The Ecological Role of Mosses in Green Roof Systems: A Systematic Review

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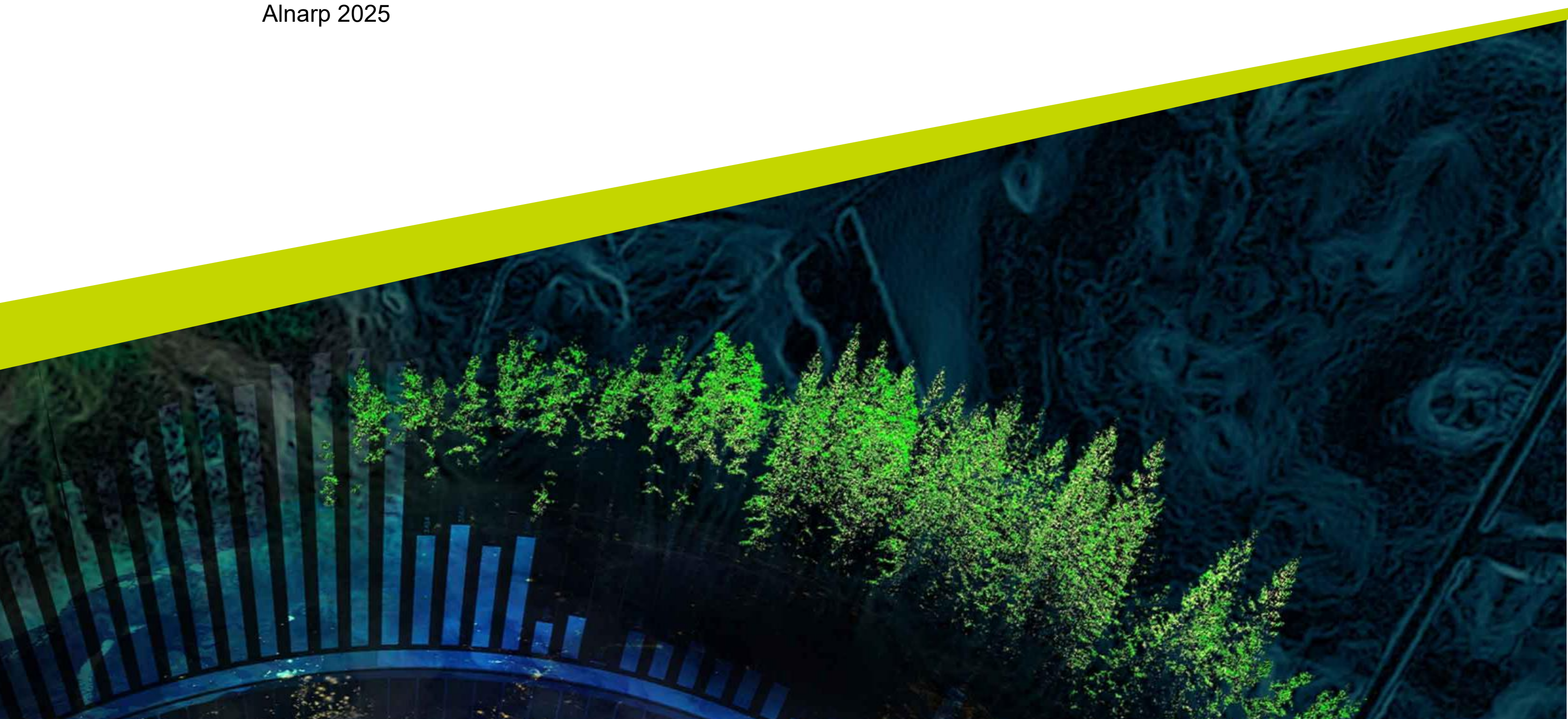

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Abstract

Green roofs are widely used on urban infrastructure, valued for their roles in stormwater management, temperature regulation, and habitat provision. While most research has focused on vascular plants, particularly *Sedum* species, mosses (bryophytes) remain comparatively understudied despite their frequent presence and ecological potential on extensive green roofs. This systematic literature review synthesizes findings from 37 peer-reviewed studies to assess the functional role of mosses in green roof ecosystems. It addresses five research questions concerning moss establishment, interactions with substrate properties, hydrological performance, growth form differences (acrocarpous vs. pleurocarpous), and interactions with vascular vegetation. Results reveal that mosses are not only frequent colonizers but also modify substrate conditions by enhancing moisture retention, reducing erosion, and buffering temperature extremes. Their poikilohydric physiology enables high water-holding capacity and rapid rehydration, contributing significantly to stormwater management. Growth form emerged as a critical functional trait, with acrocarpous species dominating in dry, exposed environments, while pleurocarpous species perform better under stable moisture conditions. Moss-vascular plant interactions were found to be highly context-dependent, shaped by substrate, microclimate, and species traits. Despite growing interest in bryophytes on green roofs, gaps remain in trait-based species selection, long-term performance data, and experimental studies of plant-plant interactions. This review provides a foundation for more intentional integration of mosses into green roof design and calls for expanded research to optimize their ecological function and practical application.

Keywords: moss, bryophyte, green roof, stormwater management, plant interactions, acrocarpous, pleurocarpous,

Table of contents

List of tables

List of figures

Abbreviations

Abbreviation	**Description**
ext.	extensive
int.	intensive
lab. con.	Laboratory conditions
man.	manipulative
MR	Meadow-Roof
obs.	observational
SMR	Sedum-Moss-Roof
TBS-RS	Trait based selection review study

1. Introduction

The concept of greening rooftops to mitigate environmental pressures in cities has evolved significantly over the past few decades. While the idea of rooftop vegetation dates back to ancient times, modern green roofs emerged in their current engineered form in Germany in the early 20th century, originally aimed at reducing fire hazards and physical damage to roof structures. Early versions involved layering sand and gravel over tar roofing, which was later colonized by vegetation, forming functional rooftop meadows (Getter & Rowe 2006; Oberndorfer et al. 2007).

This foundational phase was documented in early German works. Bornkamm (1961), for example, conducted one of the first ecological studies of spontaneously vegetated gravel roofs in Göttingen, Germany, demonstrating how substrate conditions shaped plant succession, from early ruderal colonizers to mosses, Sedum species, and eventually grassland communities on older, deeper roofs. His work illustrated the ecological potential of rooftops even without formal engineering and foreshadowed many principles of modern green roof design.

These and other early works paved the way for systematic green roof development, and by the 1970s, environmental policy shifts in Germany supported wider adoption. Technical guidelines were formalized in the 1980s by the Landscape, Research, Development and Construction Society (FLL), laying the groundwork for green roof design and implementation standards still used today.

Modern green roofs are best understood as engineered ecosystems, typically composed of multiple layers including drainage and filtration layers, a growing medium, and a vegetated layer (Getter & Rowe 2006; Oberndorfer et al. 2007). These systems are now widely recognized for their ability to provide a broad range of ecological services, such as reducing stormwater runoff, improving thermal insulation, extending roof membrane life, enhancing urban biodiversity, and contributing to urban climate regulation (Oberndorfer et al. 2007).

They are generally classified into two types based on their structural depth, vegetation type, and intended use: intensive and extensive. Intensive green roofs mimic traditional ground-level gardens with deeper substrates (typically over 20 cm), support a wide variety of vegetation including shrubs and small trees, and, as their name suggests, require intensive regular maintenance such as irrigation and fertilization. In contrast, extensive green roofs are shallower (usually less than 15 cm), lighter in weight, and designed to function with minimal maintenance. Their vegetation is typically limited to drought-tolerant, low-growing species such as Sedum species, mosses, and small (Getter & Rowe 2006; Oberndorfer et al. 2007).Due to their lower cost, reduced weight, and ease of installation, especially on existing buildings, extensive systems dominate green roof construction (Mann et al. 2021).

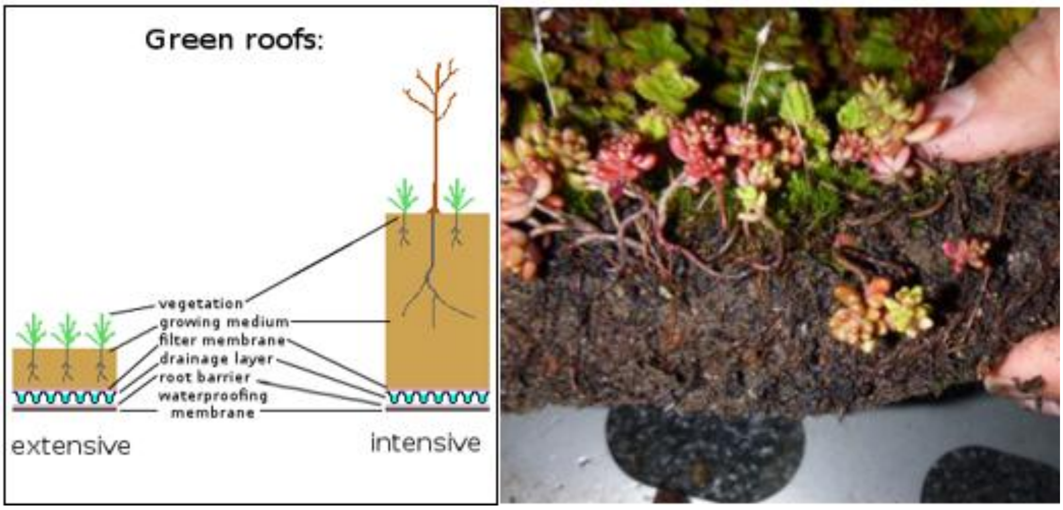

Figure 1 Structural comparison of extensive and intensive green roof systems (left) and a 2-year-old extensive Sedum roof (right). Diagram by Genetics4good 2014*, CC BY-SA 4.; photo by Mark* Mitchell.

Figure 2 Extensive green roof in Geneva, Switzerland. Photo by World Intellectual Property Organization, CC BY 2.0 (World Intellectual Property Organization 2021a).

Germany remains a global leader in green roof adoption. According to the Bundesverband GebäudeGrün e.V. (BuGG), approximately 7.84 million square meters of green roof area were added in 2020 alone, with extensive systems accounting for 82.1% of this new. Over the period from 2008 to 2020, more than 66 million square meters of green roof area were installed nationwide, with an estimated total inventory of 110-130 million square meters when including both extensive and intensive green roofs.

These extensive roofs, though primarily installed for functional benefits like stormwater retention and temperature regulation, have also become important sites for plant ecological dynamics. Despite being engineered and under harsh conditions in terms of shallow soils, exposure to heat, and water scarcity, they support a unique composition of flora often distinct from that of ground-level habitats.

Vascular plant communities on extensive roofs are commonly structured around drought-tolerant succulents from the *Sedum* genus, including *S. album*, *S. acre*, *S. spurium* (often reclassified as *Phedimus spurius*), and *S. reflexum*, valued for their shallow root systems and ability to withstand prolonged desiccation (Getter & Rowe 2006; Oberndorfer et al. 2007; Todeschini & Fett-Neto 2025). However, as highlighted in a recent global review of green roof vegetation, the composition of vascular plants on these roofs is typically broader and includes additional succulents such as *Sempervivum* and *Delosperma*, herbaceous forbs from families like Asteraceae (*Euphorbia*, *Solidago*), and drought-tolerant grasses from Poaceae, including *Festuca ovina* and *Poa compressa* (Todeschini & Fett-Neto 2025). These taxa represent dominant plant families frequently cited in green roof research and reflect a general trend toward multispecies assemblages. Such combinations not only maintain the low-maintenance and stress-tolerant qualities of Sedum-based systems but also contribute to enhanced stormwater retention, biodiversity, and functional resilience across a range of climatic and urban contexts (Todeschini & Fett-Neto 2025).

It is within this context that mosses, non-vascular, desiccation-tolerant plants, are increasingly gaining attention as an alternative or complementary green roof vegetation type, especially in thin, low-input systems where traditional vascular plants may struggle.

Figure 3 Typical Sedum plants on green roof. Photo by World Intellectual Property Organization, CC BY 2.0 (World Intellectual Property Organization 2021b).

