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The ecology and functionality of spontaneous vegetation on green roofs

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Abstract

Green roofs can provide social and ecological benefits in urban areas that lack open space, but their success relies on good vegetation cover. Ensuring sufficient plant coverage on green roofs is often difficult, especially in arid climates, where drought conditions reduce plant survival. Additionally, the high costs associated with constructing and maintaining green roofs often limit their application to wealthier areas, and in less affluent communities their implementation can exacerbate inequalities by driving up property and housing costs. A cost-effective solution is needed to encourage plant cover and make green roof benefits more accessible. Over time and without routine maintenance, the vegetation on green roofs changes as spontaneous plants, commonly viewed as ‘weeds’, colonise and become established. Although this shift might be perceived as a departure from the green roof’s original design intent, these spontaneous species, when forming good cover, could offer benefits such as rainfall retention, habitat provision, and building cooling.

Green roofs intercept and retain rainfall in substrates before it is evapotranspired or enters the urban stormwater drainage system. This reduces stormwater volumes and delays and reduces peak flow rates. Rainfall retention is significantly influenced by the type and cover of vegetation. Yet, the specific influence of spontaneous species on green roof rainfall retention are not well understood. Ideally, plants selected for rainfall retention should have high transpiration rates as this will help replenish the substrate's capacity to store water after rainfall. This is often linked to 'fast' traits like rapid growth or large leaf areas. However, 'slow' traits, such as slower growth or lower biomass, are beneficial for plant survival in dry conditions. Since spontaneous plant species can establish and survive on green roofs, they might play a role in rainfall retention. In addition to understanding the contribution of spontaneous plants to rainfall retention, understanding how their traits relate to their drought and water use strategies could also inform better plant selection for non-weedy species on green roofs.

Sedum species are commonly used on shallow 'extensive' green roofs and in drier climates may require irrigation during summer to sustain their cover. Yet, the interaction between spontaneous vegetation, *Sedum* cover, and water availability remains poorly understood. Clarifying this relationship could help reduce maintenance efforts, preserve *Sedum* cover, or maximise the diversity of spontaneously colonising species. Finally, gaining a deeper understanding of the factors that shape spontaneous plant communities on green roofs globally is crucial due to the significant role vegetation cover and composition play in green roof functionality. These insights can inform better decisions in designing and maintaining green roofs to meet specific ecological or aesthetic goals.

This thesis consists of a general introduction (Chapter 1), a literature review (Chapter 2), four experimental data chapters (Chapters 3-6) and a concluding synthesis chapter (Chapter 7) that address the following questions:

1. Can spontaneous vegetation cover help expand green roofs into areas that are funding or space limited, or does the inherent ‘weediness’ of this vegetation type make it an unwelcome addition to urban landscapes?
2. What are the water use and drought resistance strategies of spontaneous green roof plants? Are their traits, such as relative growth rate and leaf size, correlated with their drought tolerance and water consumption, and is there a trade-off between water use efficiency and drought survival?
3. What impact does the presence of existing vegetation cover (*Sedum mexicanum*) and water availability (irrigation) on a green roof have on the growth, abundance, traits, and diversity of spontaneous plant species on extensive green roofs?
4. Can spontaneous vegetation cover contribute to rainfall retention on green roofs, and how do substrate depth and rainfall patterns affect rainfall retention and spontaneous plant community diversity and composition?

5. How do factors such as roof design, accessibility, maintenance, irrigation, vegetation cover in the surrounding landscape, season, and local climate shape the species richness and functional traits of spontaneous vegetation on green roofs worldwide?

