et al., 2025b) belong to the highly desiccation-tolerant bryophytes (Wood, 2007). While this means that these mosses can survive these dry periods, with similar drought-tolerant moss species recovering from desiccation in minutes or hours, no carbon uptake can take place during desiccation (Proctor et al., 2007a; Proctor and Smirnov, 2000; Tuba et al., 1996). It is, therefore, likely necessary to keep moss moist and provide regular wetting if optimal moss growth is to be achieved, as moss hydration and growth are inexorably linked (Busby et al., 1978; Grabovik et al., 2024; Pitkin, 1975).

However, water is not the only determinant of moss growth, and the second challenge concerns establishing a suitable lighting regime. Most mosses and other bryophytes are shade-adapted plants. They have chlorophyll quantities indicative of being shade-adapted, and the fact that they have only one layer of leaf cells means their photosynthetic cells are directly exposed to sunlight (Glime, 2017c). However, light compensation (the light level at which net photosynthetic gain is achieved) and light saturation (at which photosynthetic gain is optimal) levels show significant differences between species and a high plasticity within species. Kershaw and Webber (1986) found that *Brachythecium rutabulum*, a species commonly found on concrete structures, had a light compensation point of $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (photosynthetic photon flux density; the incoming density of photons that can be used for photosynthesis) in spring, which dropped to $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ in autumn. Its light saturation point fell from $65 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $4 \mu\text{mol m}^{-2} \text{s}^{-1}$ during this period. Marschall and Proctor (2004) found that PPFD at 95 % saturation ranged from $110 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $2549 \mu\text{mol m}^{-2} \text{s}^{-1}$ when comparing 39 moss species. At the same time, different researchers have found that the light compensation point of various bryophytes ranges from 0.03 % to 7.5 % of full sunlight (Glime, 2017c). For reference, PPFD at full sunlight is approximately $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Glime, 2017c).

So, ideally, the moss is kept continuously hydrated at relatively low light levels during the initial settlement and growth period of the moss. However, while maintaining the mosses continuously hydrated may benefit their development during the settlement period, continuous wetting through an irrigation system in outdoor applications is often unwanted from a practical and economic viewpoint. Furthermore, lighting conditions will be dependent on the location of the outdoor concrete structure and the season in which it is placed and cannot always be manipulated. Instead, a two-step approach is proposed, where initial moss settlement and growth take place indoors, where optimal growing conditions can be achieved, after which the moss is hardened and moved outdoors.

However, this approach is not without its issues. Previous research has shown that mosses exhibit a species-dependent phenotypic plasticity when it comes to drought tolerance, depending on whether or not the moss previously experienced dry periods and the extent of these dry periods (e.g. Beckett, 1999; Beckett et al., 2005; Brinda et al., 2016; Schonbeck and Bewley, 1981). As the adaptations that increase drought tolerance require resources to be allocated away from reproduction and growth, mosses adapt their drought tolerance based on their environment (Vitt et al., 2014). This means that while constant hydration will likely lead to optimal growth, it may negatively impact drought tolerance and vice versa. This may be solved through a process known as 'drought hardening', where the mosses are subjected to slow drying cycles after initial settlement and growth, thereby inducing the drought tolerance necessary for outdoor moss survival. It is necessary, therefore, to strike a balance between the two in any successful growing regime, either by reducing the watering frequency, which may negatively affect growth, or by drought-hardening, introducing slow-drying cycles after an initial growing period.

A similar problem is present for light. While light is necessary for growth, excessive light can also have a detrimental effect on plants. High light intensities can damage the photosynthetic apparatus, causing photoinhibition (Glime, 2017c). Similarly, high amounts of UV-B radiation can cause damage to a range of cellular molecules, including RNA, DNA, and proteins within the moss (Robinson and Waterman, 2014). Mosses have several ways of dealing with high light intensities, including structural adaptations that limit light reaching the leaf cells, the production of pigments that can absorb harmful radiation, non-photochemical quenching of excess light energy, and cell repair mechanisms (Glime, 2017c; Robinson and Waterman, 2014). The extent to which protection mechanisms against high light intensities are present often depends on the light intensity that the moss experiences or has experienced in the past, as structural changes and increased photo-protective pigmentation have been found to be induced by changing irradiance levels (Post, 1990; Waite and Sack, 2010). Incorporating a light hardening period might therefore be a practical strategy in addition to the water-hardening method described above, to improve the successful translocation of moss-covered concrete from indoors to outdoor conditions.

Contemporary methods of growing moss either focus solely on optimising the light and hydration conditions for growth, leading to poor subsequent survivability, or rely on natural conditions, which have the opposite effect, leading to good survivability, but slow growth. This research, instead, aimed to develop a two-step protocol that combines the rapid establishment of a moss layer on bioreceptive concrete with good outdoor survivability, consisting of an initial indoor growth period followed by translocation outdoors. To achieve this, two experiments were conducted. The first focused solely on the indoor growth phase, investigating the effects of different watering and light intensities, as well as potential hardening protocols on the growth and coverage of both acrocarp and pleurocarp moss species mixtures. The aim here was to develop a growth protocol that maximises growth and coverage, whilst inducing some initial drought and light hardening. In the second experiment, we employed this newly developed protocol to grow different moss species (mixtures) on a bioreceptive concrete layer indoors, after which they were translocated outdoors to test their long-term outdoor survival.

2. Methodology

2.1. Materials

2.1.1. Bioreceptive concrete

The concrete samples used in this research measured $80 \text{ mm} \times 80 \text{ mm} \times 18 \text{ mm}$ for the first indoor-only growth experiment and $160 \text{ mm} \times 80 \text{ mm} \times 18 \text{ mm}$ for the second outdoor incubation experiment (indoor growth followed by translocation to an outdoor location). These

were made using a recipe of bioreceptive concrete based on that developed in a previous study (Veeger et al., 2021a). The mixture consisted of 280 kg/m³ CEM III/B 42.5 N, 1657 kg/m³ 0–4 mm recycled concrete aggregate, and 14 kg/m³ bone ash, with a water/cement factor of 0.90. The concrete mixture was mixed in a 5 L capacity Hobart mixer for 1.5 min and subsequently cast into plastic moulds, on the bottom of which a layer of Kiwitz CSE Pro/02 surface retarder was applied. The samples were demoulded after two days, and the top layer of cement was washed away using water. Samples were then left to cure under room conditions for 28 ± 2 days, during which they were wetted twice a week to accelerate carbonation of the surface. A total of 144 concrete samples were cast for the indoor-only growth experiment, comprising twelve growing regimes, two moss mixtures, and six replicates of each set. Another 77 were cast for the outdoor incubation experiment comprising eleven moss species mixtures, two orientations, and three replicates of each set of conditions.

2.1.2. Moss collection and preparation

Two moss mixtures were used for the indoor-only growth experiment: one containing acrocarp species and the other containing pleurocarp species (see Table 1 for species composition of each moss mixture). Both types of mosses were tested as they differ in their branching pattern and positions of the sporangia, which in turn influence their growth form, the success of fertilisation, retention capacity of water, and ability to spread horizontally across a substrate (Glime, 2017a). For the outdoor incubation experiment, six individual species

and five mixtures of these species were used (Table 1). Species selection was based on previous research (Veeger et al., 2025b), where these species were identified as common colonisers of urban concrete structures. These species were harvested from wild moss colonies growing on existing concrete structures. After collection, all moss colonies were washed under running tap water until the wash-off was clean. For the outdoor incubation experiment, the mosses were also submerged in a 70 % vol ethanol solution for 10 s, after which they were rinsed again with clean tap water. This was done to minimise algae growth seen during the first indoor growth experiment. After cleaning, all mosses were air-dried in preparation for the next step.

2.1.3. Sample inoculation

The dried mosses were pulverised in a blender until only small fragments remained. The surface of the concrete samples was wetted, after which either 105 g/m² of the pulverised pleurocarp moss (mixtures) or 235 g/m² of the pulverised acrocarp moss (mixtures) was inoculated on each sample surface. This was done by weighing the appropriate amount of pulverised moss for each individual, after which it was added to the sample surface, ensuring equal biomass weight for each sample. Afterwards, each sample was sprayed with approximately 625 mL/m² of a water-based solution containing 2 g/L of Peters Professional 10–52–10 NPK fertiliser, after which they were ready for indoor growth.