Mosses, members of the division Bryophyta, are small, non-vascular land plants that occupy a wide range of environments, from temperate forest floors to exposed rock surfaces and urban rooftops. Unlike flowering plants or ferns, mosses lack specialized vascular tissues such as xylem and phloem, which in vascular plants conduct water and nutrients internally. Instead, mosses absorb water and minerals directly across the surface of their tissues, particularly the leaves and stem-like structures of the gametophyte, the dominant stage in their life (Vanderpoorten & Goffinet 2009). This fundamental physiological trait shapes many aspects of moss ecology and adaptation.

A defining feature of mosses is their poikilohydric nature. Rather than controlling their internal water content, they adjust to the surrounding moisture level. In the presence of water, mosses perform photosynthesis and growth. During dry periods, they enter a reversible dormant state, often losing nearly all cellular water without sustaining damage. Once rehydrated, metabolic activity resumes within a short period of time, a survival strategy that allows them to withstand extreme fluctuations in water availability and temperature (Vanderpoorten & Goffinet 2009).

These physiological characteristics allow mosses to colonize nutrient-poor, shallow, and dry substrates, making them well suited to the extreme conditions often present on extensive green roofs. Their establishment does not rely on deep rooting or fertile soils, and they can persist with minimal external inputs, distinguishing them functionally from typical vascular green roof vegetation.

Mosses are commonly classified into two main growth forms: acrocarpous and pleurocarpous. Acrocarpous mosses tend to grow upright in compact, cushion-like tufts and are less strongly attached to the surface, while pleurocarpous mosses grow and spread laterally, forming mats that bind more securely to the substrate (Vanderpoorten & Goffinet 2009; Jang & Viles 2022). These structural differences have practical implications for their performance in green roof settings.

This review aims to synthesize the current state of knowledge on mosses in green roof ecosystems by examining both general trends across mosses as a functional group and variation among species, taxa, and growth forms. In particular, it considers how traits such as poikilohydry, growth form (acrocarpous vs. pleurocarpous), and substrate affinity influence moss performance and ecological roles on rooftops. Through a systematic literature review, the following five research questions are addressed:

(1) How do mosses establish on green roofs, and how does their cover change over time?

(2) What are the effects of substrate characteristics (e.g. depth, composition, organic matter content) on moss growth, and how do mosses in turn influence substrate conditions?

(3) What role do mosses play in water retention and stormwater management on green roofs?

(4) What are the functional differences between acrocarpous and pleurocarpous mosses on green roofs?

(5) What are the facilitative or suppressive effects of mosses on other members of the plant community in green roof ecosystems?

2. Methods

A systematic literature review was conducted following the PRISMA 2020 guidelines (Fig. 4) (Page et al. 2021b; a). On March 26th 2025, searches were conducted in Web of Science (Core Collection) and Scopus using the following search string:

(“moss*” OR “bryophyte*” OR “non-vascular plant*”) AND (“green roof*” OR “vegetated roof*” OR “extensive roof*” OR “eco roof*” OR “eco-roof*”).

In both databases, results were restricted to peer-reviewed articles published in English, excluding preprints and review papers, which yielded 52 records in Web of Science and 66 records in Scopus. Titles and abstracts were then screened against predefined inclusion criteria, namely, studies reporting quantitative or qualitative ecological data on mosses (e.g., cover dynamics, growth rates, microclimate effects, or biotic interactions) within green roof contexts. This screening reduced the pool to 42 Web of Science and 48 Scopus records.

Full-text articles were assessed according to exclusion criteria: non-peer-reviewed or purely conceptual works; studies that did not address mosses; publications focused exclusively on engineering, architectural, or economic aspects without ecological data; review articles; and duplicate entries. After removing 27 duplicates and excluding ineligible studies, 37 unique articles remained for analysis.

From each selected article, the following information was extracted: publication metadata (authors, year, geographic location), methodological details (substrate type, moss species, and experimental or observational design), and all findings relevant to the research questions. Quantitative and qualitative data were integrated within each thematic narrative to ensure a clear, transparent, and reproducible synthesis.

Findings were grouped and interpreted thematically according to the five predefined research questions. Quantitative data (e.g. moss cover percentages, water retention rates) were reported where available, but the synthesis focused on identifying consistent patterns, species-specific responses, and ecological mechanisms relevant to green roof performance. More detailed information, such as study location, climate, substrate depth, whether mosses were introduced or colonized spontaneously, etc. were noted and are summarized in a table (Appendix A), which provides an overview of key methodological and environmental variables for each study.

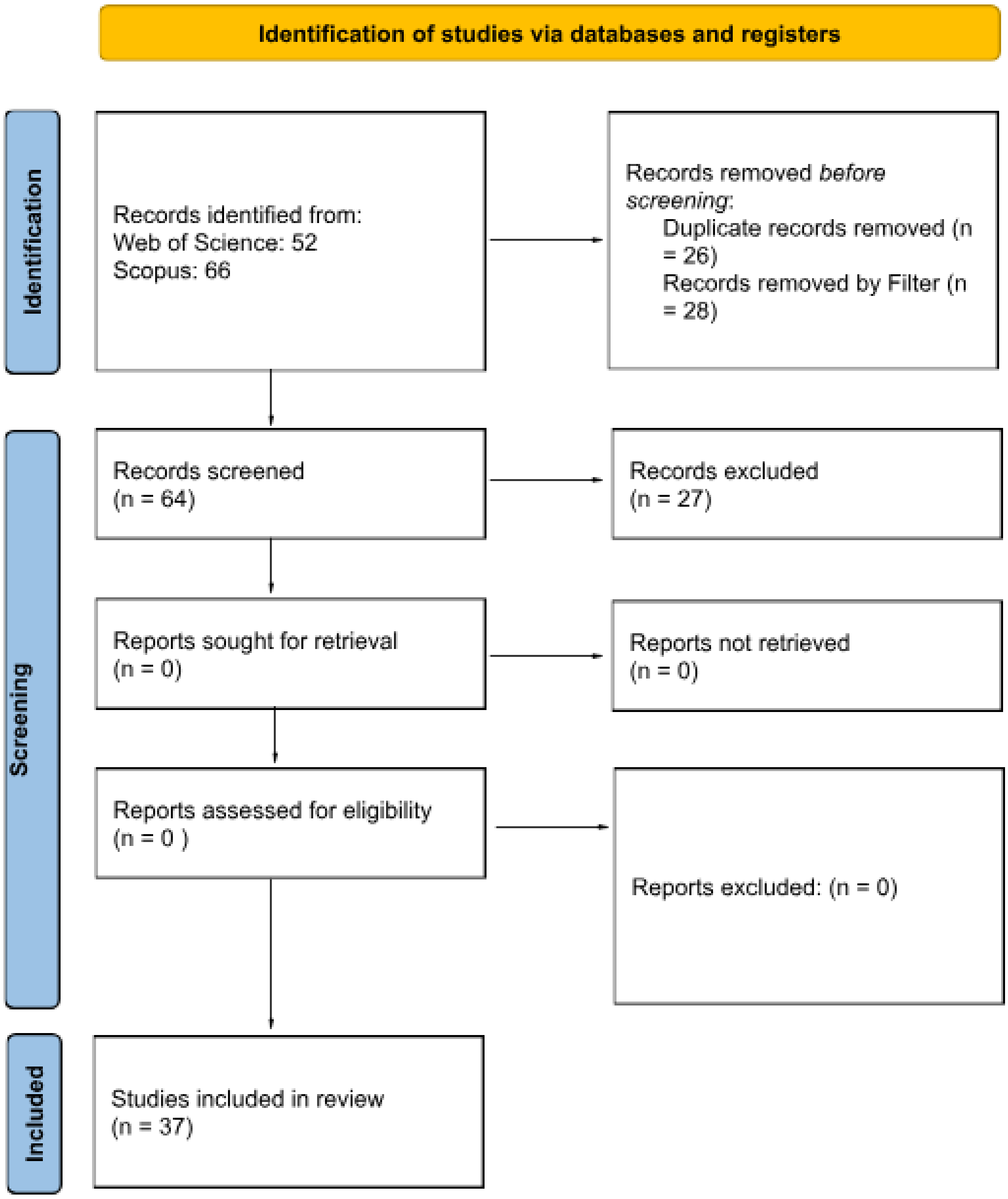

*Figure 4 PRISMA 2020 flow diagram for new systematic reviews (*PRISMA 2020 flow diagram — PRISMA statement *2025)*

3. Results

The 37 publications included in this review span from 2005 to 2025, with a notable increase in recent years. While early contributions were relatively limited and scattered, the number of studies gradually increased after 2014, peaking in 2023 with six publications. Both 2020 and 2021 also showed a higher number of publications, with five studies each (Fig. 5). However, it is important to note that these publications represent a subset of the wider green roof literature, specifically those retrieved using a specific search string focused on mosses and green roofs. Therefore, this trend likely reflects a rise in the number of green roof studies that include mosses in some capacity, rather than indicating a broader trend across the entire research field.

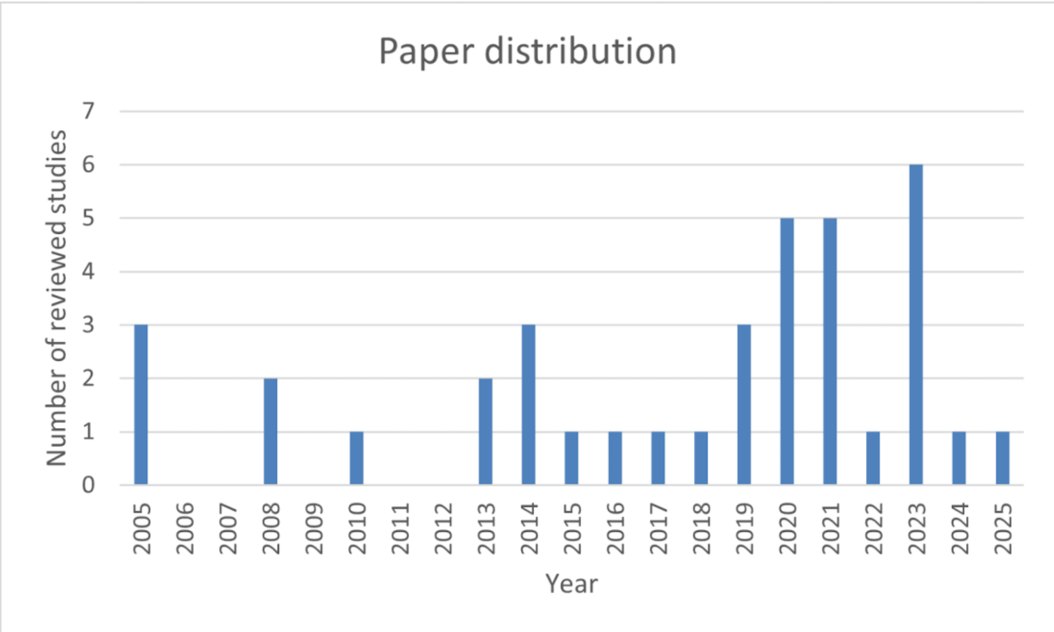

Figure 5 Publication range of studies included in the review

Geographically, these studies span many climate zones. Field investigations have been carried out in humid-continental settings such as southern Sweden and Halifax, in maritime or temperate-oceanic regions of the United Kingdom, Belgium and the Netherlands, in Mediterranean and sub-Mediterranean climates of Portugal, France, Italy and Türkiye, in humid-subtropical cities around Tokyo and in South Korea, and even in sub-arctic northern Sweden and Atlantic Canada. Interestingly, none of the included studies were conducted in the Southern Hemisphere (Fig. 6).

Figure 6 Geographic distribution of included studies. Point size is scaled to the number of publications at each location. Climate zones are categorized according to the Köppen–Geiger classification (Beck et al. 2023).

Roughly two-thirds of the papers report manipulative experiments in roof plots, or controlled-environment chambers, whereas the remainder describe observational surveys of plant and spontaneous cryptogam communities on existing roofs or conventional roofing materials. Only two studies function primarily as trait-based selection frameworks, and these were retained because they provide important species-screening criteria that are particularly relevant to Mediterranean conditions, but the framework in place can be applied worldwide. Almost every experimental field study was conducted on extensive systems with substrates no deeper than 15 cm; only two used 20 cm intensive beds. The body of evidence is therefore leaning toward the ext., low-maintenance green roofs.
Half of the manipulative trials tracked vegetation for no longer than two years, but much sparser for longer change. Nevertheless, four long-term monitoring papers analysed roofs between the ages of four to twenty-two and thus provide valuable insight into long term patterns. Reported substrate depths range from bare asphalt to 20 cm, but most fall between 3 cm and 10 cm depth. Organic-matter contents extend from strictly mineral media (0 %) to deliberately high levels of 73 %, although most experiments fall into the low-to-moderate band of roughly 3-15 % organic matter content. Several studies manipulate texture or organic inputs deliberately, providing comparative data for different substrate conditions.

