Biocentric Design: Mapping Optimal Environmental Variables for Moss Propagation on Urban Bioreceptive Surfaces

Alexandra Lăcătușu¹, Marcos Cruz¹, Brenda Parker², Anete Salmane¹

¹ Bartlett School of Architecture, UCL, London, United Kingdom a.lacatusu@ucl.ac.uk; m.cruz@ucl.ac.uk; a.salmane@ucl.ac.uk
² Department of Biochemical Engineering, UCL, London, United Kingdom brenda.parker@ucl.ac.uk

Abstract. The biocolonisation of urban building surfaces by mosses is a ubiquitous and naturally occurring phenomenon that encapsulates immense ecological value for both current and future challenges of life in cities. The miniature ecosystems facilitated by mosses capture atmospheric pollutants and maintain local biodiversity by providing shelter and nutrients for a highly diverse set of organisms across all kingdoms of life. Early establishment and growth of bryophyte communities appear to be influenced by a dynamic mix of biotic and abiotic factors, while environmental cues modulate physiological responses and biochemical exchanges. A prototype monitoring device was designed to measure carbon dioxide uptake under variable light, humidity, and temperature conditions during a 3-week experiment. By providing a non-destructive tool for understanding and visualising the impact of environmental variables on photosynthetic behaviour, the device contributes to a biocentric design practice, where an organism's ecological needs begin to drive the development of bioreceptive microenvironments.

Keywords: Living things, Bioreceptive design, Moss ecophysiology, Photosynthetic behaviour, Environmental monitoring.

1 Introduction

The practice of Bioreceptive Design challenges the modernist notion of *skin* in architecture by replacing it with a heterogenous Architectural *bark* composed of hybrid mineral-biological assemblages generated through quantitative studies and bio-digital explorations (Cruz & Beckett, 2016). Material porosity, surface macro- and micro-geometry, chemical composition, proximity to sources of diaspores and biochemical interactions between living and non-living material components are known to modulate their bioreceptivity (Guillitte & Dreesen, 1995; Heimans, 1954; Sanmartín et al., 2021). In this

context, building facades have been proposed as potential homes for dynamic multispecies interactions, which have the potential to contribute to green infrastructures by maintaining ecosystem services and urban biodiversity (Watkins et al., 2020). The application of ecological research to architectural design is facilitating a transition towards an *aesthetic of impurity* whereby material-biological interactions and façade ageing are embraced by designers rather than avoided (Cruz, 2021).

Mosses growing autonomously on urban bioreceptive surfaces are part of global cryptogamic covers and play an essential role in carbon sequestration, nutrient cycling and stormwater retention (Anderson et al., 2010; Delgado-Baquerizo et al., 2018; Elbert et al., 2012). During moss development, a range of micro-interactions with substrates and surrounding ecology may influence the development speed and fitness of colonies (Delgado-Baquerizo et al., 2013; Hornschuh et al., 2006; Schauer & Kutschera, 2011). However, the ecophysiological dynamics that enable mosses to develop on vertical building materials such as concrete, brick, stone or wood are not yet fully understood. Photosynthetic rates determine the speed at which mosses grow. However, these are known to be influenced by many factors, including colony morphology (Zotz et al., 2000), humidity (Coe & Sparks, 2014), light conditions (Griffin-Nolan et al., 2018), temperature (Osaki & Nakatsubo, 2021), and carbon dioxide availability (Coe et al., 2012).



Figure 1. Biocolonisation of a brick wall by *Tortula muralis* moss. Source: Alexandra Lăcătusu, 2019

Experiments on the physiological ecology of mosses require a mix of lab-based and field methods. Firstly, understanding how particular parameters influence plant development implies controlling the delivery of a limited number of variable conditions and observing changes in morphology, mass, colour, and gas exchange against control samples (Zotz et al., 2000). In contrast, field experiments consider dynamic environmental changes and

seasonal variations in photosynthetic activity. These span over larger timeframes and often lack detailed data sets that may reveal the dynamic relationship between growth rates and heterogenous weather conditions, daynight dynamics, or site-specific variations in light, temperature and moisture availability (Zotz & Rottenberger, 2001).

Recently, hybrid methods have been developed to pair field and laboratory experiments for tracking succession by bacteria and algae on concrete-based materials (Cruz, 2021; Manso et al., 2014). While some of these included photographic and colorimetric analysis, metagenomic testing and material tests such as porosimetry, it is not yet clear how linking the asynchronous data sets gathered at varying time resolutions and spatial scales can reveal the growth behaviours of studied organisms nor how results from empirical experiments might be re-introduced into an iterative design process.