2.2. Indoor setup

2.2.1. Growth cabinet

For the indoor growth part of both the indoor-only growth and outdoor incubation experiments, two metal cabinets with a footprint of 120 cm × 60 cm were used (Fig. 1). Each metal cabinet contained three platforms with a 60 cm vertical spacing. These cabinets were placed in a climate-controlled room with a constant temperature of 20 °C and a relative humidity of 55 %. Lighting was provided by two ViparSpectra XS1000 full-spectrum LED panels per platform, operating on a 12-h on/off schedule to simulate a day/night cycle. These LED panels consist of a combination of Samsung LM301B 3000 K and 5000 K LED diodes, and Osram 730 nm and 660 nm diodes. The panels are fully dimmable, with light intensity adjusted according to the growing regime (Fig. 2), as verified using an Apogee MQ-500 PAR sensor. Watering was provided by 16 misting nozzles per platform, controlled through an electronic valve connected to an electronic timer. The water supply was filtered using a Brita Purity C150 Quell ST filter to remove both small particles and calcium, thereby preventing clogging or mineral deposits. The addition of nutrients was performed manually using 2 g/L of Peters Professional 10–52–10 NPK fertiliser solution. A high phosphorus fertiliser was used, as previous research has shown that phosphorus supplementation is usually more important than nitrogen (Fritz et al., 2012; Gordon et al., 2001; Niinemets and Kull, 2005). This nutrient solution was applied every 2 weeks for the indoor-only growth experiment and reduced to every 4 weeks for the outdoor incubation experiment to reduce the aforementioned algae growth.

2.2.2. Growing regimes

Samples for both experiments were subjected to the indoor growing regimes for 12 weeks. For the indoor growth experiment, three different growth regime variables were applied: watering frequency, lighting intensity, and light hardening (Fig. 2). For the indoor growth part of the outdoor incubation experiment, the optimal growth regime as found during the indoor-only growth experiment was used.

2.2.2.1. Watering frequency. Three different watering frequencies were tested (Fig. 2). The first consisted of daily watering, and the second consisted of watering for three consecutive days, followed by four consecutive days of no watering (based on the research by (Antoninka

Table 1

MOSS SPECIES (MIXTURES) USED IN THE TWO EXPERIMENTS.

Experiment	Mixture	Species
(1) Indoor-only growth experiment (indoor growth only)	Acrocarps	<i>Tortula muralis</i> Hedw.
		<i>Ptychostomum capillare</i> (Hedw.) Holyoak & N.Pedersen
		<i>Orthotrichum diaphanum</i> Schrad. ex Brid.
		<i>Grimmia pulvinata</i> (Hedw.) Sm.
		<i>Rhynchostegium confertum</i> (Dicks.) Schimp.
	Pleurocarps	<i>Brachythecium rutabulum</i> (Hedw.) Schimp
		<i>Hypnum cupressiforme</i> Hedw.
		<i>Tortula muralis</i> Hedw.
		<i>Ptychostomum capillare</i> (Hedw.) Holyoak & N.Pedersen
		<i>Orthotrichum diaphanum</i> Schrad. ex Brid.
(2) Outdoor incubation experiment (indoor growth and subsequent outdoor incubation)	1	<i>Rhynchostegium confertum</i> (Dicks.) Schimp.
	2	<i>Brachythecium rutabulum</i> (Hedw.) Schimp.
	3	<i>Grimmia pulvinata</i> (Hedw.) Sm.
	4	<i>Tortula muralis</i> Hedw.
	5	<i>Grimmia pulvinata</i> (Hedw.) Sm.
	6	<i>Schistidium crassipilum</i> H.H. Blom
	7	<i>Tortula muralis</i> Hedw.
	8	<i>Rhynchostegium confertum</i> (Dicks.) Schimp.
	9	<i>Brachythecium rutabulum</i> (Hedw.) Schimp.
	10	<i>Rhynchostegium confertum</i> (Dicks.) Schimp.
	11	<i>Tortula muralis</i> Hedw.

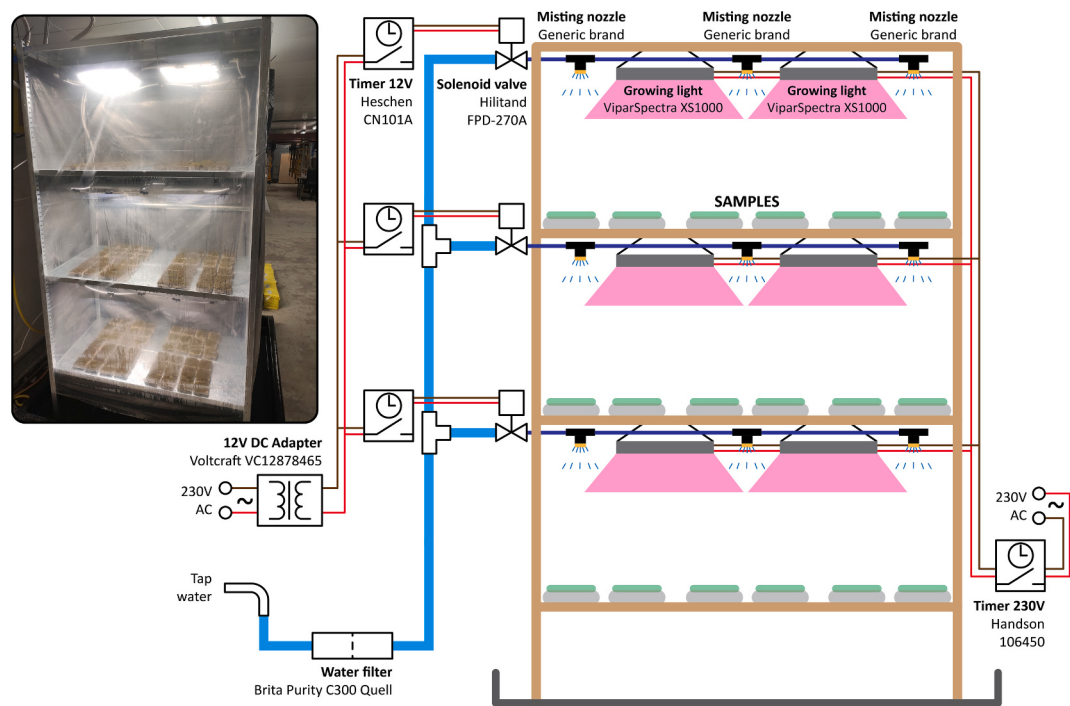


Fig. 1. Overview of the test setup used for indoor growth.

Watering frequency

	Week 1-6							Week 7-8							Week 9-10							Week 10-11						
	Ma	Tu	We	Th	Fr	Sa	Su	Ma	Tu	We	Th	Fr	Sa	Su	Ma	Tu	We	Th	Fr	Sa	Su	Ma	Tu	We	Th	Fr	Sa	Su
Daily Regime 1-4	3	3	3	3	3	3	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1
3 Days/week Regime 5-8	3	3	3					3	3	3					3	3	3					3	3	3				
Hybrid Regime 9-12	3	3	3	3	3	3	3	2		2		2		2	2		2				2			2			2	

X : x minutes of water per day

Light intensity

70μmol		Week 1-6	Week 7-8	Week 9-10	Week 10-11
no hardening Regime 2,6,10		70±10 μmol m ⁻² s ⁻¹ PAR	70±10 μmol m ⁻² s ⁻¹ PAR	70±10 μmol m ⁻² s ⁻¹ PAR	70±10 μmol m ⁻² s ⁻¹ PAR
light hardening Regime 1,5,9		70±10 μmol m ⁻² s ⁻¹ PAR	90±15 μmol m ⁻² s ⁻¹ PAR	110±15 μmol m ⁻² s ⁻¹ PAR	140±20 μmol m ⁻² s ⁻¹ PAR
130μmol		Week 1-6	Week 7-8	Week 9-10	Week 10-11
no hardening Regime 4,8,12		130±15 μmol m ⁻² s ⁻¹ PAR	130±15 μmol m ⁻² s ⁻¹ PAR	130±15 μmol m ⁻² s ⁻¹ PAR	130±15 μmol m ⁻² s ⁻¹ PAR
light hardening Regime 3,7,11		130±15 μmol m ⁻² s ⁻¹ PAR	170±20 μmol m ⁻² s ⁻¹ PAR	210±25 μmol m ⁻² s ⁻¹ PAR	260±30 μmol m ⁻² s ⁻¹ PAR

Fig. 2. Different treatments and associated regimes are used for indoor-only growth testing.

et al., 2018). The last was a hybrid regime, where, for the first 6 weeks, water was provided daily and for the last 6 weeks the regime was modified to include increasingly long periods of dry days following each day of water supply (see Fig. 2 for specifics on the watering regimes) in an effort to induce drought resistance. For all regimes, during the days when water was provided, the watering system was turned on for 1 min, followed by 2 h of no water, to allow the water to be absorbed by the moss. This process was repeated as many times as necessary to ensure

that the moss remained hydrated throughout the lighting period without being fully submerged in water throughout the day, as excessive water can also induce stress in the moss (Borkenhagen and Cooper, 2018). In all cases, water was provided before the lights were turned on to protect the moss from light-induced damage during the rehydration process (Beckett et al., 2005).