Four thematic clusters can be observed within the literature: vegetation establishment/growth and succession, hydrological and thermal regulation, biotic interactions with plant and cryptogram communities, and species- or substrate-screening for drought-resilient design. Moss propagules were intentionally introduced in twenty-one studies, the remaining ones relied on spontaneous colonisation or observed cryptogams on unaltered roof surfaces.

3.1 Moss Establishment and Cover Dynamics

Mosses have demonstrated strong potential to establish and persist on green roofs across a wide range of climates, substrate compositions, and roof types, and they show considerable variation in their establishment dynamics and patterns of cover development. Across a wide range of studies, a recurring trend is the rapid colonization potential of mosses under suitable conditions. For instance, *Leucobryum japonicum* reached 70–80% cover within just four months and maintained high survival despite drought in a rooftop tray experiment in Chiba, Japan, where moss fragments were pressed into 4 cm of substrate and left unirrigated after initial establishment. *Polytrichum commune*, under the same conditions, achieved 40–90% cover. By contrast, *Eurhynchium hians* displayed fluctuating cover under drought conditions, and *Didymodon constrictus* showed consistently low establishment across all substrates, possibly reflecting its natural preference for rocky surfaces. All trays were covered with a wind break net during the establishment period, a common propagation practice that reduced wind exposure for over a year. While not an experimental treatment, this setup may have influenced early establishment dynamics across species (Nagase et al. 2023).

Similarly, Dunnett et al. (2008) observed that mosses reached over 50% cover in their first season in shallower substrates, particularly, where moisture stress might limit vascular plant competition. Moss establishment was frequently observed as a precursor to successional changes. Some studies have found that mosses can be early colonizers, contributing significantly to early biomass and facilitating subsequent cryptogam and potential vascular plant succession (Kawakami et al. 2013). However, in harsher or more exposed environments, such as shallow substrates or drought-prone sites, mosses often persisted as the dominant ground cover over time where vascular plants failed to establish or survive (Gabrych et al. 2016; Lönnqvist et al. 2021).

Microclimate conditions, particularly roof exposure, were shown to strongly influence moss establishment. Bryophyte-rich communities were more commonly found on shaded roofs, whereas exposed roofs favoured more stress-tolerant species such as *Syntrichia ruralis* (Aszalósné Balogh et al. 2023). Higher moss cover was also observed in sheltered plots with shallow substrates, indicating that protection against exposure to solar radiation might enhance moss development (Van Mechelen et al. 2015).

On two brown roofs in Birmingham, UK, specifically designed to emulate brownfield habitats by using recycled demolition aggregates in a low-nutrient substrate, Bates et al. (2013) conducted a four-year study tracking vegetation development under varying rooftop conditions. Moss cover increased steadily over time, particularly in areas with finer-textured substrates. By the end of the study, mosses covered over 50% of the surface in these microhabitats, while coarse, rubble-dominated areas showed little moss establishment and remained largely bare. The addition of compost proved especially important. In both coarse and fine substrates, compost amendments led to dramatic increases in moss coverage, even enabling establishment in otherwise unfavourable coarse substrates. This suggests that even small increases in organic matter can significantly enhance moss development, likely by improving moisture availability. Mosses also showed high resilience during drought periods, maintaining cover while several vascular plant species declined. Rather than facilitating vascular growth, mosses tended to dominate in fine-grained, low-nutrient patches, whereas vascular diversity persisted more in coarse areas without moss cover. Overall, the study highlights how mosses can become dominant over time under the right surface conditions and low-input regimes typical of extensive brown roofs (Bates et al. 2013).
At the same time, mosses are inherently well-adapted to extreme conditions, particularly drought, which provides them with a competitive advantage over vascular plants during early stages of colonization (Kawakami et al. 2013). A comprehensive trait-based survey of Mediterranean bryophytes identified a consistent set of ecological strategies among successful green roof species. These included a predominance of acrocarpous forms (84 %), turf or cushion life-forms (79 %), and colonist or perennial life-history strategies (93 %). Such traits promote both rapid establishment and moisture retention, with structures that stabilize under fluctuating humidity and reduce water loss (Cruz de Carvalho et al. 2019). Cosmopolitan pioneers like Bryum argenteum and *Tortula muralis*, which are widely distributed and drought-resilient, show this ability to adapt. These findings highlight the potential of mosses to establish and persist even in exposed and low-irrigation environments and are consistent throughout the literature (Vanuytrecht et al. 2014; Cruz de Carvalho et al. 2019; Paço et al. 2019).
As with microclimate conditions, the speed and pattern of moss establishment can be highly species-specific, with some species consistently emerging as early colonizers that sustain long-term cover. *Ceratodon purpureus*, for instance, appeared frequently in early successional stages and maintained substantial coverage for over four years, even under challenging conditions such as drought and heatwaves, highlighting the resilience of specific moss species to green roof stresses. (Gabrych et al. 2016; Burszta-Adamiak et al. 2019; Schröder & Kiehl 2020, 2021)

In addition, when compared directly, introduced mosses established faster and more robustly than spontaneously colonizing populations. In experimental plots where mosses were introduced through raked vegetation material, cover reached 46.5% by the second year and maintained a thicker vertical layer, in contrast to only 15% cover in plots with spontaneously established acrocarpous mosses (Schröder & Kiehl 2021). These thicker moss layers were typically dominated by pleurocarpous species such as *Hypnum cupressiforme, Scleropodium purum*, and *Brachythecium albicans*, while spontaneous colonizers often included thinner, low-growing species like *Bryum argenteum* and *Ceratodon purpureus*. The origin and handling of moss material also influenced establishment success. Wild-harvested mosses outperformed lab-grown specimens on sheltered roofs in Atlantic Canada, with the latter suffering from transplant shock and slower recovery (Haughian & Lundholm 2024). These findings also demonstrate that not all moss establishment efforts are successful. The same study reported complete mortality of mosses on exposed rooftops due to wind and drought stress, highlighting the vulnerability of certain species in harsh, unprotected microhabitats (Haughian & Lundholm 2024).

In Japan, Kawakami et al. (2013) even demonstrated successful moss establishment under near-soilless conditions, while in Atlantic Canada, Haughian and Lundholm (2024) highlighted the potential for mosses to colonize asphalt directly. These findings, while preliminary in some cases, support the notion that moss-only or moss-complemented green roof systems could offer a low-maintenance alternative to vascular-based vegetation, particularly in weight- or water-limited contexts.

Moss cover patterns evolved over time, often reflecting broader ecological processes such as succession. In many cases, mosses gradually became the dominant functional group. For example, mosses overtook vascular plants as the primary ground cover by the third or fourth year in long-term studies (Schröder & Kiehl 2020, 2021) and moss cover correlated positively with succulent cover (e.g., Sedum spp.) and negatively with vascular plant species richness in the Mediterranean (Van Mechelen et al. 2015). A similar shift was noted by Gabrych et al. (2016) and Mitchell et al. (2021), where older roofs became increasingly moss-dominated, and moss cover positively correlated with roof age. Lönnqvist et al. (2021) observed moss cover exceeding 60% on younger roofs and reaching up to 82% on older ones, supporting the trend that mosses increasingly dominate on older roofs. Additionally, Vidaller et al. (2023) found that mosses became the principal vegetation type in exposed areas where vascular plants declined, highlighting mosses' ability to adapt and thrive in high-stress environments over time.

3.2 Effects of Substrate Characteristics on Moss Growth

A number of field and tray experiments across Europe demonstrate that mosses establish readily on substrates with relatively low organic matter content, and that only modest amendments are needed to support long-term cover. In Malmö, Sweden, Emilsson (2008) compared 4 cm-deep trays of crushed-tile substrates amended to 3 % versus 10 % organic matter as well as a commercial lava-and-peat mix and found that moss cover not only increased steadily in all treatments but exceeded 80 % by the end of the 3-year trial, showing that substrates with only a few percent organics matter can sustain moss growth. Likewise, in Wrocław, Poland, Burszta-Adamiak et al. (2019) achieved 60–73 % moss cover over four years on a 7 cm-deep commercial medium containing just 2 % organic matter; these moss layers persisted through droughts and heatwaves without any irrigation or fertilization. In Birmingham, UK, Bates et al. (2013) manipulated compost additions (0 %-15 %) within fine- and coarse-grained recycled demolition aggregates (4-12 cm depths). They found that both fine + compost and coarse + compost treatments reached the highest early moss cover, whereas unamended coarse substrates never supported substantial moss cover and unamended fine substrates lagged until the third year, showing that even small organic amendments can make the difference between bare ground and substantial moss cover.

Taken together, these studies indicate that substrates containing as little as 2–10 % organic matter, when combined with a suitable mineral base, can be sufficient for moss establishment and sustained cover on green roofs. However, organic content alone does not determine substrate suitability. Other physical properties, like porosity and water-holding capacity, also play an important role in shaping moss performance under rooftop conditions.

3.3 Porosity and Water-Holding Capacity

Across the reviewed studies, substrate porosity and water-holding capacity showed importance in shaping moss growth on green roofs. Substrates with moderate to high capillary properties generally favoured moss establishment, while poorly retentive materials often constrained moss persistence (Perini et al. 2020; Nagase et al. 2023)

Nagase et al. (2023) examined moss performance on different substrate types, demonstrating the relationship between substrate moisture retention and moss survival. Specifically, substrates like clay/compost mixtures supported increased moss growth due to their higher organic content and associated moisture retention capacity. By contrast, river sand, characterized by its low water-holding capacity, severely constrained moss establishment and growth, especially affecting more moisture-dependent species like *Polytrichum commune*. Interestingly, some moss species such as *Racomitrium japonicum* showed a broader tolerance, growing similarly well across substrates, indicating variability among species regarding their reliance on substrate water retention properties (Nagase et al. 2023).

These findings align with Perini et al. (2020), who conducted a comparative study on several construction materials in Genoa, Italy, and found that moss cover was highest on surfaces with high water retention capacity and porosity. Capillary matting and lime/cement plasters supported moss coverage of 72 % and 67 %, respectively, while quartzite, a low-porosity and fast-draining substrate, achieved only 8 % coverage, showing how substrates, capable of retaining more moisture, can enhance moss establishment and cover.

Additionally, Deska et al. (2020) showed that moss survival was limited in thin substrates (~3 cm) that dried out rapidly, highlighting the importance of sustained moisture availability for early establishment. However, the same study also found that as moisture-enhancing amendments like hydrogels lost effectiveness over time, the resulting stress conditions eventually promoted moss colonization. This indicates that while an initial lack of water can limit moss growth, prolonged substrate stress and therefore reduced competition, may later create favourable conditions for moss establishment. In this context, mosses may act as indicators of declining substrate performance, particularly with respect to water retention capacity.

Conversely, Van Mechelen et al. (2015) observed that green roofs with a water retention layer beneath the substrate supported lower moss cover compared to those without one. While such layers are designed to increase overall water-holding capacity, the authors suggested that the retention layer may have drawn moisture downward too quickly, reducing the availability of water near the substrate surface, where mosses absorb moisture. This shift may have resulted in drier surface conditions that hindered moss establishment. Additionally, green roofs with water retention layers also tended to support higher vascular plant cover, which might have increased competition for light, space, or nutrients. Together, these factors may have contributed to the lower moss cover observed, suggesting that both altered surface moisture dynamics and increased vascular plant performance could play a role under such conditions.

3.4 Substrate Depth

In addition to porosity and water holding capacity, substrate depth also plays an important role in moss establishment and development. Multiple studies indicate that mosses often achieve greater cover in shallower substrates, not necessarily because of the depth itself, but due to the reduced competition and distinct moisture dynamics associated with thinner growing media (Dunnett et al. 2008; Gabrych et al. 2016).