Echoing planetary and agricultural scale green space monitoring, non-destructive image-based methods for quantifying in-situ moss photosynthesis have already been developed (Pettorelli et al., 2005; Valle et al., 2017). The Normalised Difference Vegetation Index (NDVI) analysis represents one of these methods and was paired with lab tests and colorimetric analysis of reflected light wavelengths to monitor the photosynthetic activity of mosses (Burgheimer et al., 2006; Graham et al., 2006; Young & Reed, 2017).

By combining methods from the fields of bryology, ecology, design and engineering into cross-disciplinary research and design practice, this project aims to create an integrated workflow for introducing the physiological needs of biocrust mosses into bioreceptive design. In this context, this study proposes a hybrid method that includes gas exchange monitoring and image analysis for quantifying photosynthetic performance in bespoke conditions to quantitatively assess the environmental factors that impact the growth of biocrust mosses.

2 Methodology

2.1 Monitoring Device

A small-scale monitoring system for tracking moss growth, health and carbon dynamics was designed and manufactured. Based on research into critical environmental parameters, its purpose was to verify and extract optimal conditions for the growth of the biocrust moss *Syntrichia ruralis*. The prototype closed-loop system contained sensors and a near-infrared image capture module that recorded the photosynthetic activity of the moss specimen by measuring carbon dioxide (CO₂) uptake and oxygen (O₂) production in relation to temperature, humidity, light intensity, and light colour. The monitoring device was placed within a plant growth chamber (CONVIRON, GEN2000 TC) on a 22h-2h day-night cycle at 25-15°C.

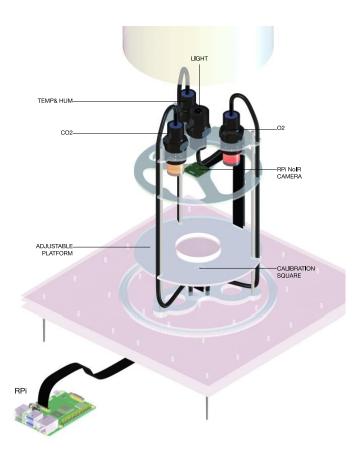


Figure 2. Moss Monitoring Device components. Source: Alexandra Lăcătușu, 2021

2.2 Sample Collection and Preparation

A tuft of *S. ruralis* moss was collected from a concrete surface located next to a riverbank in London (51.560932, -0.043466). Before the experiment, the sample was placed into a petri dish and sprayed with sterile water until saturation. Excess water was discarded, and the specimen was placed at a marked location on the observation platform within the monitoring device. The device was sealed to provide an airtight closed-loop microenvironment for the whole duration of the experiment.

2.3 Sensor Readings

A series of factory-calibrated sensors (EZO series, Atlas Scientific) located within the device recorded CO₂, O₂, air humidity, temperature, dew point and light intensity levels. All sensors were placed at the top level of the device,

facing the sample at approximately 15cm, except for the light intensity and light colour sensor, which faced upwards to capture environmental light levels. Sensor recordings were done at 15-minute intervals throughout the 3-week experiment and recorded on a Raspberry Pi microcontroller.

2.4 Image Capture and NDVI Image Analysis

Image data was captured with a Raspberry Pi NoIR camera at the same 15-minute intervals for complementing sensor readings and measuring the surface area of the studied sample. The absence of an infrared filter on the camera module allowed for reflected infrared light to be recorded and the Normalised Difference Vegetation Index to be calculated (Young & Reed, 2017).

$$NDVI = (NIR - RED)/(NIR + RED)$$
 (1)

Values range from -1 to 1, and pixels with an index above 0.33 indicate active photosynthetic areas.

2.5 Net Photosynthesis Equation

The basic equation for a closed-loop system was used (Field et al., 1989).

$$An = ((Cf - Cb) * V)/\Delta tL$$
 (2)

Here Cb is the initial concentration of CO_2 , Cf is the final concentration, V is the total volume of air within the chamber, Δt is the time elapsed from the beginning of the experiment until its end, and L is the surface area of the moss sample estimated from image recordings. Final photosynthetic rates were calculated based on chamber CO_2 levels and the estimated sample area at 15-minute intervals and as an absolute cumulative value for the whole experiment duration. All values were expressed as ppm/m²/s.