2.2.2.2. Light intensity and hardening. Two different light intensities

were tested (Fig. 2). The first was $70 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR (photosynthetically active radiation), as this was found to be the optimal light intensity for growing mosses by (Hao and Chu, 2021). The second was $130 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, which is the highest light compensation point for mosses listed by (Glime, 2017c), which means that at this light intensity, every moss species tested would be able to reach a net-positive photosynthetic gain. This was then further divided into groups with or without light hardening. The light hardening regime consisted of a 33 % increase in light intensity after 6 weeks, a 66 % increase after 8 weeks, and a 100 % increase after 10 weeks to induce the structural and chemical changes necessary for protection against light-induced damage.

2.3. Outdoor setup

The setup for the outdoor part of the outdoor incubation experiment consisted of two wooden frames that held four rows of samples in a staggered manner (Fig. 3). Each wooden frame hosted three samples of each species (or species mixture) and was placed in the Hortus Botanicus in Delft, The Netherlands. One frame was placed facing north, the other facing south. In general, moss is expected to grow better on northern aspects in the northern hemisphere, as this aspect receives the lowest amount of solar radiation and is, therefore, usually also more humid. Both these aspects were therefore chosen as best- and worst-case scenarios, respectively. After the samples were moved from the indoor growth setup to the outdoor incubation setup in October 2023, the samples were initially covered with a light-blocking nylon-weave mesh cloth with a light permeability of 50 % for a period of 3 months, as (Antoninka et al., 2018) found that this significantly improved the outdoor adaptation and survival of biocrusts that were pre-cultivated indoors. In total, the samples spent 15 months in this location (including the 3-month light adaptation period), after which the characteristics of the moss layer were measured.

2.4. Moss coverage, layer thickness and health measurements

To determine the overall change in biomass presence and health condition of the moss layer, three different indicators were measured: green coverage, layer thickness, and photosynthetic efficiency.

2.4.1. Green coverage

Photographs were taken of the surface of each sample at the end of each experiment (week 12 indoors for the indoor-only growth experiment and month 15 outdoors for the outdoor incubation experiment).



Fig. 3. Outdoor incubation setup with moss-covered concrete samples immediately after removing the light-blocking mesh cloth (following 3 months of outdoor incubation).

These photographs were then analysed using the Canopeo for Windows software (Patrignani and Ochsner, 2015) using the following settings: Red Ratio 1.050, Blue Ratio 0.400, Noise Reduction 100. This provides the percentage of the surface which is covered by organic (green) material.

2.4.2. Layer thickness

The layer thickness of the moss was measured at the end of each experiment (week 12 indoors for the indoor-only growth experiment and month 15 outdoors for the outdoor incubation experiment). This was done by measuring the distance between the concrete surface and the top of the moss layer in three positions along a line (one in the middle of the surface and two 2 cm from the edge) using a calliper. If no growth was present at that exact location, the layer thickness of the growth closest to this point was measured instead. The three values were then averaged to obtain a single value for the average layer thickness.

2.4.3. Photosynthetic efficiency

Chlorophyll α fluorescence measurements were carried out using a Walz MINI-PAMII Pulsed Amplitude Fluorometer (PAM) only at the end of the outdoor incubation experiment. This gives the chlorophyll fluorescence parameter F_v/F_m , a value reflecting the potential quantum efficiency of photosystem II (PSII) (an indicator of plant photosynthetic performance), with lower values indicating that the plant has been exposed to stress (Maxwell and Johnson, 2000). In healthy, unstressed bryophytes, this value is generally between 0.76 and 0.83 (Proctor, 2003). Before the measurements, samples were kept in a fully hydrated condition in a room with no PAR for at least 20 min to ensure all samples were dark-adapted. Each sample was measured by placing the sensor at a 60° angle relative to its surface using the Walz 2060-A Fiberoptics Holder for Surfaces in three locations on its surface: one in the centre of the surface and two 2 cm from the edge. If no biomass was present at that location, the biomass closest to this point was measured. Settings used on the MINI-PAMII were as proposed by Murchie and Lawson (2013): Measuring Light OFF, with a Saturating Pulse intensity of $5000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and a duration of 0.8 s. All other settings were left on their default value.

2.5. Data analysis

To determine significant differences between regimes in the indoor-only growth experiment for the moss species mixtures (Acrocarp and Pleurocarp), two Kruskal-Wallis analyses were performed in R version 4.4.3 (R Core Team, 2023) using the 'PMCMRplus' package (Pohlert, 2024), with either Green coverage or Layer thickness as the dependent variable. This was followed by a post-hoc Conover-Iman test with a Benjamini-Hochberg correction. The post hoc test results were then used to create homogeneous subsets (i.e., factor levels of the independent variable that show no significant differences between them) with an alpha level of 0.05.

To test the effects of the two individual environmental variables (Watering frequency and Light intensity) and their interaction, two Aligned Rank-Transformed ANOVAs were performed with either Green coverage or Layer thickness as the dependent variable. For this purpose, the data was first rank-transformed in R (R Core Team, 2023) with the 'ARTool' package (Wobbrock et al., 2011) and then analysed using a factorial ANOVA test. To determine pairwise differences, a statistically significant result ($p < 0.05$) was followed by a post-hoc contrast test using the ART-C contrast testing procedure (Elkin et al., 2021). The results of this post-hoc test were then used to create homogeneous subsets at an alpha level of 0.05.

This last procedure was repeated for the results of the outdoor incubation experiment, except that this time, Orientation (North or South), Species (mixture), and their interaction term were used as independent variables, and either Green coverage, Layer thickness, or PAM result was used as the dependent variable.

3. Results

3.1. Results of the indoor-only growth experiment

Whilst all samples showed growth to some extent (Fig. 4), some clear differences were visible. For the acrocarp species mixture, the differences between regimes were statistically significant with a large effect size for both Layer thickness ($\chi^2[11] = 51.443$, $p < 0.001$) and Green coverage ($\chi^2[11] = 45.919$, $p < 0.001$). Regime 10 (hybrid watering regime with a light intensity of $70 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR and no light hardening) performed best overall in terms of layer thickness ($M = 11.2 \text{ mm}$ [IQR $10.6 \text{ mm} - 12.2 \text{ mm}$]). However, the differences between it and Regimes 2 and 4 were not statistically significant (Fig. 5a). Regime 10 also performed best in terms of green coverage ($M = 15.1 \%$ [IQR 13.2% – 17.9%]) for the acrocarp mixture, although the differences with it and Regimes 1 and 4 were not statistically significant (Fig. 6a).

For the pleurocarp species mixture, the differences between regimes were also statistically significant for both Layer thickness ($\chi^2[11] = 51.996$, $p < 0.001$) and Green coverage ($\chi^2[11] = 43.423$, $p < 0.001$). For layer thickness, Regime 4 (daily watering regime with $130 \mu\text{mol}$

$\text{m}^{-2} \text{s}^{-1}$ PAR light intensity and no light hardening) and 10 performed best ($M = 15.5 \text{ mm}$ [IQR $15.2 \text{ mm} - 15.9 \text{ mm}$] and $M = 16.0$ [IQR $13.3 \text{ mm} - 16.5 \text{ mm}$], respectively). However, the difference between these and Regime 2 was not statistically significant (Fig. 5a). Regimes 8 ($M = 51.7 \%$ [IQR 49.2% – 52.3%]) and 10 ($M = 51.3 \%$ [IQR 51.2% – 52.7%]) performed best in terms of green coverage, although these did not significantly differ from Regimes 2, 4, and 12 (Fig. 6a).

When considering the separate environmental variables, it was found that the Watering frequency significantly affected the Layer thickness ($F[2,60] = 37.259$, $p < 0.001$, $\eta^2 = 0.554$) and Green coverage ($F[2,60] = 39.975$, $p < 0.001$, $\eta^2 = 0.571$) of the acrocarps species, as well as the Layer thickness ($F[2,60] = 8.827$, $p < 0.001$, $\eta^2 = 0.227$) and Green coverage ($F[2,60] = 5.829$, $p = 0.005$, $\eta^2 = 0.163$) of the pleurocarp species, with large effect sizes. The regimes with hybrid and daily watering frequencies performed similarly in most cases. However, the hybrid regimes significantly outperformed the daily regimes regarding coverage of the pleurocarp species (Figs. 5b and 6b).