In Sheffield, Dunnett et al. (2008) found that moss cover reached an average of 52.9 % in 10 cm deep substrates, more than twice the 20.8 % observed in deeper 20 cm trays. This difference was primarily attributed to reduced competition from vascular plants, which were less able to establish in the more moisture-stressed shallow layers, creating open patches more easily colonized by mosses. A similar pattern emerged in the study by Van Mechelen et al. (2015), where bryophyte cover peaked on 5 cm substrates without water retention layers, especially in sheltered plots. In contrast, 10 cm substrates with retention layers supported denser vascular vegetation, likely suppressing mosses through competition.

Supporting the viability of even thinner substrates, Mitchell et al. (2021) observed substantial moss accumulation on green roofs with just 2.5–3 cm of substrate, highlighting mosses' ability to dominate low-input systems over time. Gabrych et al. (2016) examined a broader range of depths (2–24 cm) on sedum-moss and meadow roofs in Helsinki and found only a slight, statistically non-significant increase in moss abundance with depth. This suggested that other factors, such as roof age, dispersal opportunities, or plant competition, may be equally or more important than substrate depth alone as determinants of moss cover.

In subarctic and continental climates, Lönnqvist et al. (2021) documented moss cover exceeding 60 % on younger roofs and up to 82 % on older ones with lightweight substrates between 3-10 cm. While vascular plant cover and species richness increased with depth, mosses continued to dominate wherever competition remained limited, further reinforcing that shallow substrates may indirectly benefit mosses by restricting vascular plant species.

Finally, long-term observations Burszta-Adamiak et al. (2019) showed moss persistence on shallow 7 cm substrates composed of expanded clay, lava, and brick, even in the absence of irrigation. These findings collectively indicate that while deeper substrates may offer more stable moisture availability, moss performance is more consistently shaped by the interplay of multiple factors like competition, microclimate, and stress tolerance factors.

3.5 Substrate Composition & Texture

Building on the importance of moisture dynamics and depth discussed above, the mineral makeup and grain size of green-roof substrates can be equally important for moss success, yet they operate through slightly different mechanisms than depth or porosity alone. Rather than simply holding water, the texture of a substrate determines where and for how long that moisture stays and how easily mosses can anchor on the substrate.

Fine-textured, moderately porous media, such as crushed tile or scoria blends, support continuous bryophyte mats by offering capillary cracks that pull water to the surface. For example, Emilsson (2008) showed that crushed-tile substrates with only 3-10 % organic matter supported moss over of 80 % within two years and held steady thereafter. In the UK's brown roofs, Bates et al. (2013) found that fine-grained crushed aggregates (e.g. brick, sand, concrete) supported dense (> 50 %) moss mats, while the same roof's large brick and concrete fragments created dry, bare-ground microhabitats, valuable for biodiversity but not for blanket bryophyte cover.

Conversely, coarse media can still serve mosses by creating moisture refugia beneath clasts. Coarse aggregate resisted direct colonization yet maintained water pockets under overhangs, supporting small, persistent plant colonies and maintaining plant diversity even during drier conditions (Bates et al. 2013). Similarly, Burszta-Adamiak et al. (2019) demonstrated that a low-fertility mix of lava, pumice, gravel, and brick (2 % organic matter) sustained moss layers for four years without irrigation, emphasising the adaptation of mosses to extreme conditions.

On the flat roofs of Debrecen, Hungary, Aszalósné Balogh et al. (2023) surveyed cryptogamic communities across ten urban rooftops differing in age, exposure, and construction material. The study found that *Racomitrium canescens*, a stress-tolerant acrocarpous moss, was almost exclusively associated with siliceous substrates, particularly coarse gravel fractions ranging from 10 to 60 mm laid over bituminous felt. The species' occurrence on these acidic, mineral-rich surfaces, and absence from concrete-based (calcareous) rooftops, shows its acidophilous preference and ecological affinity for well-drained, nutrient-poor microhabitats. This points to the importance of chemical composition and substrate pH, not just texture or grain size, in shaping moss species distribution, but more research is needed in that regard.

In contrast, broader ecological generalists like *Bryum argenteum* and *Ceratodon purpureus* demonstrated greater adaptability across diverse substrate types. As reported in the Mediterranean-wide trait-based analysis by Cruz de Carvalho et al. (2019), both species were recorded in over 27 countries, colonizing a variety of rooftop materials, including scoria, pumice, crushed tile, and even lime-based concrete. This survey characterized the prevailing traits of green roof mosses in the region, identifying species that were most frequently observed across a wide range of Mediterranean green roofs. *Bryum argenteum and Ceratodon purpureus* stood out as particularly successful, found on rooftops in over 27 countries. These two species were among the most commonly encountered and consistently exhibited traits typical of successful green roof mosses: an acrocarpous growth form, compact cushion or turf-like structure, and a life-history strategy adapted for colonization and long-term persistence. Their ability to establish on both fine and coarse mineral substrates, as well as tolerate a range of pH and moisture conditions, highlights their role as cosmopolitan species well-suited for green roofs with variable or harsh substrate conditions (Cruz de Carvalho et al. 2019). This functional versatility contrasts sharply with the habitat-specific requirements of specialists like *R. canescens*, highlighting not only the role of substrate chemistry and texture but also how species-specific traits, such as substrate affinity, stress tolerance, and growth form shape moss distribution and performance on green roofs (Aszalósné Balogh et al. 2023).

3.6 Effects of Moss on Substrate Properties

Mosses on green roofs may exert a range of effects on the substrates they colonize, potentially modifying substrate behaviour in ways that contribute to improved roof function and reduced maintenance requirements. While green roof research often focused on how substrate characteristics influence moss and plant establishment, an increasing number of studies suggest that mosses might also play an active role in stabilizing, hydrating, and thermally insulating the substrate surface (Heim & Lundholm 2014; Paço et al. 2019; Nagase et al. 2023). These effects, though still under investigation in many contexts, have been observed across a variety of climates, roof types, and substrate compositions, indicating that mosses may function as subtle ecosystem engineers within green roof systems.

A key potential benefit of moss cover is surface stabilization. In this context, moss layers can help reduce substrate erosion by binding loose particles through their dense rhizoid networks and mat-forming growth habits. For instance,Nagase et al. (2023) reported that moss mats reduced particle displacement in 4 cm-deep substrates in the Tokyo region, especially in those amended with clay or compost. Similar observations were made by Schröder and Kiehl (2021) in Germany, where cryptogam cover increased rapidly on lightly raked plots and bare substrate patches were nearly eliminated by year four. These moss mats appeared to contribute to substrate cohesion, particularly in porous or coarse-grained media where erosion might otherwise be more pronounced under wind or rainfall. In such coarser substrates, microhabitat effects may also arise. For example, Bates et al. (2013) found that while mosses did not fully colonize large aggregates, they did persist in moisture-retaining pockets within the substrate, suggesting that even partial cover could contribute to surface stability.

Thermal buffering is another shown potential benefit of moss colonization. Moss carpets can reduce substrate temperature fluctuations by shading the surface and increasing latent heat loss through evapotranspiration. Kawakami et al. (2013), working in Toyokawa, Japan, showed that *Racomitrium japonicum* reduced surface temperatures by up to 2 °C, with modelling results indicating a strong link between moss evapotranspiration and cooling. In Halifax, Heim and Lundholm (2014) found that moss and lichen treatments consistently exhibited lower substrate temperatures compared to bare or vascular-plant controls, likely due to shading and a mulching effect that moderated substrate temperature. This pattern was broadly supported by Family et al. (2020), who associated mosses' high leaf area index with increased radiative cooling and reduced thermal conductivity, potentially improving the insulating properties of rooftop surfaces. Although these thermal effects may vary by species and exposure, moss layers appear capable of contributing to surface temperature regulation under varying climate conditions.

In some contexts, mosses might also facilitate the establishment of vascular plants by creating favourable microclimates within the substrate. (Schröder & Kiehl 2021) observed increased vascular plant cover in plots where mosses and lichens had established from vegetative fragments, attributing this facilitation to lower surface temperature and moisture stress. However, facilitative interactions remain context-dependent and can be influenced by moss identity, substrate properties, and climate stressors.

Over longer time scales, mosses can support the substrate by dampening extremes in temperature and moisture, potentially slowing nutrient leaching or reducing physical weathering of the medium. In Malmö, Mitchell et al. (2021) reported stable moss cover over time on green roofs with only 2.5–3 cm of substrate depth, despite low organic content and minimal fertilization.

Mosses can also play a role in mediating hydrological performance by intercepting rainfall, retaining moisture at the substrate surface, and gradually releasing it to reduce peak runoff. Several studies report that cushion- or turf-forming mosses function like living sponges, absorbing water rapidly and slowing its movement through the substrate profile (Anderson et al. 2010; Paço et al. 2019). These effects, ranging from delayed runoff and enhanced surface moisture retention to increased water storage in shallow or low-input systems, have been observed across a variety of contexts (Bengtsson 2005; Brandão et al. 2017). Their hydrological functions, including contributions to stormwater regulation and evapotranspiration dynamics, are explored in more detail in the following section.

Finally, moss mats may also enhance substrate-level biodiversity by offering habitat and stable conditions for other organisms. In the Mediterranean setting of Avignon, Vidaller et al. (2023) recorded higher densities of mesofauna such as Springtails *(Collembola*) in moss-covered plots, likely due to the buffering effect of mosses on moisture availability. Whether these effects extend to broader ecosystem functioning remains to be tested, but they hint at the potential for moss layers to support biodiversity even in simplified green roof systems.

Taken together, the studies suggest that mosses might play an important, if often underrepresented, role in shaping the physical and biological functioning of green roof substrates. While the extent and consistency of these effects likely depend on moss species, substrate composition, and climatic conditions, the available evidence points to a substantial contribution by mosses to substrate stability, water regulation, thermal moderation, and ecological facilitation. Further research could help clarify the mechanisms involved and support more intentional integration of mosses into green roof design, particularly in systems aiming for high resilience with minimal inputs.

3.7 Mosses’ Role in Water Retention and Stormwater Management

Across the reviewed studies, mosses were found to enhanced water retention and contributed to the regulation of stormwater dynamics on green roofs. Owing to their poikilohydric physiology, mosses can absorb large amounts of water directly across their surfaces and tolerate complete desiccation, resuming metabolic activity when moisture returns (Cruz de Carvalho et al. 2019; Nagase et al. 2023). This capacity, combined with their high water-holding potential, typically retaining 8-10 times their dry weight in water, makes them especially effective at buffering short-term moisture fluctuations and delaying surface runoff (Anderson et al. 2010; Cruz de Carvalho et al. 2019; Paço et al. 2019). Through these mechanisms, mosses help moderate stormwater discharge and increase substrate resilience, particularly on shallow, extensive green roofs where deeper water retention is limited.

This functional capacity was clearly demonstrated by Anderson et al. (2010), who conducted comparative trials in Oregon using green roof modules planted with *Racomitrium canescens*. Moss-covered modules retained 12-24 % more stormwater than bare substrate or vascular-only roofs during natural rainfall events. The authors attributed this enhanced retention to surface-level water storage within the moss mat, which temporarily held rainwater and delayed runoff without depending on deeper substrate saturation.

Similar results were observed in Southern Europe. In Lisbon, Paço et al. (2019) found that moss-vascular plant mixtures exhibited 1.2 times higher evapotranspiration rates compared to vascular-only treatments. This increase suggested that mosses improved moisture availability in the upper substrate layers, contributing to prolonged plant activity. Furthermore, biocrust roofs, defined in the study as thin, living layers composed primarily of mosses, were able to survive extended dry periods without irrigation, reactivating quickly following seasonal rainfall due to the desiccation tolerance of their moss components. These biocrust-dominated roofs also contributed to flash flood mitigation, as moss layers stored water temporarily at the surface and slowed water movement into the substrate and drainage layers.

The stabilizing effect of mosses on stormwater dynamics was also highlighted by Brandão et al. (2017), who tested mixed-vegetation beds containing shrubs, grasses, and mosses under simulated rainfall in Lisbon. These mixed systems achieved near-complete retention of water during short-duration rain events, with many replicates in the moss-inclusive treatments retaining close to 100% of rainfall, outperforming vascular plant monocultures. The authors emphasized mosses' role in stabilizing moisture availability, particularly during high-intensity rainfall events where surface-level buffering is critical.