3 Results

3.1 Photosynthesis and Respiration

Daytime CO₂ values within the device fluctuated between 150 and 460 ppm during the experiment. A steady decrease in overall CO₂ levels was observed for the first four days, which may show its uptake by moss, followed by an equivalent increase between day 5 and day 8, potentially indicating respiration from moss tissues. Following this period, CO₂ levels went through a plateau phase, stabilising around the value of 300 ppm. An increase in the

initial CO_2 levels within the device followed the plateau phase, indicating higher respiration rates than photosynthesis. For the night cycles, a rhythmic set of spikes in CO_2 levels between 50-80 ppm correlated with a humidity increase from 70% to 100% and a decrease in O_2 levels.

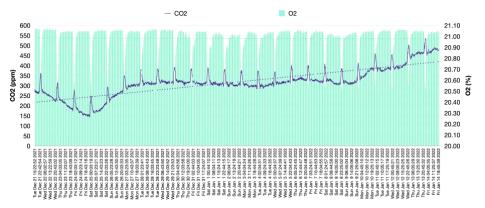


Figure 3. Fluctuations between daytime and night CO₂ and O₂ levels within monitoring device. Source: Alexandra Lăcătușu, 2022

3.2 Photosynthetic Rates

The photosynthetic rate at 15-minute intervals showed substantial variations throughout the experiment, ranging from an average CO_2 gain of 5.84 ppm/m²/s to a loss of 6.44 ppm/m²/s. The cumulative rate of -0.1 ppm/m²/s calculated for the 3-week experiment indicated an overall negative CO_2 balance in the moss sample.

3.3 Environmental Monitoring

Throughout the experiment, there was a clearly defined diurnal pattern in overall environmental conditions, with light and temperature levels influenced by the plant growth chamber's environmental schedule. Temperature levels within the monitoring device oscillated from 15°C during night cycles to just below 30°C during the day. While the lower limit was in line with the chamber's night cycle setpoint, the daytime temperature exceeded it by about 5°C, indicating overheating within the device. In line with the lighting settings of the chamber, the light intensity levels recorded were relatively stable and low, varying between 1.5% and 2.5% of full sun, with the first part of the day characterised by lower values (1500-2000 lux), and higher light intensity for the rest of the day cycle (up to 2500 lux). Daytime air humidity (80%) was recorded at high temperatures (29°C), while sudden drops in temperature (15°C) and light intensity during the night cycle matched drops in air humidity (70%). A rise in humidity above daytime levels was recorded toward the end of each night cycle.

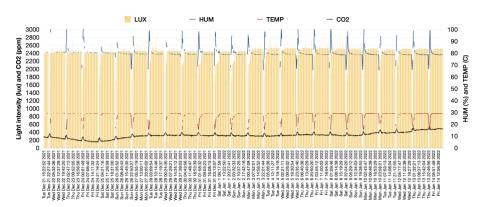


Figure 4. Interaction between environmental parameters and CO_2 levels. Source: Alexandra Lăcătuşu, 2022

3.4 NDVI Image Analysis

Results from NDVI analysis show that photosynthetic activity was maintained for longer in the middle of the sample as opposed to its edges. This is indicated by red areas with an NDVI value between 0.66 and 1, while yellow and green areas were the least active, shown by values below 0.66 and 0.33, respectively. Since image data gathered throughout the experiment showed drying and shrinkage of moss starting from the edges of the sample and moving toward the centre, the NDVI pattern shows a correlation between the presence of liquid water and photosynthetic activity.

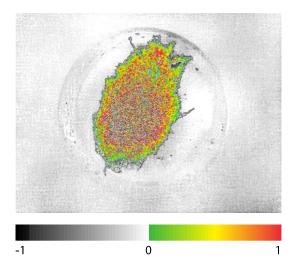


Figure 5. NDVI results for *S. ruralis* moss sample. Colourised pixels represent NDVI values between 0 and 1. Source: Alexandra Lăcătușu, 2022

4 Discussion

The results from this pilot experiment revealed the short and mid-term effects of variable light intensity, temperature, and air humidity on the photosynthetic activity of the selected moss species, *S. ruralis*. The rhythmic day-night cycles, environmental conditions provided by the plant growth chamber, and the single watering event at the beginning of the experiment provided a controlled set of variables for observing patterns in photosynthetic activity. Pairing sensor data and zooming in and out at different time scales within the data set allowed for correlations to be monitored and interpreted against existing literature on how individual variables such as light intensity, temperature, humidity, and CO₂ influence photosynthesis.