The Lighting intensity used was also found to significantly affect the Layer thickness ($F[3,60] = 26.231$, $p < 0.001$, $\eta^2 = 0.567$) and Green coverage ($F[3,60] = 4.2564$, $p = 0.009$, $\eta^2 = 0.175$) of the acrocarp

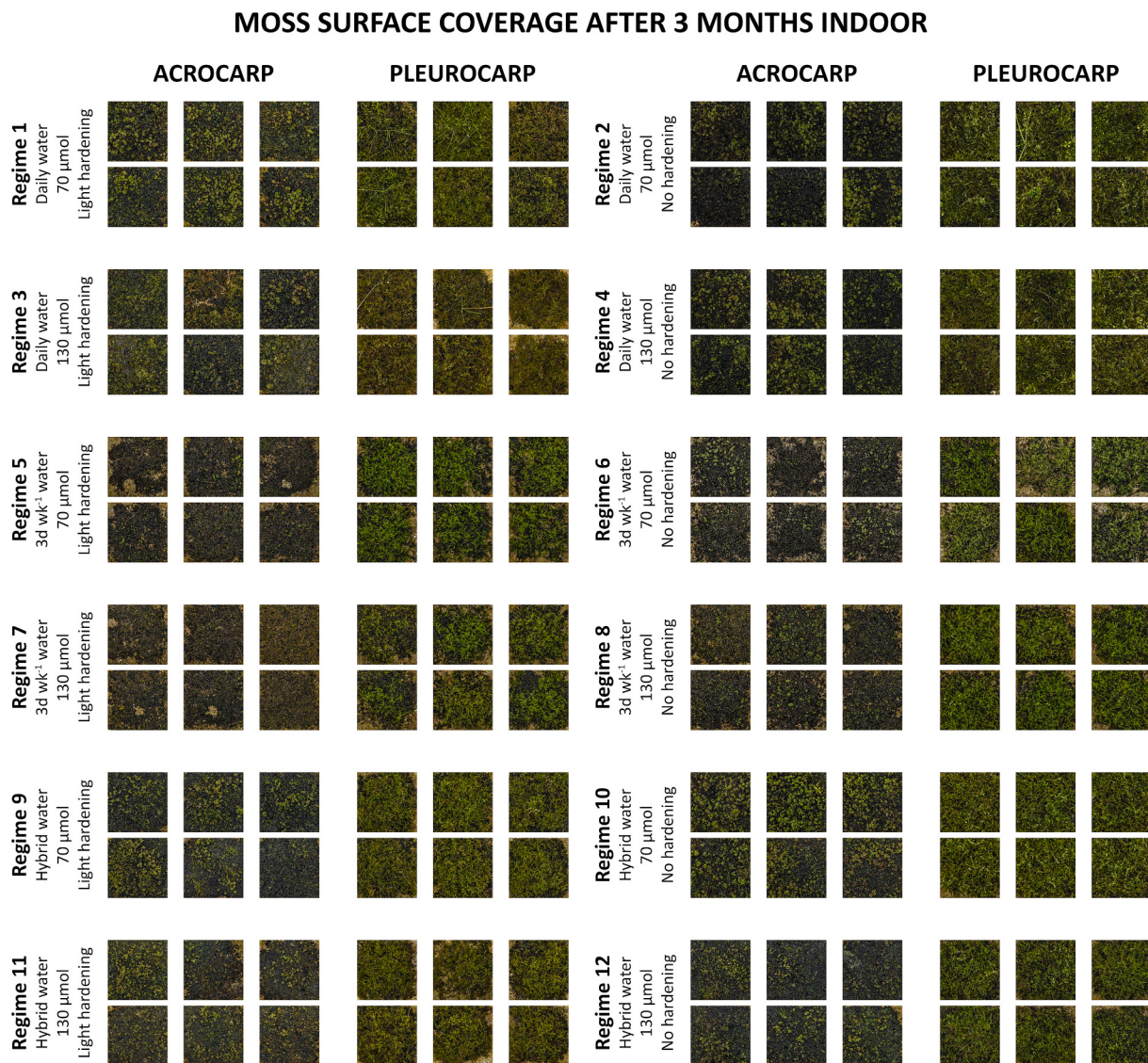


Fig. 4. Top-down pictures showing the green coverage for each growth regime after 12 weeks of indoor growth. Most specimens were almost completely covered by biomass, although green moss coverage differed between samples. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

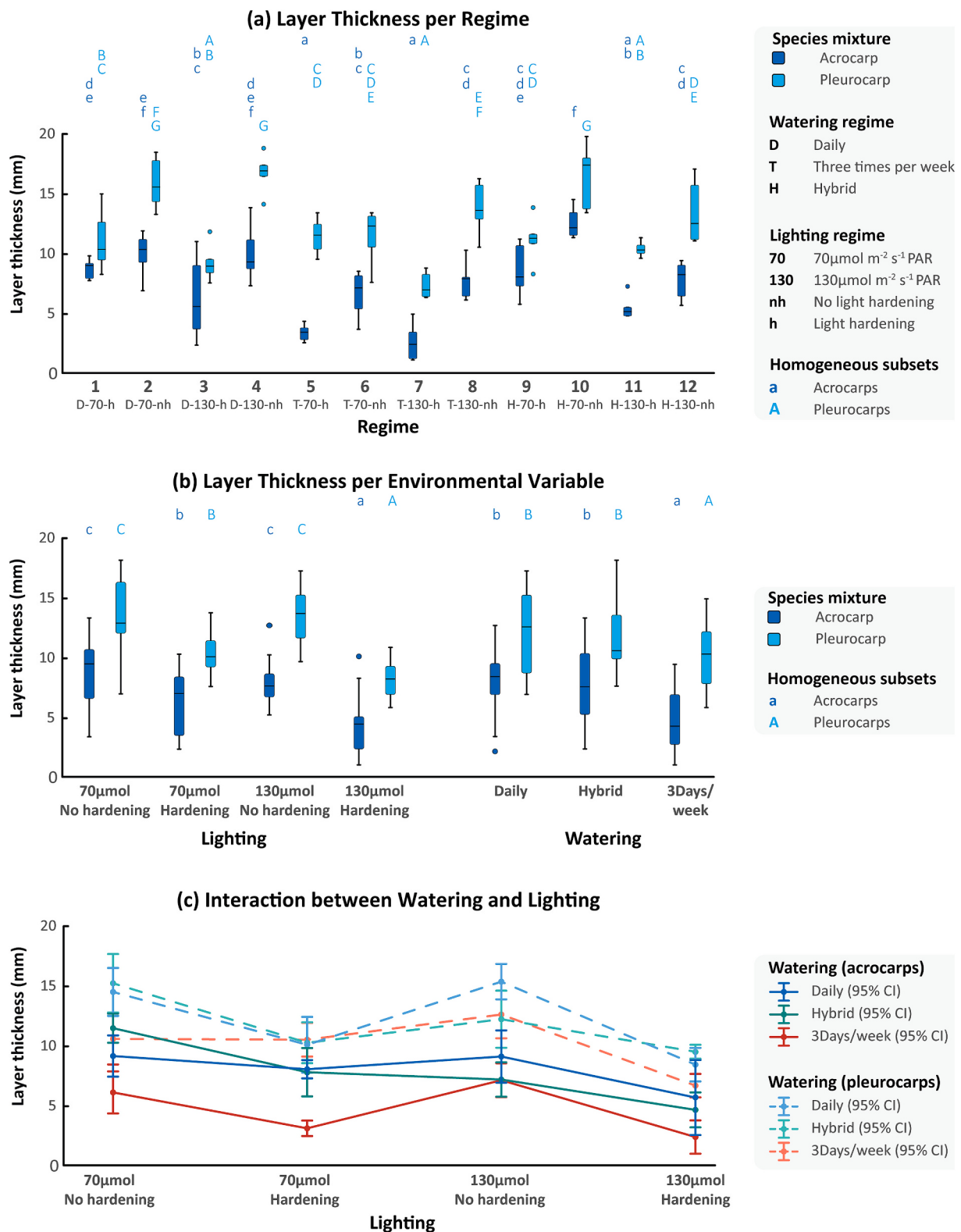


Fig. 5. (a) Layer thickness results per growing regime (1–12) for the acrocarp (dark blue) and pleurocarp (light blue) species mixtures. The letters above the box plots denote the homogeneous subsets with an alpha level of 0.05 formed based on the post-hoc contrasts test. If two groups share a letter, it means that the differences between the two groups are not statistically significant. Letters are assigned alphabetically, from the lowest to the highest values. (b) Layer thickness results per environmental variable (watering and lighting) for the acrocarp (dark blue) and pleurocarp (light blue) species mixtures. Letters above the box plots denote the homogeneous subsets based on the post-hoc contrasts test. (c) Graph showcasing the interaction between the lighting and watering variables on layer thickness. Bars denote the 95 % confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