While few studies isolate mosses' hydrological effects completely from other vegetation, findings from Bengtsson (2005) offer insight into their function in sedum-moss combinations. On a 3 cm-deep green roof in Malmö, the annual runoff was reduced to 50 % of total rainfall, with a field capacity of 9 mm determining the threshold for runoff initiation. During rainfall events, runoff began only after this storage capacity was exceeded, and during summer, increased evapotranspiration further reduced discharge. Mosses, integrated into the thin vegetative layer, helped delay the onset of runoff, especially during short, intense rainfall events, contributing both to total runoff reduction and peak flow reduction.

These hydrological effects were supported by Nagase et al. (2023), who found that moss presence improved water retention across multiple substrate types. Mosses acted as a surface-level sponge, increasing moisture stability near the top of the substrate and reducing immediate water loss to runoff, especially important in shallow or fast-draining systems. As shown in earlier sections, this effect complements mosses' broader ecological role as low-input vegetation that buffers both thermal and hydrological stress in substrate-limited environments (Kawakami et al. 2013; Heim & Lundholm 2014).

Overall, mosses not only enhance stormwater retention capacity through their own biomass but also modify substrate hydrology by delaying saturation thresholds and increasing evaporation rates. Their physiological ability to absorb and hold large volumes of water, combined with their rapid rehydration and surface coverage, make mosses especially effective in managing stormwater on extensive green roofs.

Together, these studies demonstrate that mosses contribute meaningfully to stormwater regulation on green roofs through their ability to intercept, store, and gradually release water at the substrate surface. Their poikilohydric physiology and high water-holding capacity enable them to function as a hydrologically active layer that buffers short-term moisture fluctuations, delays the onset of runoff, and supports prolonged evaporation, effects particularly valuable in shallow or fast-draining systems. Whether integrated into mixed vegetation beds or forming biocrust-dominated layers, mosses enhanced water retention, reduced peak flows during high-intensity rainfall, and improved substrate moisture stability across a range of climatic contexts. While their hydrological impact is sometimes studied in combination with vascular plants, findings from moss-specific trials showed that even thin moss mats can retain significant volumes of water and prolong infiltration (Anderson et al. 2010; Cruz de Carvalho et al. 2019; Nagase et al. 2023). These traits position mosses as effective stormwater management regulators in extensive green roof systems, complementing their broader ecological role as low-input, stress-tolerant plants capable of improving both thermal and hydrological performance in substrate-limited environments (Kawakami et al. 2013; Heim & Lundholm 2014).

3.8 Growth Form and Function: Acrocarpous vs. Pleurocarpous Mosses

The ecological relevance of moss growth form becomes particularly apparent under the exposed and moisture-variable conditions of green roofs. While the basic distinction between acrocarpous and pleurocarpous mosses is well established, their contrasting growth strategies also shape how they respond to environmental stressors such as drought, substrate dryness, and radiation exposure. Acrocarpous species, with their compact, upright morphology, often dominate in arid or sun-exposed rooftop environments due to their higher desiccation tolerance. Pleurocarpous mosses, on the other hand, are typically more dependent on sustained surface moisture and tend to decline under extended dry periods unless sheltered or partially shaded (Cruz de Carvalho et al. 2019; Nagase et al. 2023). These functional differences play a key role in determining species distribution and persistence across roof types and climates.

Figure 7 Acrocarpous moss Bryum argenteum (top) and pleurocarpous moss Brachythecium rutabulum (bottom). Top image by Michael Becker (Becker 2005), CC BY-SA 3.0; bottom image by Scott Zona (Zona 2014),CC BY-NC 2.0

Nagase et al. (2023) provided detailed insights into the contrasting performances of acrocarpous and pleurocarpous moss species. The acrocarpous species *Racomitrium japonicum* and *Polytrichum commune* showed strong drought resilience, maintaining high coverage over two years (70–80%) despite moisture-limited conditions. This resilience was attributed to their upright growth forms and morphological adaptations, such as hyaline hair points in *R. japonicum*, which increase dew and fog collection, making it easier for the moss to stay hydrated. However, another acrocarpous moss, *Didymodon constrictus*, demonstrated poor establishment across all tested substrates, likely due to its specific habitat preference for rocky or concrete surfaces rather than soil-based substrates common on green roofs. In contrast, the pleurocarpous moss *Eurhynchium hians* showed highly variable coverage strongly tied to moisture availability. Rather than dying during dry periods, *E. hians* entered a dormant state, turning visibly brown when substrate moisture was lacking and rehydrating rapidly once water became available again. This pattern of browning and recovery, with green cover increasing again shortly after rewetting, highlights its dependence on stable surface moisture. With its horizontally spreading growth habit and limited structural adaptations, *E. hians* appears less equipped to persist through prolonged droughts common in exposed rooftop environments (Nagase et al. 2023).

Cruz de Carvalho et al. (2019) further support the suitability of acrocarpous mosses for drought-prone green roofs by showing that 84% of the species identified in Mediterranean regions had this upright, acrocarpous growth form. As discussed previously, this growth type is commonly associated with greater resilience to environmental stress, particularly under dry and exposed conditions (Nagase et al. 2023). Acrocarpous mosses are generally smaller than their pleurocarpous counterparts and form dense colonies that equilibrate more slowly with surrounding humidity. As a result, they tend to exist in distinct physiological states, either fully hydrated and metabolically active or desiccated and dormant, making them well-suited to environments with intermittent water availability (Cruz de Carvalho et al. 2019). These traits help explain why acrocarpous mosses are predominantly found in open, dry habitats, whereas pleurocarpous mosses are more common in shaded, moist environments. Widely distributed species like *Bryum argenteum* and *Tortula muralis* exemplify this adaptability and are frequently encountered across Mediterranean and temperate rooftop environments.

Building on these distinctions, (Veeger et al. 2025) observed further ecological differences in habitat preferences, noting that acrocarpous mosses like *Tortula muralis* were more common in exposed, sunlit locations, while pleurocarpous species such as *Brachythecium rutabulum* tended to occur in more shaded environments.

In sum, functional differences between acrocarpous and pleurocarpous mosses can significantly influence their performance and suitability on green roofs. Acrocarpous mosses, with their specialized structures and vertical growth forms, can offer greater drought tolerance and are better suited for exposed, low-maintenance roofs. In contrast, pleurocarpous mosses may require more shaded or irrigated conditions, where their horizontal growth can rapidly cover surfaces, provided moisture stress is limited. Nonetheless, species-level differences within growth forms remain, again emphasizing the need for careful consideration when selecting moss species for green roofs (Nagase et al. 2023).

3.9 Moss-Vascular Plant Interactions: Facilitation and Suppression

Facilitative and suppressive effects between mosses and vascular plant communities in green roof ecosystems vary considerably across studies, highlighting the context-dependent nature of these interactions.

Several studies indicate that mosses could facilitate the establishment and survival of vascular plants by improving microclimatic conditions. For instance, Schröder and Kiehl (2020, 2021) reported that cryptogam communities, comprising a mix of pleurocarpous mosses, acrocarpous mosses, and lichens, provided significant facilitative benefits on green roofs in Germany. In their experiment, plots treated with raked cryptogamic material developed a dense moss-lichen layer, which can reduce substrate evapotranspiration by limiting direct solar radiation and stabilizing moisture at the substrate surface. There was higher vascular plant cover during drought periods in those plots compared to non-raked plots, with vascular coverage being approximately three times greater (22% vs. 8–9%) in raked treatments during severe drought.

Paço et al. (2019) further showed the potential for facilitative effects, documenting mosses' role as moisture buffers on roofs in Lisbon, Portugal. Mosses enhanced water availability in the substrate, indirectly improving conditions for other plants. Moreover, taller vascular plants in return protected mosses from excessive evaporation and stress caused by solar radiation and wind, suggesting a mutual facilitative interaction in this case. However, in other contexts, increased vascular plant cover has been linked to reduced moss presence, likely due to competition for light and space (Van Mechelen et al. 2015).

Similarly, Brandão et al. (2017) indicated potential indirect facilitation, reporting that mosses improved substrate moisture retention, which could in turn support the survival of associated vascular plants. However, their study involved test beds with and without mosses but did not include vascular plants in the experimental setup, so direct facilitative or suppressive interactions between mosses and higher plants were not examined.

But, moss-vascular plant interactions can also show suppressive tendencies, particularly affecting seedling germination and establishment. Drake et al. (2018) found that moss presence inhibited seed germination in their experiment due to dense moss canopies restricting seed-to-soil contact. Particularly, dense and tall moss species such *as Polytrichum commune* created competitive conditions under drought stress by rapidly absorbing available moisture. This suppression was strongest for small-seeded species requiring direct soil contact, while some plants like Festuca rubra with narrow leaves and vertical seed orientation were less affected.

Bates et al. (2013) also observed a primarily suppressive role of mosses, with expanding moss colonies negatively impacting annual plants like *Papaver rhoeas* through competition for space and possibly moisture. Interestingly, as discussed before, coarse substrates reduced moss cover, opening up space for vascular plants, suggesting substrate structure as a key factor for shaping the composition of an ecosystem.

The complexity of these interactions is underscored by the mixed results reported by Heim et al. (2014) and Heim and Lundholm (2014). While moss presence increased survival and post-drought recovery for certain vascular species like *Panicum lanuginosum and Festuca rubra*, others (e.g. *Deschampsia flexuosa* and *Anaphalis margaritacea*) exhibited poorer performance or failed to recover from drought stress completely. They additionally noted no net facilitative effect from moss neighbours on *Solidago bicolor* despite reduced substrate temperatures, suggesting context-specific rather than broadly facilitative outcomes (Heim & Lundholm 2014).

Some studies explicitly highlighted neutral interactions or coexistence without clear facilitative or suppressive effects. Emilsson and Rolf (2005) described moss coexistence with succulent plants without significant suppression or facilitation. Emilsson (2008) found moss dominance, primarily *Ceratodon purpureus*, coincided with reduced spontaneous vascular plant establishment, although causality remained speculative. Similarly, Lönnqvist et al. (2021) reported a negative correlation between moss and vascular plant cover, indicating potential suppression yet acknowledging the coexistence of both groups without complete exclusion of one or the other.

Esfahani et al. (2022) examined interactions between mosses and selected drought-tolerant native vascular plants in Portugal. The study specifically investigated how the inclusion of the moss species *Pleurochaete squarrosa* influenced the ground coverage and survival of four vascular plant species (*Antirrhinum linkianum*, *Sedum sediforme*, *Asphodelus fistulosus*, and *Centranthus ruber*). Moss presence coincided with the complete mortality of *A. fistulosus*, though this outcome could not be specifically attributed to the presence of moss. Additionally, *A. linkianum* and *S. sediforme* showed reduced ground coverage when mosses were present, although these differences were not statistically significant. The results highlight that there can be facilitative and suppressive effects between mosses and vascular plants although species-specific moss-plant interactions dependent on many factors, demonstrating how mosses can simultaneously suppress some species while potentially benefiting others under certain conditions (Esfahani et al. 2022).

Aszalósné Balogh et al. (2023) studied moss-lichen interactions on urban green roofs, specifically focusing on the relationship between the moss *Ceratodon* *purpureus* and the lichen *Cladonia rei*. Their observations indicated a mutual facilitative effect, where *C. purpureus* established stable, moisture-rich microhabitats on gravel substrates, enabling *C. rei* to successfully colonize these areas. Conversely, *C. rei* appeared to aid the moss by collecting and directing moisture, such as fog and rain, toward the moss base, thereby enhancing moisture availability and retention. Lichen presence did not seem to suppress moss growth but rather contributed positively to microhabitat stability. Although the study did not explicitly investigate implications for vascular plants, the stabilizing effect of the moss-lichen interaction on substrate moisture conditions may indirectly promote opportunities for subsequent vascular plant colonization and establishment on green roofs, but this will be highly context and species specific as we have seen above.

While much of the current literature emphasizes the influence of mosses on vascular plant performance, potential reverse effects remain less well studied. A few studies, such as Paço et al. (2019), suggest that taller vascular plants may offer shelter to mosses by buffering against evaporative stress and intense solar radiation, though this benefit may reverse under conditions of excessive shading. Similarly, Heim and Lundholm (2014) noted that mosses survived equally well across treatments with and without vascular plants, and in some cases appeared to benefit from reduced vascular competition. However, direct experimental evidence on how vascular plants influence moss establishment and growth remains limited. Despite occasional references to protective or neutral co-occurrence, few studies have systematically assessed the extent, direction, or mechanisms of such effects, highlighting a notable gap for future studies.