4.1 Photosynthetic Behaviour

The most critical factor for photosynthesis in mosses is the presence of water. Studies have shown that the optimal relative water content (RWC) for maximum photosynthetic rates in drought-tolerant moss S. ruralis is 40% to 70% (Tuba et al., 1996). Water content above this range causes low CO2 diffusion through the water pellicle gliding on the leaf surface and inhibiting photosynthesis, while a lower RWC does not fulfil the cell's water potential for the photosynthetic activity to be maintained (Coe & Sparks, 2014). Although the RWC of the sample could not be measured for this experiment, the drying pattern recorded on camera over the 3-week timeframe, paired with NDVI image analysis, data on air humidity and CO2 levels were sufficient for observing the photosynthetic behaviour of the studied specimen. Following the initial watering, the gradual decrease of CO₂ levels within the chamber over the first four days of the experiment is hypothesised to correlate with increasing photosynthetic rates in the moss. Image data showed surplus water evaporating from the sample, followed by gradually drying of the moss tuft inwards. This pattern was in line with the NDVI analysis showing that dry tissues reflected less infrared light, indicating the reduction of photosynthetic activity within the sample.

Light is observed to be another highly limiting factor for photosynthesis. With few exceptions, the light compensation and saturation points for sunadapted species are between 1000-2000 lux (Bazzaz et al., 1970) and 10000-30000 lux, respectively (Glime, 2017). In *S. ruralis*, 95% light saturation and maximum photosynthetic rates occur at a photosynthetic photon flux density (PPFD) of 832-935 μ m/m²/s and full saturation at >1000 μ m/m²/s (Coe & Sparks, 2014; Marschall & Proctor, 2004), the equivalent of about 36000-40000 lux and 43500 lux respectively. In this experiment, daytime lighting levels were just over the compensation point, at about 2.5% of full sunlight (1500-2500 lux).

Insufficient excitation of electrons due to light intensity levels below the compensation point is known to halt photosynthesis and activate dark

respiration processes, causing CO_2 loss from plant tissues and limiting growth (Glime, 2017). As a result, the CO_2 uptake rates recorded for this experiment show the lowest range of photosynthetic capacity for the moss species, which was about 5.84 ppm/m²/s. The sudden switch from light to darkness was followed by increased levels of CO_2 and humidity within the device, which indicates dark respiration (Zotz et al., 2000).

The optimal temperature levels for *S. ruralis* range between 10 - 20°C, while at temperatures above 25-35°C, the organism's photosynthetic activity becomes inhibited by a series of biochemical, physiological and environmental factors, which include increased respiration rates and the reduction of water availability due to faster evaporation (Coe et al., 2012). The daytime temperature within the monitoring device was around 30°C, exceeding the optimal range for this species and consequently creating unfavourable conditions for photosynthesis.

The photosynthetic performance of *S. ruralis* must be assessed against suboptimal conditions since the negative carbon balance was influenced by the low light intensity paired with high temperature and limited water availability. Due to *in vivo* yearly climatic dynamics, which include irradiance factors, temperature oscillations, and magnitudes and length of rain events, biocrust mosses may not always maintain a positive annual carbon balance (Coe & Sparks, 2014), and the results from this 3-week experiment showed how variations in humidity, light and temperature below or above optimal levels affect the carbon balance of wall-dwelling moss *S. ruralis*. In this context, bioreceptive design projects that seek to sequester CO₂ from urban environments through moss biocolonisation need to include strategies for maintaining environmental conditions within optimal ranges to match the ecophysiological needs of selected species.

4.2 Device optimisation and further research

The environmental variables monitored in this experiment were generated by the plant growth chamber with pre-set schedule and a single watering event, setting a predictable rhythm of photosynthesis. However, temperature, moisture, and lighting conditions vary more widely across days and seasons in the outdoor environment. Introducing wider variations in light intensity, temperature, and water availability would allow for more correlations and a higher resolution in understanding optimal conditions for maximum photosynthetic rates in mosses.

Further calibration of the camera hardware and software enabling automated tracking of total green surface area measurements would allow photosynthetic rates to be calculated in real-time. Script amendments, including automatic NDVI gradient analysis, will generate more accurate results on the photosynthetic potential of different moss species. At the same time, the assessment of relative photosynthetic rates for larger biocolonised

surfaces and different mosses growing *in vivo* could be done remotely (Graham et al., 2006; Young & Reed, 2017).