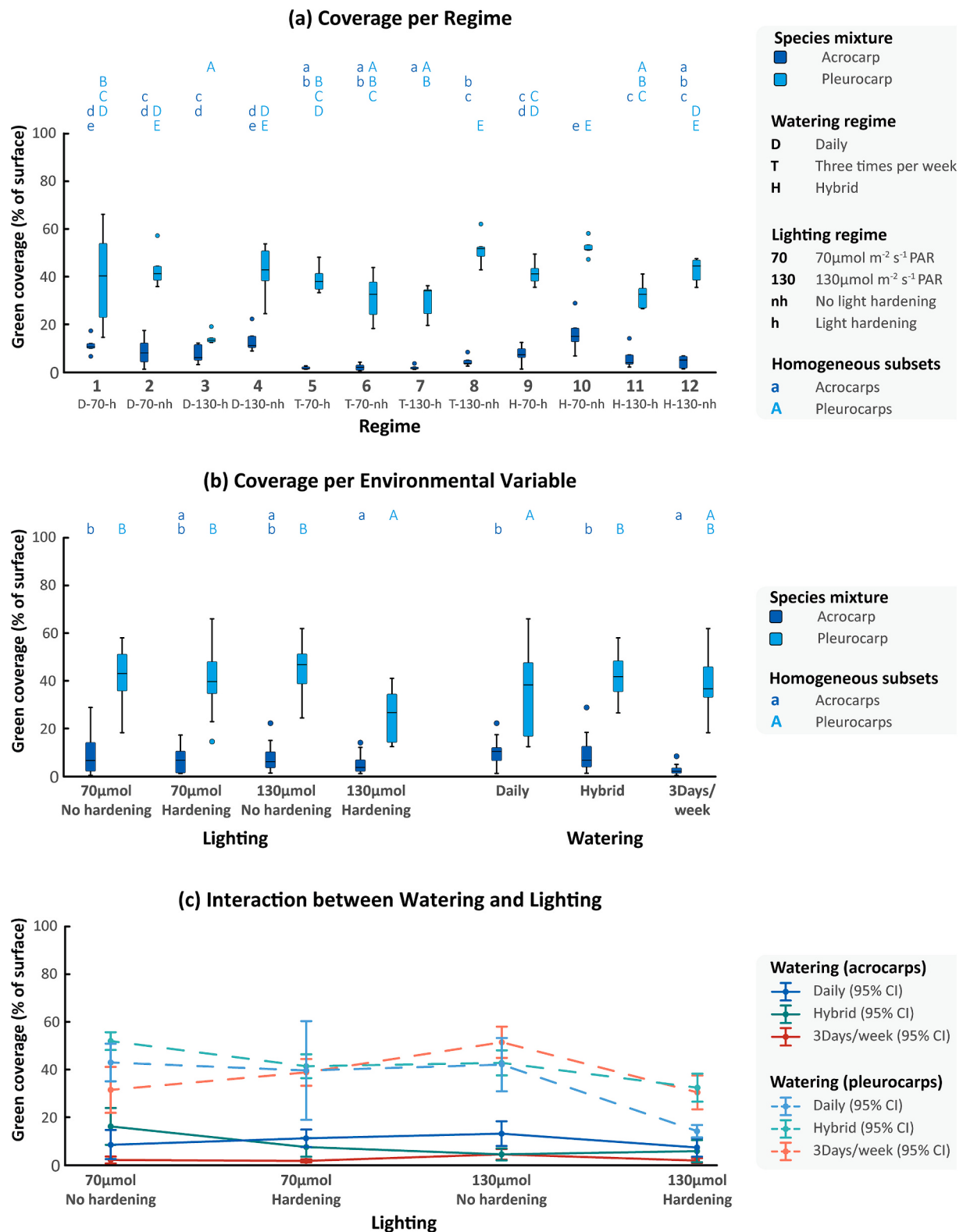


Fig. 6. (a) Green coverage results per growing regime (1–12) for the acrocarp (dark blue) and pleurocarp (light blue) species mixtures. The letters above the box plots denote the homogeneous subsets with an alpha level of 0.05 formed based on the post-hoc contrasts test. If two groups share a letter, it means that the differences between the two groups are not statistically significant. Letters are assigned alphabetically, from the lowest to the highest values. (b) Green coverage results per environmental variable (watering and lighting) for the acrocarp (dark blue) and pleurocarp (light blue) species mixtures. Letters above the box plots denote the homogeneous subsets based on the post-hoc contrasts test. (c) Graph showcasing the interaction between the lighting and watering variables on green coverage. Bars denote the 95 % confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species, as well as the Layer thickness ($F[3,60] = 41.373$, $p < 0.001$, $\eta^2 = 0.674$) and Green coverage ($F[3,60] = 21.187$, $p < 0.001$, $\eta^2 = 0.514$) of the pleurocarp species, again with large effect sizes. In most cases, using $70 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR with no hardening performed best but was closely followed by the regimes with $130 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR and no hardening (Figs. 5b and 6b). In all cases, however, the differences were not statistically significant between the two. For both Light intensities, the introduction of light hardening significantly decreased Layer thickness and Green coverage for both acrocarps and pleurocarps, although the effect was strongest for the $130 \mu\text{mol m}^{-2} \text{s}^{-1}$ light intensity regimes.

Finally, the interaction between Lighting and Watering was found to be significant for the Layer thickness ($F[6,60] = 5.004$, $p < 0.001$, $\eta^2 = 0.334$) and Green coverage ($F[6,60] = 6.505$, $p < 0.001$, $\eta^2 = 0.394$) of the acrocarp species, as well as the Layer thickness ($F[6,60] = 3.867$, $p = 0.003$, $\eta^2 = 0.279$) and Green coverage ($F[6,60] = 6.880$, $p < 0.001$, $\eta^2 = 0.408$) of the pleurocarp species. More specifically, the hybrid watering frequency performed the best of all watering frequencies at the lowest light intensity ($70 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR with no hardening), but results for both green coverage and layer thickness strongly declined with increased light intensity for both species, especially with added light hardening, as can be seen in Figs. 5c and 6c. On the other hand, when watering only 3 days a week, a much smaller negative response to the light-hardening conditions was observed, and there was even a positive response to the increased light intensity without added light hardening. The daily watering frequency showed a response roughly in between the two, with a roughly neutral response to an increase in light intensity without added light hardening and a moderately negative

response to light hardening.

3.2. Results of the outdoor incubation experiment

Based on the results of the indoor-only growth experiment for the Acrocarp and Pleurocarp moss species mixtures, Regime 10 was selected as the indoor growing regime for the individual moss species and species mixtures (see Table 1) used in the outdoor incubation experiment. Results from the outdoor experiment showed that all species (and species mixtures) suffered from indoor to outdoor translocation, as most specimens lost a significant amount of their biomass (Fig. 7).

PAM results (Fig. 8a) showed that of the still present biomass, all Species (mixtures) had Fv/Fm values roughly between 0.6 and 0.7, with no statistical differences between Species (mixtures) ($F[9,39] = 1.3499$, $p = 0.244$, $\eta^2 = 0.238$), although one sample from the *O. diaphanum* group showed an insufficient PAM response to be measured properly and was therefore excluded from these results. On the other hand, the effect of sample Orientation was significant ($F[1,39] = 46.436$, $p < 0.001$, $\eta^2 = 0.544$), with samples facing North (0.71 [IQR 0.68–0.72]) exhibiting somewhat higher values than those facing South (0.62 [IQR 0.57–0.67]). The interaction between Species (mixture) and Orientation was not significant for the PAM results ($F[9,39] = 0.8695$, $p = 0.560$, $\eta^2 = 0.167$).

For the Layer thickness (Fig. 8b), both the Species (mixture) used ($F[9,40] = 12.385$, $p < 0.001$, $\eta^2 = 0.736$) and their Orientation ($F[1,40] = 50.829$, $p < 0.001$, $\eta^2 = 0.560$) had a significant effect. The best-performing single-species groups were *P. capillare* (8.5 mm [IQR 6.8