Overall, these findings reveal that moss-vascular plant interactions on green roofs are highly context-dependent and shaped by a complex interplay of species traits, substrate conditions, and microclimatic factors. Mosses can function as facilitators by stabilizing microhabitats, reducing thermal stress, and improving moisture retention, indirectly supporting vascular plant establishment. At the same time, mosses may suppress plant recruitment through dense growth forms that hinder seed-soil contact or intensify competition for moisture. Conversely, vascular plants may in turn modify moss performance, though this dynamic remains underexplored. Therefore, moss integration into green roof ecosystems requires careful consideration of species-specific interactions and environmental contexts to balance potential facilitative and suppressive effects and ensure optimal ecosystem functioning.

4. Discussion

This section discusses the main findings of the review in relation to the original research questions and broader ecological and design implications. Each question is addressed in turn, followed by an interpretation of the main findings.

This review successfully addresses all five of its research questions, although the strength and clarity of the evidence vary across topics. The first two questions, regarding moss establishment and the mutual relationship between mosses and substrate characteristics, are well-supported by a broad base of studies. Consistent patterns emerge, showing that mosses establish readily under a range of roof conditions (Dunnett et al. 2008; Cruz de Carvalho et al. 2019; Lönnqvist et al. 2021) and that differences in substrate depth, porosity, or composition can significantly influence moss cover (Emilsson 2008; Bates et al. 2013; Perini et al. 2020; Nagase et al. 2023). Equally, multiple sources show that mosses can actively modify substrate conditions, improving surface moisture retention, reducing erosion, and buffering temperatures (Heim & Lundholm 2014; Paço et al. 2019; Schröder & Kiehl 2021; Nagase et al. 2023).

The third question, concerning mosses' role in water retention and stormwater regulation, is one of the most robustly answered. Multiple studies, including both experimental and observational designs, document mosses' ability to intercept rainfall, delay runoff, and enhance evapotranspiration, even in thin substrate systems (Bengtsson 2005; Anderson et al. 2010; Brandão et al. 2017; Paço et al. 2019). These findings consistently demonstrate that mosses contribute meaningfully to the hydrological performance of green roofs.

The fourth question, how growth form influences moss function, is also addressed with reasonable clarity. The dominance of acrocarpous species in exposed, drought-prone settings, and the moisture sensitivity of pleurocarpous forms, are recurrent themes across multiple studies (Vanderpoorten & Goffinet 2009; Cruz de Carvalho et al. 2019; Aszalósné Balogh et al. 2023; Nagase et al. 2023). While some inconsistencies remain in species-level reporting, there is sufficient evidence to suggest that growth form is a key functional trait relevant to their success on green roofs.

The last question, concerning moss interactions with other vegetation, is somewhat less consistently answered. While several studies report facilitative effects under stress and some note competitive dynamics (Van Mechelen et al. 2015; Paço et al. 2019; Schröder & Kiehl 2021), few isolate moss-vascular plant interactions experimentally. As such, the evidence is not definitive. Further targeted research is needed to clarify the mechanisms, conditions, and outcomes of these interactions in more detail.

4.1 Strengths and Limitations

A key strength of this review lies in its focused synthesis of a relatively underexplored topic: the ecological role of mosses on green roofs. While green roof research has been conducted for decades, it has often prioritized and concentrated on broader functional outcomes such as optimizing stormwater retention (e.g. Sedum-based systems), improving energy efficiency, or enhancing urban biodiversity, with comparatively little attention paid to the ecological roles of mosses. This study provides a targeted analysis of mosses across diverse climates, substrates, and design contexts. The inclusion of over 35 peer-reviewed sources, ranging from manipulative experiments to observational surveys, allows for a robust understanding of the current research state on moss function, performance, and interactions on green roofs.

The review also highlights how several studies link moss performance to functional traits. By distinguishing between growth forms (acrocarpous vs. pleurocarpous), ecological strategies (desiccation tolerance, substrate affinity), and functional contributions (e.g. hydrological buffering, erosion control), it shows how mosses contribute to green roof ecosystems. This perspective strengthens the practical relevance of the findings for green roof design, species selection, and planning.

However, the review also faces limitations. First, there is significant heterogeneity in methods across studies. Differences in study duration, climate, substrate composition, and measurement methodology make direct comparisons difficult. Second, few studies isolate mosses from other vegetation types, meaning that their functional contributions are often inferred rather than tested directly. In several cases, mosses are mentioned incidentally or grouped with other cryptogams, limiting the resolution of species-specific effects.

Another limitation is the geographic bias in the literature. Most studies are concentrated in Europe, particularly in temperate and Mediterranean climates. Regions such as North America, Asia, and the tropics are underrepresented, whereas the Southern Hemisphere is entirely unrepresented in the reviewed literature, highlighting a significant geographic gap. Additionally, many studies lack long-term data, making it difficult to assess the stability or successional role of mosses beyond 3-5 years.

4.2 Interpretation of findings

This review demonstrates that mosses are not only frequent colonizers of green roofs but also play active and functionally significant roles in their ecological performance. Across a wide range of climatic conditions, roof types, and substrates, mosses, especially acrocarpous species, readily establish and persist, often in systems where vascular plants are limited by drought, shallow substrate, or low fertility (Dunnett et al. 2008; Cruz de Carvalho et al. 2019; Lönnqvist et al. 2021).

Their success is closely tied to key adaptive traits such as poikilohydry, minimal nutrient requirements, and compact growth forms, which allow them to survive extreme surface conditions and thrive with little or no maintenance input. This suggests that mosses are not merely tolerating extreme conditions, but are functionally adapted to the constraints of extensive green roofs, filling a niche where vascular plants often fail.

Substrate characteristics were found to both influence and be influenced by mosses. Establishment was strongly associated with substrate depth, porosity, and organic content, with finer, moderately porous materials promoting higher moss cover and persistence (Bates et al. 2013; Perini et al. 2020; Nagase et al. 2023). At the same time, mosses themselves modify substrate properties through their dense, mat-forming structures, reducing erosion, buffering temperatures, and enhancing surface moisture retention, especially important in low-input systems with minimal growing medium (Heim & Lundholm 2014; Paço et al. 2019; Nagase et al. 2023). These findings suggest that mosses do not just respond to substrate conditions, but actively shape them, influencing it in ways that affect the overall functioning of the green roof.

Their role in regulating rooftop hydrology emerged as one of the most consistent and functionally relevant themes. Mosses were repeatedly shown to delay runoff, retain water through direct absorption, and increase evapotranspiration, contributions that are especially pronounced during short, intense rainfall events typical of urban climates (Anderson et al. 2010; Brandão et al. 2017; Paço et al. 2019). These functions position mosses as effective stormwater regulators, particularly in extensive systems where deeper retention layers are absent.

Growth form further shaped moss performance and ecological function. Acrocarpous mosses dominated in exposed, drought-prone settings, reflecting their higher desiccation tolerance and ability to maintain compact, resource-efficient structures. Pleurocarpous species, while potentially offering broader surface coverage and stronger substrate binding, were more sensitive to moisture availability and typically declined under prolonged drought (Cruz de Carvalho et al. 2019; Nagase et al. 2023). These differences suggest that growth form is not merely a morphological category but a key trait determining moss suitability under specific roof conditions. This points to the value of using trait-based approaches in green roof planning, allowing to match species to site-specific conditions more effectively.

Finally, moss interactions with vascular plants were shown to be dynamic and context-dependent, shaped not only by environmental factors like roof design, moisture, and substrate depth, but also by the traits and characteristics of the species involved. In some cases, mosses facilitated vascular plant establishment by improving surface moisture and reducing microclimatic stress, particularly in shallow or drought-stressed substrates (Paço et al. 2019; Schröder & Kiehl 2021).

In other contexts, however, dense moss mats appeared to suppress vascular seedling emergence, potentially by limiting light, space, or seed-soil contact (Bates et al. 2013). This complexity highlights the need to treat moss-vascular plant interactions not as fixed outcomes, but as dynamic relationships shaped by roof design, environmental conditions, and the species-specific traits of the interacting species. While this review identifies clear patterns in moss establishment, function, and interaction on green roofs, several research gaps remain. Few studies explicitly apply a trait-based framework to moss selection or performance, despite the clear influence of traits like growth form and desiccation tolerance. Expanding this approach to include physiological characteristics such as water-holding capacity, substrate affinity, or light response could improve predictability in species selection. Secondly, most studies are concentrated in Europe and focus on short- to medium-term timescales. Broader geographic representation and long-term experimental designs are needed to assess moss persistence, successional roles, and functional contributions across diverse climates. Finally, moss-vascular plant interactions remain one of the least experimentally resolved aspects of green roof ecology. While some studies suggest mosses can facilitate vascular plant establishment, others report potential suppressive effects due to reduced seed-soil contact or light availability, and some report no effect at all. However, these conclusions are largely inferred rather than directly tested. Few studies have directly isolated these interactions under controlled conditions or tracked their dynamics over time. Future research should aim to disentangle these mechanisms through factorial experiments, long-term monitoring, and species-specific assessments, ideally across a range of substrate depths and climate contexts. Understanding the conditions under which mosses act as facilitators versus competitors would be critical for understanding plant community interactions and optimizing species combinations for green roofs.

5. Conclusion

Taken together, this review positions mosses not only as incidental green roof colonizers, but as ecologically functional and resilient vegetation types with significant potential. Their capacity to regulate moisture and temperature, stabilize substrates, and coexist, at times competitively or facilitatively, with vascular plants suggests that mosses can contribute meaningfully to the long-term sustainability of extensive green roofs. These findings provide a foundation for recognizing mosses not only as part of rooftop biodiversity but as strategic components of climate-adaptive, low-input design.

By synthesizing existing studies across diverse climates, substrates, and roof systems, this review outlines what is currently known and identifies key functional traits, such as growth form, desiccation tolerance, and water retention capacity, that influence moss performance. In doing so, it offers a platform for future research and application. Integrating mosses into green roof design based on functional traits offers a promising direction for optimizing system performance under varied environmental conditions. This review provides a baseline for future studies to build on, particularly in exploring species selection and interaction, trait-based implementation, and long-term dynamics in rooftop environments.

As research in this field advances, mosses should be more consistently considered in both experimental and applied contexts, not merely as incidental colonizers, but as central vegetation types uniquely adapted to occupy niches that are too challenging even for many stress-tolerant vascular plants, and with distinct ecological functions that contribute meaningfully to green roof performance.