Data gathered from similar experiments testing other urban moss species may contribute to a standardised model for identifying optimal environmental conditions. This is necessary for identifying and evaluating the potential of other mosses to propagate and thrive on building materials. The designed monitoring device is a prototype tool for simulating the interaction between different *in vivo* environmental variables and the photosynthetic behaviour of cryptogams in dynamic microclimatic settings. This research constitutes a critical step toward a data-driven bioreceptive design practice based on biological experimentation (Cruz & Beckett, 2016), where the needs of particular moss species are captured and analysed through quantitative research, beginning to drive what can be seen as a biocentric approach to both design and material bioreceptivity.

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References

- Anderson, M., Lambrinos, J., & Schroll, E. (2010). The potential value of mosses for stormwater management in urban environments. *Urban Ecosystems*, 13(3), 319– 332. https://doi.org/10.1007/s11252-010-0121-z
- Bazzaz, F., Paolillo, D., & Jagels, R. (1970). Photosynthesis and Respiration of Forest and Alpine Populations of *Polytrichum juniperinum*. *American Bryological and Lichenological Society*, 73(3), 579–585.
- Burgheimer, J., Wilske, B., Maseyk, K., Karnieli, A., Zaady, E., Yakir, D., & Kesselmeier, J. (2006). Relationships between Normalized Difference Vegetation Index (NDVI) and carbon fluxes of biologic soil crusts assessed by ground measurements. *Journal of Arid Environments*, *64*(4), 651–669. https://doi.org/10.1016/j.jaridenv.2005.06.025
- Coe, K. K., Belnap, J., Grote, E. E., & Sparks, J. P. (2012). Physiological ecology of desert biocrust moss following 10 years exposure to elevated CO₂: Evidence for enhanced photosynthetic thermotolerance. *Physiologia Plantarum*, *144*(4), 346–356. https://doi.org/10.1111/j.1399-3054.2012.01566.x
- Coe, K. K., & Sparks, J. P. (2014). Physiological Ecology of Dryland Biocrust Mosses. In D. T. Hanson & S. K. Rice (Eds.), *Photosynthesis in Bryophytes and Early Land Plants* (pp. 291–308). Springer. https://doi.org/10.1007/978-94-007-6988-5

- Cruz, M. (2021). Design for Ageing Buildings. In L. Duanfang (Ed.), *The Routledge Companion to Contemporary Architectural History* (pp. 384–400). Routledge.
- Cruz, M., & Beckett, R. (2016). Bioreceptive design: A novel approach to biodigital materiality. *Architectural Research Quarterly*, 20(1), 51–64. https://doi.org/10.1017/S1359135516000130
- Delgado-Baquerizo, M., Maestre, F. T., Eldridge, D. J., Bowker, M. A., Jeffries, T. C., & Singh, B. K. (2018). Biocrust-forming mosses mitigate the impact of aridity on soil microbial communities in drylands: observational evidence from three continents. New Phytologist, 220(3), 824–835. https://doi.org/10.1111/nph.15120
- Delgado-Baquerizo, M., Morillas, L., Maestre, F. T., & Gallardo, A. (2013). Biocrusts control the nitrogen dynamics and microbial functional diversity of semi-arid soils in response to nutrient additions. *Plant and Soil*, 372(1–2), 643–654. https://doi.org/10.1007/s11104-013-1779-9
- Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M. O., & Pöschl, U. (2012). Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nature Geoscience*, *5*(7), 459–462. https://doi.org/10.1038/ngeo1486
- Field, C. B., Ball, T. J., & Berry, J. A. (1989). Photosynthesis: Principles and field techniques. In R. W. Pearcy, J. Ehleringer, H. A. Mooney, & P. W. Rundel (Eds.), Plant Physiological Ecology. Field methods and instrumentation (pp. 209–253). Chapman and Hall.
- Glime, J. (2017). Photosynthesis: The Process. In J. Glime (Ed.), *Bryophyte Ecology, Volume 1: Physiological Ecology* (Vol. 1). Michigan Tech. http://digitalcommons.mtu.edu/bryophyte-ecology/
- Graham, E. A., Hamilton, M. P., Mishler, B. D., Rundel, P. W., & Hansen, M. H. (2006). Use of a networked digital camera to estimate net CO2 uptake of a desiccation-tolerant moss. *International Journal of Plant Sciences*, 167(4), 751–758. https://doi.org/10.1086/503786
- Griffin-Nolan, R. J., Zelehowsky, A., Hamilton, J. G., & Melcher, P. J. (2018). Green light drives photosynthesis in mosses. *Journal of Bryology*, 40(4), 342–349. https://doi.org/10.1080/03736687.2018.1516434
- Guillitte, O., & Dreesen, R. (1995). Laboratory chamber studies and petrographical analysis as bioreceptivity assessment tools of building materials. *Science of the Total Environment*, 167(1–3), 365–374. https://doi.org/10.1016/0048-9697(95)04596-S
- Heimans, J. (1954). L' accessibilité, terme nouveau en phytogéographie. *Vegetatio*, 5(1), 142–146.
- Hornschuh, M., Grotha, R., & Kutschera, U. (2006). Moss-associated methylobacteria as phytosymbionts: An experimental study. *Naturwissenschaften*, *93*(10), 480–486. https://doi.org/10.1007/s00114-006-0137-7
- Manso, S., De Muynck, W., Segura, I., Aguado, A., Steppe, K., Boon, N., & De Belie, N. (2014). Bioreceptivity evaluation of cementitious materials designed to stimulate biological growth. Science of the Total Environment, 481(1), 232–241. https://doi.org/10.1016/j.scitotenv.2014.02.059