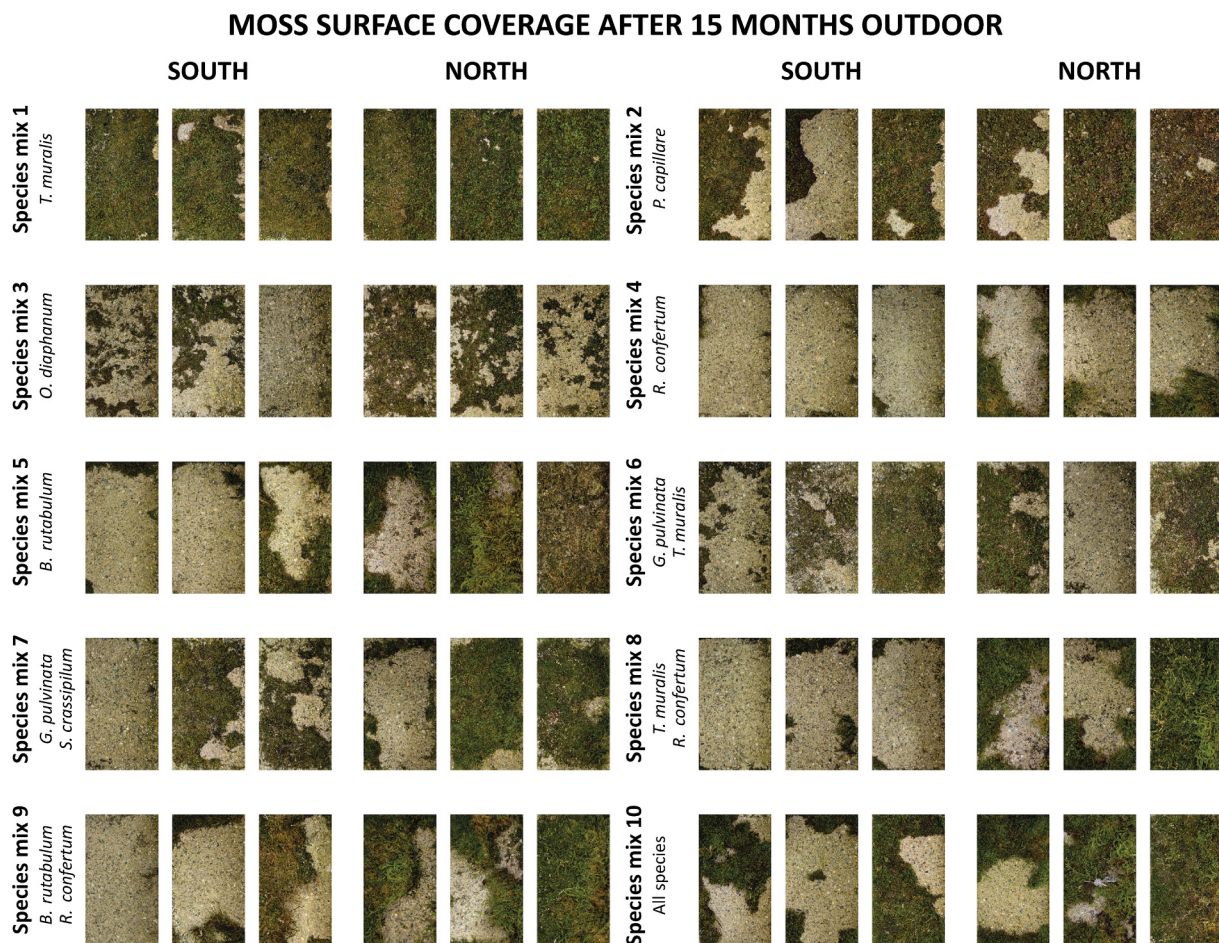


Fig. 7. Top-down pictures showing the green coverage for each species (mixture) after 15 months of outdoor growth. Most specimens lost a significant portion of their moss coverage, with the exception of those covered with *T. muralis*. The loss of coverage was often stronger on south-facing samples, as compared to north-facing ones. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

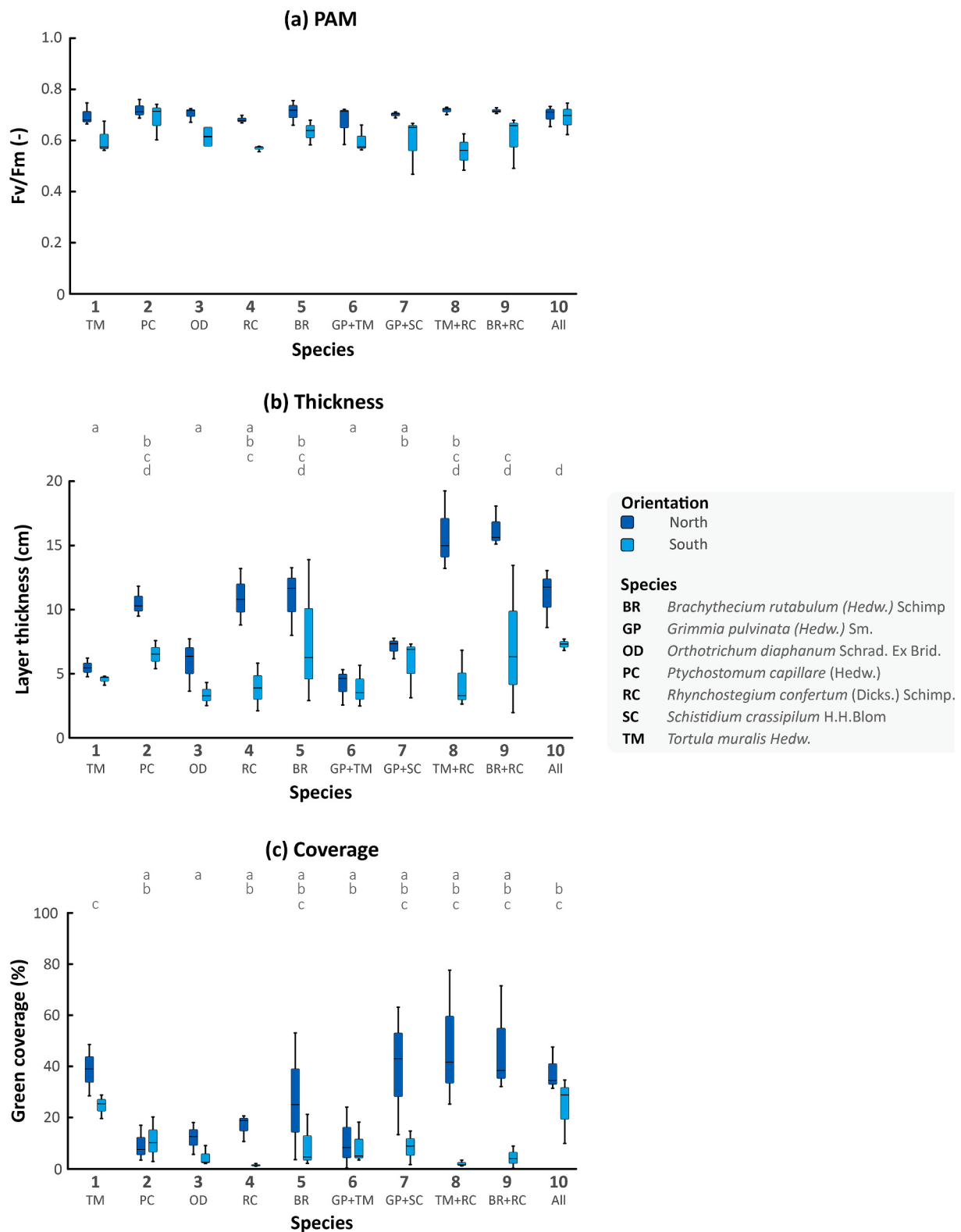


Fig. 8. (a) PAM results per species (mixture) for the two tested orientations: North (dark blue) and South (light blue). As the differences were not statistically significant, no homogeneous subsets were created. (b) Layer thickness results per species (mixture) for the two tested orientations: North (dark blue) and South (light blue). The letters above the box plots denote the homogeneous subsets with an alpha level of 0.05 formed based on the post-hoc contrasts test. If two groups share a letter, it means that the differences between the two groups are not statistically significant. Letters are assigned alphabetically, from the lowest to the highest values. (c) Green coverage results per species (mixture) for the two tested orientations: North (dark blue) and South (light blue). Letters above the box plots denote the homogeneous subsets based on the post-hoc contrasts test. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mm – 10.1 mm]) and *B. rutabulum* (9.8 mm [IQR 6.7 mm – 12.9 mm])). The groups with mixtures of *T. muralis* and *R. confertum* (10.0 mm [IQR 4.2 mm – 14.6 mm]), *B. rutabulum* and *R. confertum* (14.3 mm [IQR 8.1 mm – 15.5 mm]) and of all species (15.6 mm [IQR 9.3 mm – 19.1 mm]) performed even better. Still, differences between these groups and *P. capillare* and *B. rutabulum* were not statistically significant. Furthermore, the overall layer thickness was higher on the North-facing samples (9.9 mm [IQR 6.3 mm – 14.6 mm]) than on the South-facing samples (5.1 mm [IQR 3.3 mm – 6.8 mm]). Not only that, there was also a significant interaction between Species and Orientation ($F(9,40) = 4.69$, $p < 0.001$, $\eta^2 = 0.513$), which seems to be primarily due to the groups (4, 5, 8, 9, and 10) containing one or more pleurocarp species (*B. rutabulum* and *R. confertum*) showing a much more substantial decline in layer thickness when comparing North to South, as compared to those with only acrocarp species (*G. pulvinata*, *O. diaphanum*, *P. capillare*, *S. crassipilum*, and *T. muralis*).