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/FIGURES/2

Aszalósné Balogh, R., Matus, G., Lőkös, L., Adorján, B., Freytag, C., Mészáros, I., Oláh, V., Szűcs, P., Erzberger, P. & Farkas, E. (2023). Cryptogamic communities on flatroofs in the city of Debrecen (East Hungary). *Biologia Futura*, 74 (1–2), 183–197. https://doi.org/10.1007/S42977-023-00166-3/FIGURES/5

Bates, A.J., Sadler, J.P. & Mackay, R. (2013). Vegetation development over four years on two green roofs in the UK. *Urban Forestry & Urban Greening*, 12 (1), 98–108. https://doi.org/10.1016/J.UFUG.2012.12.003

Beck, H.E., McVicar, T.R., Vergopolan, N., Berg, A., Lutsko, N.J., Dufour, A., Zeng, Z., Jiang, X., van Dijk, A.I.J.M. & Miralles, D.G. (2023). High-resolution (1 km) Köppen-Geiger maps for 1901–2099 based on constrained CMIP6 projections. *Scientific Data 2023 10:1*, 10 (1), 1–16. https://doi.org/10.1038/s41597-023-02549-6

Becker, M. (2005). Acrocarpous moss Bryum argenteum . https://commons.wikimedia.org/wiki/File:Bryum_argenteum_2005.03.29_15.52.55.jpg [2025-05-23]

Bengtsson, L. (2005). Peak flows from thin sedum-moss roof. *Hydrology Research*, 36 (3), 269–280. https://doi.org/10.2166/NH.2005.0020

Bornkamm, R. (1961). Vegetation und vegetations-entwicklung auf kiesdächern - Mit 5 abbildungen und 11 tabellen. *Vegetatio*, 10 (1), 1–24. https://doi.org/10.1007/BF00452954/METRICS

Brandão, C., Cameira, M. do R., Valente, F., Cruz de Carvalho, R. & Paço, T.A. (2017). Wet season hydrological performance of green roofs using native species under Mediterranean climate. *Ecological Engineering*, 102, 596–611. https://doi.org/10.1016/J.ECOLENG.2017.02.025

Burszta-Adamiak, E., Fudali, E., Łomotowski, J. & Kolasińska, K. (2019). A pilot study on improve the functioning of extensive green roofs in city centers using mosses. *Scientific Review Engineering and Environmental Sciences*, 2019 (vol.28(1)), 118–130. https://doi.org/10.22630/PNIKS.2019.28.1.11

Cruz de Carvalho, R., Varela, Z., do Paço, T.A. & Branquinho, C. (2019). Selecting Potential Moss Species for Green Roofs in the Mediterranean Basin. *Urban Science 2019, Vol. 3, Page 57*, 3 (2), 57. https://doi.org/10.3390/URBANSCI3020057

Deska, I., Mrowiec, M., Ociepa, E. & Lewandowska, A. (2020). Influence of the Hydrogel Amendment on the Water Retention Capacity of Extensive Green

Roof Models. *Journal of Ecological Engineering*, 21 (1), 195–204. https://doi.org/10.12911/22998993/112763

Drake, P., Grimshaw-Surette, H., Heim, A. & Lundholm, J. (2018). Mosses inhibit germination of vascular plants on an extensive green roof. *Ecological Engineering*, 117, 111–114. https://doi.org/10.1016/J.ECOLENG.2018.04.002

Dunnett, N., Nagase, A. & Hallam, A. (2008). The dynamics of planted and colonising species on a green roof over six growing seasons 2001-2006: Influence of substrate depth. *Urban Ecosystems*, 11 (4), 373–384. https://doi.org/10.1007/S11252-007-0042-7/TABLES/8

Emilsson, T. (2008). Vegetation development on extensive vegetated green roofs: Influence of substrate composition, establishment method and species mix. *Ecological Engineering*, 33 (3–4), 265–277. https://doi.org/10.1016/J.ECOLENG.2008.05.005

Emilsson, T. & Rolf, K. (2005). Comparison of establishment methods for extensive green roofs in southern Sweden. *Urban Forestry & Urban Greening*, 3 (2), 103–111. https://doi.org/10.1016/J.UFUG.2004.07.001

Esfahani, R.E., Paço, T.A., Martins, D. & Arsénio, P. (2022). Increasing the resistance of Mediterranean extensive green roofs by using native plants from old roofs and walls. *Ecological Engineering*, 178, 106576. https://doi.org/10.1016/J.ECOLENG.2022.106576

Family, R., Celik, S. & Mengüç, M.P. (2020). Coupled heat transfer analysis and experiments to evaluate the radiative cooling potential of concrete and green roofs for buildings. *Heat and Mass Transfer/Waerme- und Stoffuebertragung*, 56 (8), 2605–2617. https://doi.org/10.1007/S00231-020-02891-0/FIGURES/13

Gabrych, M., Kotze, D.J. & Lehvävirta, S. (2016). Substrate depth and roof age strongly affect plant abundances on sedum-moss and meadow green roofs in Helsinki, Finland. *Ecological Engineering*, 86, 95–104. https://doi.org/10.1016/J.ECOLENG.2015.10.022

Genetics4good (2014). Structural comparison of extensive and intensive green roof systems. . https://commons.wikimedia.org/wiki/File:Intensive_extensive_green_roofs.png [2025-05-19]

Getter, K.L. & Rowe, D.B. (2006). The role of extensive green roofs in sustainable development. *HortScience*, 41 (5), 1276–1285. https://doi.org/10.21273/HORTSCI.41.5.1276

Haughian, S.R. & Lundholm, J.L. (2024). Mosses for minimalist green roofs: A preliminary study of the effects of rooftop exposure, species selection, and lab-grown vs. wild-harvested propagule sources. *Nature-Based Solutions*, 5, 100119. https://doi.org/10.1016/J.NBSJ.2024.100119

Heim, A. & Lundholm, J. (2014). Species interactions in green roof vegetation suggest complementary planting mixtures. *Landscape and Urban Planning*, 130 (1), 125–133. https://doi.org/10.1016/J.LANDURBPLAN.2014.07.007

Heim, A., Lundholm, J. & Philip, L. (2014). The impact of mosses on the growth of neighbouring vascular plants, substrate temperature and evapotranspiration on an extensive green roof. *Urban Ecosystems*, 17 (4), 1119–1133. https://doi.org/10.1007/S11252-014-0367-Y/TABLES/4

Jang, K. & Viles, H. (2022). Moisture Interactions Between Mosses and Their Underlying Stone Substrates. *Studies in Conservation*, 67 (8), 532–544. https://doi.org/10.1080/00393630.2021.1892430

Kawakami, N., Murase, H. & Fukuda, H. (2013). Analysis of the transpiration properties in Sunagoke moss. *Acta Horticulturae*, 1011, 473–478. https://doi.org/10.17660/ACTAHORTIC.2013.1011.60

Lönnqvist, J., Blecken, G.T. & Viklander, M. (2021). Vegetation cover and plant diversity on cold climate green roofs. *Journal of Urban Ecology*, 7 (1). https://doi.org/10.1093/JUE/JUAA035

Mann, G., Gohlke, R., Wolff, F., Supported, R., Renneberg, M., Bruchmüller, S., Herfort, S., Luck, F., Mollenhauer, P., LastNameLastNameStruß, S., Van Meegen, L. & Vötig, T.W. (2021). BuGG-Market Report on Building Greening 2021 Green roofs, green facades, and interior greening Germany. www.gebaeudegruen.info [2025-05-06]

Van Mechelen, C., Dutoit, T. & Hermy, M. (2015). Vegetation development on different extensive green roof types in a Mediterranean and temperate maritime climate. *Ecological Engineering*, 82, 571–582. https://doi.org/10.1016/J.ECOLENG.2015.05.011

Mitchell, M.E., Emilsson, T. & Buffam, I. (2021). Carbon, nitrogen, and phosphorus variation along a green roof chronosequence: Implications for green roof ecosystem development. *Ecological Engineering*, 164. https://doi.org/10.1016/j.ecoleng.2021.106211

Nagase, A., Katagiri, T. & Lundholm, J. (2023). Investigation of moss species selection and substrate for extensive green roofs. *Ecological Engineering*, 189, 106899. https://doi.org/10.1016/J.ECOLENG.2023.106899

Oberndorfer, E., Lundholm, J., Bass, B., Coffman, R.R., Doshi, H., Dunnett, N., Gaffin, S., Köhler, M., Liu, K.K.Y. & Rowe, B. (2007). Green Roofs as Urban Ecosystems: Ecological Structures, Functions, and Services. *BioScience*, 57 (10), 823–833. https://doi.org/10.1641/B571005

Paço, T.A., Cruz de Carvalho, R., Arsénio, P. & Martins, D. (2019). Green Roof Design Techniques to Improve Water Use under Mediterranean Conditions. *Urban Science 2019, Vol. 3, Page 14*, 3 (1), 14. https://doi.org/10.3390/URBANSCI3010014

Page, M.J., McKenzie, J.E., Bossuyt, P.M., Boutron, I., Hoffmann, T.C., Mulrow, C.D., Shamseer, L., Tetzlaff, J.M., Akl, E.A., Brennan, S.E., Chou, R., Glanville, J., Grimshaw, J.M., Hróbjartsson, A., Lalu, M.M., Li, T., Loder, E.W., Mayo-Wilson, E., McDonald, S., McGuinness, L.A., Stewart, L.A., Thomas, J., Tricco, A.C., Welch, V.A., Whiting, P. & Moher, D. (2021a). The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *BMJ*, 372. https://doi.org/10.1136/BMJ.N71

Page, M.J., Moher, D., Bossuyt, P.M., Boutron, I., Hoffmann, T.C., Mulrow, C.D., Shamseer, L., Tetzlaff, J.M., Akl, E.A., Brennan, S.E., Chou, R., Glanville, J., Grimshaw, J.M., Hróbjartsson, A., Lalu, M.M., Li, T., Loder, E.W., Mayo-Wilson, E., Mcdonald, S., Mcguinness, L.A., Stewart, L.A., Thomas, J., Tricco, A.C., Welch, V.A., Whiting, P. & Mckenzie, J.E. (2021b). PRISMA 2020 explanation and elaboration: updated guidance and exemplars for reporting systematic reviews. *BMJ*, 372. https://doi.org/10.1136/BMJ.N160

Perini, K., Castellari, P., Giachetta, A., Turcato, C. & Roccotiello, E. (2020). Experiencing innovative biomaterials for buildings: Potentialities of mosses. *Building and Environment*, 172, 106708. https://doi.org/10.1016/J.BUILDENV.2020.106708

PRISMA 2020 flow diagram — PRISMA statement (2025). https://www.prisma-statement.org/prisma-2020-flow-diagram [2025-04-12]

Schröder, R. & Kiehl, K. (2020). Extensive roof greening with native sandy dry grassland species: Effects of different greening methods on vegetation development over four years. *Ecological Engineering*, 145, 105728. https://doi.org/10.1016/J.ECOLENG.2020.105728

Schröder, R. & Kiehl, K. (2021). Testing standard growth substrates for establishing native dry sandy grassland species on extensive green roofs in Northern Germany. *Basic and Applied Ecology*, 56, 181–191. https://doi.org/10.1016/J.BAAE.2021.07.010

Todeschini, C.C. & Fett-Neto, A.G. (2025). Life at the Top: Extensive Green Roof Plant Species and Their Traits for Urban Use. *Plants*, 14 (5), 735. https://doi.org/10.3390/PLANTS14050735/S1

Vanderpoorten, A. & Goffinet, B. (2009). Moss. In: *Introduction to Bryophytes*. Cambridge University Press. . 70–105.

Vanuytrecht, E., Van Mechelen, C., Van Meerbeek, K., Willems, P., Hermy, M. & Raes, D. (2014). Runoff and vegetation stress of green roofs under different climate change scenarios. *Landscape and Urban Planning*, 122, 68–77. https://doi.org/10.1016/J.LANDURBPLAN.2013.11.001

Veeger, M., Veenendaal, E.M., Limpens, J., Ottelé, M. & Jonkers, H.M. (2025). Moss species for bioreceptive concrete: A survey of epilithic urban moss communities and their dynamics. *Ecological Engineering*, 212, 107502. https://doi.org/10.1016/J.ECOLENG.2024.107502

Vidaller, C., Jouet, A., Van Mechelen, C., De Almeida, T., Cortet, J., Rivière, L., Mahy, G., Hermy, M. & Dutoit, T. (2023). Coexistence and Succession of Spontaneous and Planted Vegetation on Extensive Mediterranean Green Roofs: Impacts on Soil, Seed Banks, and Mesofauna. *Land 2023, Vol. 12, Page 1726*, 12 (9), 1726. https://doi.org/10.3390/LAND12091726

World Intellectual Property Organization (2021a). Extensive green roof in Geneva, Switzerland. https://www.flickr.com/photos/wipo/51253935367/in/album-72157719428846151 [2025-05-19]

World Intellectual Property Organization (2021b). Typical Sedum plants on green roof . https://www.flickr.com/photos/wipo/51254666221/ [2025-05-19]

Zona, S. (2014). Pleurocarpous moss Brachythecium rutabulum. https://www.flickr.com/photos/scottzona/14619961714/in/photostream/ [2025-05-23]

Appendix 1

Table 1 Overview of studies included in the systematic review.

Summary of 37 publications on mosses in green roof systems, detailing study location, climate zone (Köppen–Geiger classification), study type, roof type, age, substrate depth and organic matter content, key treatments or focus, and whether moss was introduced intentionally.