- Marschall, M., & Proctor, M. C. F. (2004). Are bryophytes shade plants? Photosynthetic light responses and proportions of chlorophyll a, chlorophyll b and total carotenoids. *Annals of Botany*, *94*(4), 593–603. https://doi.org/10.1093/aob/mch178
- Osaki, S., & Nakatsubo, T. (2021). Effects of climate warming on the production of the pioneer moss *Racomitrium japonicum*: seasonal and year-to-year variations. *Journal of Plant Research*, *134*(1), 115–126. https://doi.org/10.1007/s10265-020-01240-w
- Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution*, *20*(9), 503–510. https://doi.org/10.1016/j.tree.2005.05.011
- Sanmartín, P., Miller, A. Z., Prieto, B., & Viles, H. A. (2021). Revisiting and reanalysing the concept of bioreceptivity 25 years on. *Science of the Total Environment*, 770, 145314. https://doi.org/10.1016/j.scitotenv.2021.145314
- Schauer, S., & Kutschera, U. (2011). A novel growth-promoting microbe, Methylobacterium funariae sp. nov., isolated from the leaf surface of a common moss. Plant Signaling & Behaviour, 6(4), 510–515. https://doi.org/10.4161/psb.6.4.14335
- Tuba, Z., Csintalan, Z., & Proctor, M. C. F. (1996). Photosynthetic responses of a moss, *Tortula ruralis*, *ssp. ruralis*, and the lichens *Cladonia convoluta* and *C. furcata* to water deficit and short periods of desiccation, and their ecophysiological significance: A baseline study at present-day CO₂ concentration. *New Phytologist*, 133(2), 353–361. https://doi.org/10.1111/j.1469-8137.1996.tb01902.x
- Valle, B., Simonneau, T., Boulord, R., Sourd, F., Frisson, T., Ryckewaert, M., Hamard, P., Brichet, N., Dauzat, M., & Christophe, A. (2017). PYM: A new, affordable, image-based method using a Raspberry Pi to phenotype plant leaf area in a wide diversity of environments. *Plant Methods*, 13(1), 1–17. https://doi.org/10.1186/s13007-017-0248-5
- Watkins, H., Robinson, J. M., Breed, M. F., Parker, B., & Weinstein, P. (2020). Microbiome-Inspired Green Infrastructure: A Toolkit for Multidisciplinary Landscape Design. *Trends in Biotechnology*, *xx*(xx), 4–7. https://doi.org/10.1016/j.tibtech.2020.04.009
- Young, K. E., & Reed, S. C. (2017). Spectrally monitoring the response of the biocrust moss *Syntrichia caninervis* to altered precipitation regimes. *Scientific Reports*, 7(July 2016), 1–10. https://doi.org/10.1038/srep41793
- Zotz, G., & Rottenberger, S. (2001). Seasonal changes in diel CO₂ exchange of three central European moss species: A one-year field study. *Plant Biology*, *3*(6), 661–669. https://doi.org/10.1055/s-2001-19363
- Zotz, G., Schweikert, A., Jetz, W., & Westerman, H. (2000). Water relations and carbon gain are closely related to cushion size in the moss *Grimmia pulvinata*. *New Phytologist*, *148*(1), 59–67. https://doi.org/10.1046/j.1469-8137.2000.00745.x