Finally, for Green Coverage (Fig. 8c), both the Species (mixture) ($F[9,40] = 4.1205$, $p < 0.001$, $\eta^2 = 0.481$) used and the Orientation ($F[1,40] = 38.178$, $p < 0.001$, $\eta^2 = 0.488$) again had a significant effect. In this case, the best-performing single-species groups were *T. muralis* (28.8 % [IQR 26.2 % - 36.5 %]) and *B. rutabulum* (13.0 % [IQR 3.9 % - 24.2 %]), and all mixtures of species (groups 6–10) showed similar results to these best-performing single-species groups. Coverage was once again higher for those samples facing North (25.2 % [IQR 12.9 % - 41.1 %]) than for those facing South (4.9 % [IQR 2.2 % - 17.4 %]). A statistically significant interaction was also found between Species (mixture) and Orientation ($F[9,40] = 2.949$, $p = 0.009$, $\eta^2 = 0.399$). As with the Layer thickness results, this seems primarily due to the groups containing pleurocarp species (groups 4, 5, 8, 9, and 10) showing a much stronger negative response to the Southern orientation than those with only acrocarp species, although the group with *G. pulvinata* and *S. crassipilum* also had a similarly strong negative response. It should be noted, however, that compared to the difference in the amount of horizontal growth observed in the indoor-only experiment, this time, the differences in green coverage are primarily due to variations in how well the species (mixtures) are attached to the surface. As shown in Fig. 7, many species (mixtures) lost a significant portion of their surface coverage due to insufficient anchorage to the concrete surface.

4. Discussion

4.1. The role of water and light in the optimal indoor growing regime

As achieving optimal moss growth outdoors is not always practically or economically feasible, a two-step approach was proposed, where initial settlement and growth take place indoors, after which the moss-covered concrete is subsequently translocated to its outdoor location. Water and light were hypothesised as likely being the most critical components of the initial indoor moss-growing regime before the start of this experiment. This hypothesis is indeed supported by the results obtained. Both water and light had a statistically significant influence on the green coverage and layer thickness of both the acrocarp and pleurocarp moss mixtures. The results from the first indoor-only growth experiment indicate that thicker moss layers with better coverage can be achieved under wetter conditions with lower light intensity. One might initially expect the moss species that were used to perform better under dry conditions with higher light intensities, as this more closely resembles the often exposed and dry habitat on urban concrete from which they were harvested. However, what was found in this experiment does agree with the conclusions of Marschall and Proctor (2004), who found that even moss species in exposed habitats cannot truly be considered what they call 'sun-plants'. The findings also align with findings by Vitt (1989) and Zotz and Rottenberger (2001) who found that under natural conditions, the growth rate of drought-tolerant moss species is positively related to the wetness of its environment and with Doherty et al. (2018), who found increased growth for wetter regimes in their growth

experiments with *S. ruralis*, another drought-tolerant species. As such, even for drought-tolerant species, lower light intensity and more frequent watering will stimulate overall growth.

However, watering moss more frequently can be expected to reduce its outdoor survival, as was shown by Antoninka et al. (2018), who found that moss-containing greenhouse-grown biocrusts had reduced outdoor survivability when watered more frequently in the greenhouse. Nevertheless, as the moss growth results presented in this paper show, using a drier 3-days-a-week watering regime throughout the indoor growing period also leads to significantly reduced growth. The proposed hybrid watering treatment, which starts with daily watering and gradually introduces increasingly longer periods of drought, however, had no significant impact on the two growth parameters. At the same time, just a single drying event has been shown to induce drought hardening in moss, with maximal hardening achieved after 3 days of drought (Beckett, 1999; Beckett et al., 2005). Therefore, the hybrid watering regime will likely induce similar drought hardening to the 3-days-a-week watering regimes. This is encouraging as it means that measures against drought, such as irrigation, are not necessary during the outdoor growth stage if a hybrid watering regime is employed during the indoor growth phase.

Notably, the hybrid watering regime even outperformed the daily watering regime in the experiments at the lowest light intensity, despite the moss receiving less water in the second half of the indoor-only growing period. This suggests that it is also possible to provide too much water, causing physiological stress and thereby hampering growth, a phenomenon that has been previously observed in moss (Busby et al., 1978; Busby, 1976; Mulligan and Gignac, 2001). As the moss colony grows, it can be expected to exhibit increased water absorption (Zotz et al., 2000), which, in turn, will keep it wet for a longer period. To compensate for this and avoid flooding the moss, the amount of water received per day on which water was provided was already reduced in the indoor-only experiment for the wetter regimes (Fig. 2). However, this reduction might not have been enough for the mosses growing under the lowest light intensity. As LED growing lights also produce a small amount of heat, the samples under the higher light intensity lamps may have experienced somewhat higher levels of evaporation, compensating for the excess in water in these samples, but not those growing under lower light intensity. Thus, higher amounts of water benefit moss development, as long as the moss is not left too saturated for an extended period.

Regarding light intensity, the overall difference between using 70 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR and 130 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR was not statistically significant. However, this is mainly due to the differences in the response to increased light intensity between different watering frequencies used. Under the driest watering treatment, where water was provided for three consecutive days, followed by four consecutive days of drought, layer thickness and coverage showed a slight to moderate tendency to increase with higher light intensity for both the acrocarp and pleurocarp species mixture. Under the wettest treatment, where water was provided daily, both layer thickness and green coverage were similar across light intensities for both species mixtures. Contrarily, there was a reduction in layer thickness and coverage for all species under the higher light intensity for the hybrid watering treatment. This may confirm the hypothesis by Beckett et al. (2005), who suggested that the photosystem of mosses may express along a spectrum with, on the one hand, a 'high efficiency' state and, on the other hand, a 'photo-protected' state. The former end of the spectrum is characterised by faster growth but slower recovery from dehydration due to the creation of light-induced ROS (reactive oxygen species, which can cause damage to cellular organic molecules). In contrast, the latter 'photoprotected' end of the spectrum is characterised by slower growth due to the metabolic costs associated with this state. Still, mosses in this state are less likely to suffer from light-induced ROS when rehydrated due to higher non-photochemical quenching (a process through which excess light energy is converted into heat or fluorescence to protect the

photosynthetic apparatus from damage). The mosses on the wettest water treatment can be expected to be on the 'high-efficiency' end of the spectrum. However, as they are constantly hydrated, no light-induced damage can occur as there are no rehydration events. The mosses on the driest treatment do experience frequent rehydration. However, they can be expected to be on the 'photoprotected' end of the spectrum (which would also explain their slow growth, as it is less efficient), as they have been drought-hardened; thus, light-induced damage is negated. Moreover, mosses under this treatment appear to benefit somewhat from higher light intensities, as this may offset the lower efficiency of the 'photoprotected' state. The mosses under the hybrid treatment, however, are not initially drought-hardened. During the first six weeks, they are likely in the 'high-efficiency' state and gradually transition to the 'photoprotected' state over the next six weeks. However, during this transition, they remain susceptible to light-induced damage during rehydration, a situation that they now experience due to the longer time between watering events. As such, this would explain why the mosses under the hybrid water treatment respond so negatively to increased light intensity.

On the one hand, this does show the effect that (even slowly) increasing the light intensity can have on moss and thereby highlights the importance of letting the moss gradually adjust to the higher light intensity. On the other hand, it also shows that drought hardening and light hardening are best not done simultaneously. As light-hardening can be relatively easily achieved outside using light-blocking mesh, and drought-hardening requires either labour-intensive manual watering or an automated irrigation system, it is generally best to induce drought-hardening indoors and light-hardening outdoors. Furthermore, the resulting growing regime, consisting of a hybrid watering treatment combined with a light intensity of $70 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR and no light hardening, yielded either the best or nearly the best results in both growth metrics for both species.

Finally, during the subsequent outdoor incubation experiment, all species and species mixtures, except the single-species samples of *G. pulvinata*, exhibited some degree of moss growth after the initial indoor growing period, using the regime developed during the indoor-only growth experiment. This suggests that this regime is suitable for a large range of moss species, but some species may need an adjusted growing regime, or the use of additional phytohormones, as this has previously been found to be necessary for the gametophore formation of certain moss species (Szweykowska, 1963).

4.2. Response of indoor-grown moss communities to translocation to outdoor conditions

Based on the outdoor survival of the moss communities after translocation during the outdoor incubation experiment, several inferences can be made. While mosses growing on the south-facing samples show a lower overall health of their photosynthetic systems than those growing on the north-facing samples, the range of PAM values found for the former (0.62 [IQR 0.57–0.67]) is well within the range of values found for naturally occurring moss colonies (Jägerbrand and Kudo, 2016; Lan et al., 2012). This suggests that all moss species can at least survive on both north and south-facing substrates using the developed cultivation method.