Study	**Location**	**Climate**	**Study Type**	**Roof type**	**Age (year)**	**Subst rate depth**	**Organic matter**	**Key Treatment / Focus**	**Moss Intro duction**
Bengtsson et al. (2005). Hydrological function of a thin ext. green roof in southern Sweden	Malmö, Sweden	Humid continental climate	obs.	ext.	-	3 cm	10%	Hydrological function / runoff of Sedum-moss roofs	Yes
Bengtsson, L. (2005). Peak flows from thin sedum-moss roof	Malmö, Sweden	Humid continental climate	obs.	ext.	-	3 cm	10%	Hydrological function / runoff	Yes
Emilsson, T., & Rolf, K. (2005). Comparison of establishment methods for ext. green roofs in southern Sweden	Malmö, Sweden	Humid continental climate	man.	ext.	1	4 cm	3% / 10%	Comparison of establishment methods / diff. substrates	No
Emilsson, T. (2008). Vegetation development on ext. vegetated green roofs: Influence of substrate	Malmö, Sweden	Humid continental climate	man.	ext.	1	4 cm	N.A. /3% / 10%	Vegetation development / diff. substrates	No

Study	Location	Climate	Study Type	Roof type	Age (year)	Substrate depth	Organic matter	Key Treatment / Focus	Moss Introduction
composition, establishment method and species mix									
Dunnett et al. (2008). The dynamics of planted and colonising species on a green roof over six growing seasons 2001-2006: Influence of substrate depth	Sheffield, UK	Maritime climate	man.	ext.	5	10 cm/20 cm	35%	Vegetation development / diff. Substrate depth	No
Anderson et al. (2010). The potential value of mosses for stormwater management in urban environments	Corvallis, USA	Mediterranean climate	man.	ext.	1	10.16 cm / 12.7 cm	-	Storm water management potential of mosses	Yes
Bates et al. (2013). Vegetation development over four years on two green roofs in the UK	Birmingham, UK	Maritime climate	man.	ext.	4	4-12 cm*	0-15%*	Vegetation development on varying substrate	No
Kawakami et al. (2013). Analysis of the transpiration properties in Sunagoke moss	Toyokawa, Japan	Humid subtropical climate	obs.	ext.	-	-	-	Transpiration properties of Sunagoke moss for cooling	No

Study	Location	Climate	Study Type	Roof type	Age (year)	Subst rate depth	Organic matter	Key Treatment / Focus	Moss Intro duction
Heim et al. (2014). The impact of mosses on the growth of neighbouring vascular plants, substrate temperature and evapotranspiration on an ext. green roof	Halifax, Canada	Humid continental climate	man.	ext.	< 1	-	-	Mosses impact on vascular plants, substrate temperature and evapotranspiration	Yes
Heim, A., & Lundholm, J. (2014). Species interactions in green roof vegetation suggest complementary planting mixtures	Halifax, Canada	Humid continental climate	man.	ext.	1	7.5 cm	5.9 %	Species interaction (facilitation/supression) of moss/lichen/ grass on forb *Solidago bicolor*	Yes
Vanuytrecht et al. (2014). Runoff and vegetation stress of green roofs under different climate change scenarios	Flemish Region, Belgium	Maritime climate	man.	ext.	-	5 cm	-		No
van Mechelen et al. (2015). Vegetation development on different ext. green roof types in a Mediterranean and temperate maritime climate	Avignon, France and Heverlee, Belgium	Mediterranaian climate (Avignon) / Maritime climate (Heverlee)	man.	ext.	2	5 cm / 10 cm	-	Comparing drought adapted plants in Mediterranean and temperate maritime climate and varying substrate depth	No

Study	Location	Climate	Study Type	Roof type	Age (year)	Substrate depth	Organic matter	Key Treatment / Focus	Moss Introduction
Gabrych et al. (2016). Substrate depth and roof age strongly affect plant abundances on sedum-moss and meadow green roofs in Helsinki, Finland	Helsinki, Finland	Humid continental climate	obs.	ext. & int.	n=51, age: 1-41	2-5 (SMR) / 3-24 (MR)	10.5 % (Sedum moss roof) / 16.5 % (MR)	Effects of substrate depth and roof age on plant abundance	No
Brandão et al. (2017). Wet season hydrological performance of green roofs using native species under Mediterranean climate	Lisbon, Portugal	Mediterranean climate	man.	ext.	< 1	15 cm	-	Three native vegetation treatments (including a shrub-grass-moss mixture) plus control to assess how they influenced stormwater retention, peak attenuation, and runoff timing under Mediterranean autumn/winter rainfall	Yes
Drake et al. (2018). Mosses inhibit germination of vascular plants on an ext. green roof	Halifax, Canada	Humid continental climate	man.	ext.	< 1	11 cm	-	Impact of moss cover on vascular plant seed germination	Yes
Paço et al. (2019). Green Roof Design Techniques to Improve Water Use under Mediterranean Conditions	Lisbon, Portugal	Mediterranean climate	man.	int.	<1	20 cm	73 % / 36.5 % / 20 %	Testing design strategies (native plants, biocrusts, installation techniques) to optimize water use and minimize irrigation needs in Mediterranean	Yes

Study	Location	Climate	Study Type	Roof type	Age (year)	Subst rate depth	Organic matter	Key Treatment / Focus	Moss Intro duction
Cruz de Carvalho et al. (2019). Selecting Potential Moss Species for Green Roofs in the Mediterranean Basin	-	-	TBS-RS	-	-	-	-	Defining moss selection criteria for non-irrigated Mediterranean green roofs based on ecological traits	-
Burszta-Adamiak et al. (2019). A pilot study on improve the functioning of ext. green roofs in city centers using mosses	Wrocław, Poland	Humid continental climate	man.	ext.	4	7 cm	2 %	Testing if mosses can develop and be sustained on simplified, lightweight roofs, offering an alternative to traditional vascular plant green roofs	Yes
Cruz de Carvalho et al. (2020). Using Chlorophyll a Fluorescence Imaging to Select Desiccation-Tolerant Native Moss Species for Water-Sustainable Green Roofs	Southern Portugal	Mediterranea n climate	man.	lab con.	-	-	-	Screening desiccation-tolerant native moss species for drought-resilient green roofs using chlorophyll a fluorescence imaging	-
Schröder, R., & Kiehl, K. (2020). ext. roof greening with native sandy dry grassland species: Effects of different greening methods on vegetation development over four years	Osnabrüc k, Germany	Maritime climate	man.	ext.	4	9 cm	4 %	Testing different greening methods (seed sowing vs. raked material) to establish native sandy dry grassland species and evaluating long-term vegetation development	Yes

Study	Location	Climate	Study Type	Roof type	Age (year)	Subst rate depth	Organic matter	Key Treatment / Focus	Moss Intro duction
Perini et al. (2020). Experiencing innovative biomaterials for buildings: Potentialities of mosses	Genoa, Italy	Mediterranaian climate	man.	ext.	<1	0 cm	0 %	Assessing the growth ability of mosses on various building and low-cost materials	Yes
Family et al. (2020). Coupled heat transfer analysis and experiments to evaluate the radiative cooling potential of concrete and green roofs for buildings	Istanbul, Türkiye	Mediterranaian climate	man.	ext.	< 1	0 cm	0 %	Evaluating the radiative cooling and insulation potential of moss compared to other plant-based and concrete roof surfaces	Yes
Deska et al. (2020). Influence of the Hydrogel Amendment on the Water Retention Capacity of ext. Green Roof Models	Częstochowa, Poland	Humid continental climate	man.	ext.	< 1	3.2 cm	-	Assessing how hydrogel amendments and vegetation influence the water retention capacity of ext. green roof models over time	Yes
Mitchell et al. (2021). Carbon, nitrogen, and phosphorus variation along a green roof chronosequence: Implications for green roof ecosystem development	Malmö, Sweden	Humid continental climate	man.	ext.	n= 15 age: 2-22	2.5 cm / 3 cm	5.3 %	Investigating how nutrient content and vegetation traits change over time on green roofs	No

Study	**Location**	**Climate**	**Study Type**	**Roof type**	**Age (year)**	**Substrate depth**	**Organic matter**	**Key Treatment / Focus**	**Moss Introduction**
Schröder, R., & Kiehl, K. (2021). Testing standard growth substrates for establishing native dry sandy grassland species on ext. green roofs in Northern Germany	Osnabrück, Germany	Maritime climate	man.	ext.	4	9 cm	10 %	Testing different substrates for establishing native dry sandy grassland species / how substrate composition affects vegetation development over four years	No
Lönnqvist et al. (2021). Vegetation cover and plant diversity on cold climate green roofs	Kiruna / Luleå / Umeå, Sweden	Humid continental climate (Umeå) / Subarctic climate (Kiruna, Luleå)	obs.	ext.	n = 11 age: 2-15	3-10 cm	-	Assessing how vascular plant / moss cover, and species composition change over time on cold-climate green roofs	-
Rajandu et al. (2021). Bryophyte species and communities on various roofing materials, Estonia	Estonia	Humid continental climate	obs.	ext.	-	-	-	Surveying spontaneous bryophyte species and community patterns across different roofing materials in Estonia	-

Study	Location	Climate	Study Type	Roof type	Age (year)	Subst rate depth	Organic matter	Key Treatment / Focus	Moss Intro duction
Varela et al. (2021). Optimising Artificial Moss Growth for Environmental Studies in the Mediterranean Area	Mediterra nean	Mediterranea n climate	man.	Lab con.	-	5 cm	-	Testing optimal conditions (temperature, substrate) for cultivating Mediterranean moss species	Yes
Esfahani et al. (2022). Increasing the resistance of Mediterranean ext. green roofs by using native plants from old roofs and walls	Lisbon, Portugal	Mediterranea n climate	man.	ext.	< 1	11 cm	-	Testing drought-tolerant native vascular plant species for sustainable Mediterranean ext. green roofs, evaluating performance under reduced irrigation levels.	No
van Dijck et al. (2023). Sedum as host plants for caterpillars? Introducing gut content metabarcoding to green roof research	Flemish region, Belgum	Maritime climate	obs.	ext.	n = 7 age: 4-14	4-5-8.3 cm	-	Investigating whether Sedum-dominated ext. green roofs can serve as larval habitat for moth species (moss cover was measured)	No
Nagase et al. (2023). Investigation of moss species selection and substrate for ext. green roofs.	Chiba, Japan	Humid subtropical climate	man.	ext.	2	4 cm	-	Assessing the establishment success of four moss species on different substrates	Yes
Vidaller et al. (2023). Coexistence and Succession of Spontaneous and Planted	Avignon, France	Mediterranea n climate	man.	ext.	7	5 cm / 10 cm	-	Investigating long-term vegetation dynamics and soil properties / comparing effects of exposure,	No

Study	Location	Climate	Study Type	Roof type	Age (year)	Subst rate depth	Organic matter	Key Treatment / Focus	Moss Intro duction
Vegetation on ext. Mediterranean Green Roofs: Impacts on Soil, Seed Banks, and Mesofauna								substrate depth, and planting vs. spontaneous colonization.	
Seo et al. (2023). CO2 removal characteristics of a novel type of moss and its potential for urban green roof applications	South Korea	Humid continental climate	man.	Lab con.	1 / 3	-	-	Assessing the CO_2 removal capacity of moss under varying environmental conditions	Yes
Laguerre et al. (2023). Characterization of volatile organic compound emissions and CO2 uptake from eco-roof plants	Portland, USA	Mediterranea n climate	man.	Lab con.	< 1	-	-	Measuring CO_2 uptake and BVOC emissions from succulents and one moss species	Yes
Aszalósné Balogh et al. (2023). Cr yptogamic communities on flatroofs in the city of Debrecen (East Hungary)	Debrecen , Hungary	Humid continental climate	obs.	ext.	n = 10 age: 11-50	1-6 cm	-	Surveying the bryophyte and lichen diversity on green roofs and analysing how substrate, shading, and roof age affect cryptogamic communities	-
Haughian, S. R., & Lundholm, J. L. (2024). Mosses for minimalist green roofs: A preliminary study of the effects of rooftop exposure, species selection,	New Brunswic k, Canada	Humid continental climate	man.	ext.	3	0 cm	0 %	Testing moss establishment on asphalt roofs and comparing survival between wild-harvested and lab-grown moss propagules	Yes

Study	Location	Climate	Study Type	Roof type	Age (year)	Substrate depth	Organic matter	Key Treatment / Focus	Moss Introduction
and lab-grown vs. wild-harvested propagule sources									
Veeger et al.(2025). Moss species for bioreceptive concrete: A survey of epilithic urban moss communities and their dynamics.	Netherlands	Maritime climate	obs.	ext.	-	-	-	Surveying urban moss communities on concrete to identify species best suited for colonizing bioreceptive concrete surfaces	-

* They created a non-uniform substrate with varying depth and composition

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