However, it should be noted that both the season of translocation and climate might affect these results. The moss species used in this experiment have a cosmopolitan distribution and are mostly very drought-resistant (Veeger et al., 2025b; Wood, 2007), suggesting they can survive under a variety of weather conditions. However, as mentioned previously, this drought resistance must be induced first. When the moss is translocated in autumn in the Netherlands, as was done in this experiment, high light intensity and rapid dehydration – two of the main damaging mechanisms in moss (Heber and Lüttge, 2011) – are less likely to occur. This is especially true when a light-blocking mesh is used to induce light hardening. If translocation is to occur in spring or summer,

or in hotter climates, the transition from indoor to outdoor might still be too extreme, in which case additional measures may be required. One potential measure that could be investigated in this case is the employment of a longer light hardening period, potentially with different subsequent mesh densities (for example 70 %, 50 %, and 30 %).

When it comes to differences between the tested species, pleurocarp species are characterised mainly by a high growth rate and coverage, as can be seen in the results of both the indoor-only and outdoor experiments. This makes them an interesting candidate for use on bioreceptive concrete, as they enable rapid and extensive surface coverage. However, pleurocarp species (mixtures) also appear more susceptible to growth inhibition on south-facing surfaces, exhibiting a large drop in layer thickness and green coverage on south-facing substrates compared to north-facing ones. This finding concurs with previous research, which has shown that pleurocarp species tend to occur in more shaded and humid environments than acrocarp species (Gimingham and Birse, 1957; Grace, 1995; Tarja and Paul, 2009; Veeger et al., 2025b). Pleurocarp species (mixtures) are, therefore, likely best suited for use in a more shaded environment. Nevertheless, these species' relatively high PAM values on the south-facing samples suggest passable to good photosystem health. This may indicate their potential to grow on more exposed surfaces, warranting further research. Of the tested pleurocarp species, *B. rutabulum* showed the best overall results.

Acrocarp species, on the other hand, are slower-growing but appear more resilient to the increased environmental stress experienced on south-facing surfaces, although they are also affected. *T. muralis* was the most resilient species, exhibiting decent growth on both north- and south-facing surfaces, making it an interesting species to use in harsh environments. However, it is hindered by its slow growth rate, resulting in a relatively thin layer thickness. *P. capillare*, on the other hand, can grow much thicker layers but is very susceptible to a loss of adhesion to the surface, especially on a south-facing surface, resulting in a low green coverage.

4.3. Options for improving moss adhesion

Except for *T. muralis*, most moss species showed only partial surface coverage after 15 months outside. This reduction in moss surface coverage is not unusual and is a common phenomenon that often occurs when indoor-grown mosses are moved outside (e.g. Antoninka et al., 2018; Bowker et al., 2023; Doherty et al., 2020). However, the low green coverage of most samples appears not to be due to poor moss health, as the moss falling off from the surface still seemed to be in good health (Fig. 9), nor did the PAM results reveal any undue amounts of stress in any of the samples. While the lower coverage on the south-facing samples might suggest that some environmentally induced stress was



Fig. 9. The mosses that lost adhesion to the concrete surface still appeared healthy in most cases.

involved, this may simply be due to the south-facing samples being placed in a windier location, causing more mechanical stress on the moss. Instead, for all species except *T. muralis*, the low green coverage results seem to be more due to insufficient adhesion to the surface. As such, improving surface adhesion would be an obvious next step.

Moss uses rhizoids – small, filamentous tissue similar to root hairs – to adhere to the surface on which it grows. As such, the primary cause of poor adhesion is likely to be a poorly developed rhizosphere. The cause of this underdeveloped rhizosphere system might be the watering treatment used during the initial indoor development of the moss layer. As discussed before, frequent watering is beneficial for growth and, as such, was used to develop a moss layer on the concrete surface quickly. However, it has previously been observed by other researchers that moss prioritises shoot development over rhizoid development when well-watered (Berdaguer et al., 2024). The exact mechanism through which this occurs has not been investigated. However, rhizoid development has been found to be controlled by the plant hormone auxin (Ashton et al., 1979; Bennett et al., 2014; Chopra and Vashistha, 1990; Kurepa and Smalle, 2022; Lavy et al., 2016; Sakakibara et al., 2003), and auxin production has been shown in vascular plants to be increased when the plant experiences drought (Sharma et al., 2023). As such, it stands to reason that the low adhesion observed on the outdoor moss samples arises from the reduced rhizoid development resulting from the low auxin production caused by the watering treatment used. The differences in adhesion between moss species may thus be linked to either differences in baseline auxin production or auxin sensitivity, or may instead be caused by differences in overall rhizoid morphology.

One solution for the poor adhesion of the moss might, therefore, be the application of exogenous auxin. Previous research has shown that this can increase rhizoid production in moss at the expense of shoot and leaf development, with the extent of the effect dependent on the concentration of exogenous hormone used (Chopra and Vashistha, 1990; Kurepa and Smalle, 2022; Sakakibara et al., 2003). This could stimulate rhizoid development, even under the wetter conditions used in indoor growth.

Another option would be to increase the adhesion of the moss to the surfaces artificially. For example, tackifiers (soil-adhesive agents), consisting of psyllium or polyacrylamide, have successfully improved soil adherence in moss biocrust restoration (Blankenship et al., 2020). Similarly, a biodegradable glue consisting of cornstarch, maltodextrin, gums, and montmorillonite clay has successfully been used to aid moss biocrust restoration (Oliveira et al., 2025). Therefore, applying these adhesives might aid in keeping the moss attached to the concrete, although the effectiveness of this type of adhesive on concrete remains to be seen.

As found in this research, one final option is using a multispecies mixture rather than monospecies mixtures. Overall, the multispecies mixtures performed better than monospecies mixtures in terms of green coverage, potentially due to the differences in rhizoid structure between species complementing one another (Odu, 1978). Not only that, but multispecies colonies also performed better in terms of layer thickness compared to their individual constituents in most cases. This suggests these species can complement one another, in line with previous findings (Veeger et al., 2025b). However, the benefits, while statistically significant, are mostly relatively minor, and even the multispecies colonies suffer from a lack of adhesion. Furthermore, the results are not always positive, as is the case when combining *T. muralis* and *R. confertum* on a southern surface, where layer thickness and coverage are worse than the matching monospecies samples, suggesting competition can occur under harsh environments, once again in line with previous findings (Veeger et al., 2025b).

5. Conclusion

This research aimed to develop a moss layer on bioreceptive concrete quickly while still exhibiting good long-term outdoor survival. For this

purpose, a two-step approach was proposed: an initial indoor growth period during which optimal conditions are provided for moss settlement and growth, followed by a translocation to the outdoor location. This approach was tested through two experiments. Based on our findings, the following conclusions can be drawn:

- Frequent watering and a lower light intensity ($70 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR) are ideal for indoor moss growth, applicable to both moss growth forms (acrocarp and pleurocarp), although overwatering should be prevented
- Drought hardening can be induced by reducing the watering frequency during the second half of the indoor growth period without significantly impacting the moss layer thickness or coverage.
- Light hardening, through the slow increase in light intensity during the second half of the indoor growing period, is detrimental to coverage and layer thickness, especially when combined with drought hardening. Light hardening can instead be done outdoors with light-blocking mesh.
- *T. muralis* was the most reliable moss species, with good coverage outdoors on both north- and south-facing surfaces, but it is characterised by slow growth.
- *P. capillare* and *B. rutabulum* exhibited significantly faster growth than *T. muralis* but struggled to remain attached to the concrete surface outdoors, particularly when facing south.
- *O. diaphanum* and *R. confertum* showed only minimal growth and coverage outdoors, and *G. pulvinata* showed no growth indoors, suggesting this growing regime is not suited for all moss species.
- Surface adhesion is still problematic for most species but could be improved using exogenous plant hormones, adhesives, or multispecies moss colonies.

As such, the most reliable way of developing a durable moss layer on concrete currently is by using *T. muralis*, which is grown for 12 weeks indoors under a light intensity of $70 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, with initial daily watering reduced to one watering event every 4 days to induce drought hardening. Then, during the first months of exterior growth, the moss is best covered with a light-blocking cloth that reduces the incoming solar radiation by 50 % to induce gradual light hardening.

In future research, the use of either plant hormones, adhesives or multispecies colonies could be tested on *P. capillare* and/or *B. rutabulum*, to see if they could replace *T. muralis*, as the former two showed significantly faster growth but have worse surface adhesion. Furthermore, the need for, and effectiveness of, optimisation of the outdoor light-hardening period could be investigated, which could include the use of different light-blocking mesh densities.

CRedit authorship contribution statement

M. Veeger: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **M. Ottel :** Writing – review & editing, Supervision, Methodology, Conceptualization. **H.M. Jonkers:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

M. Veeger reports a relationship with ReSpyre B.V. that includes: consulting or advisory.

M. Ottele reports a relationship with ReSpyre B.V. that includes:

equity or stocks.

H.M. Jonkers reports a relationship with ReSpyre B.V. that includes: equity or stocks.

If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data is available on Mendeley Data under the following DOI: [10.17632/rfmhn8cr3t](https://doi.org/10.17632/rfmhn8cr3t).

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