In Chapter 2, I reviewed existing research to understand how spontaneous vegetation impacts the social and ecological aspects of green roofs. While some people may view spontaneous plants as undesirable 'weeds’, studies indicate that these plants become more accepted as their coverage on green roofs increases. Spontaneous species, which can grow without needing irrigation or fertilisers, could also lower the costs of green roofs. This would be particularly beneficial in areas with lower socio-economic demographics or without an established green roof industry. Additionally, in hot and dry climates where deeper substrate layers or irrigation are needed for plant survival, spontaneous species can be advantageous as they can grow in thinner soils and regenerate from their seeds. Using spontaneous vegetation based on social and ecological needs could make green roofs more affordable and prevent them from contributing to increased property values and housing costs, thereby helping urban communities become more resilient.

In Chapter 3, I conducted an eight-week glasshouse experiment to determine the water use and drought response of nine spontaneous green roof species under well-watered (WW) and water-deficit (WD) conditions. Under WW conditions, higher transpiration was associated with 'fast' traits such as increased biomass, leaf area, and growth rate. A clear trade-off emerged between water use under WW conditions and drought resistance under WD. 'Fast' species, while reducing transpiration by 57-72% and biomass by up to 50% under WD, failed to maintain adequate leaf water content (leaf RWC <90%) to avoid drought stress. Conversely, 'slow' species, with their smaller biomass, used less water in both WW and WD conditions, successfully maintaining their leaf water status and showing greater drought resistance. This diversity in water use and drought responses among the spontaneous species mirrors the variable conditions on green roofs, suggesting different strategies may be advantageous at different times. Spontaneous species are likely to offer rainfall retention comparable to planted species, particularly where good plant coverage is achieved.

In Chapter 4, I conducted a 10-month study to investigate the interaction between planted vegetation cover (*Sedum mexicanum*) with increasing coverage (0%, 25%, 50%, 75% and 100% cover) subjected to two irrigation treatments (well-watered; WW, or water-deficit; WD). The microcosms were seeded with a mix of 14 species typically found as spontaneous vegetation on green roofs. I measured the abundance, community biomass, and functional traits like specific leaf area (SLA), leaf dry matter content, and relative growth rate, and assessed species and functional richness of the spontaneous vegetation communities. Increasing *S. mexicanum* cover inversely affected the abundance and richness of spontaneous species but did not significantly impact community biomass or functional richness. The interaction between *S. mexicanum* cover and irrigation treatment played a key role in determining species richness, with the highest richness observed in WW microcosms devoid of *S. mexicanum* cover. The biomass of spontaneous plants was greater in WW than WD modules. The SLA of spontaneous communities was significantly higher in WW conditions where *S. mexicanum* cover was less than 100%. These results suggest that maximising *Sedum* cover while restricting water availability would likely reduce the abundance, biomass, and diversity of spontaneous vegetation on green roofs. In contrast, green roofs that embrace spontaneous species could benefit from increased water availability via occasional irrigation, leading to a richer and more diverse community.

In Chapter 5, I conducted a 100-day rainfall simulation study with green roof modules planted with 14 spontaneous plant species typically found on green roofs in Mediterranean-type climates to determine their rainfall retention. For this study, green roof modules were prepared with either 7 cm (shallow) or 14 cm (deep) substrate layers. These were either left bare or planted with a community of spontaneous species, which achieved approximately 100% coverage before commencement of the experiment. The rainfall simulation consisted of two phases – a 'dry' phase replicating the driest period on record, and a 'wet' phase with rainfall depths based on the highest recorded rainfall percentiles (90th, 95th, and 99th) in Melbourne, Australia. Across 17 rainfall events, I measured rainfall retention, evapotranspiration, runoff initiation time, and soil water content. Additionally, I assessed the spontaneous vegetation cover, and species and functional diversity at the end of each rainfall phase, and biomass at the conclusion of the wet phase. Results showed that during the dry phase, modules with spontaneous vegetation retained 88% of the applied rainfall, irrespective of substrate depth, outperforming bare substrates by 6%. In the wet phase, modules with deep substrates and spontaneous vegetation achieved 30% greater rainfall retention compared to other combinations. By the end of the wet phase, spontaneous vegetation in deeper substrates had 42% higher biomass, 19% greater coverage, and over twice the functional richness than in the shallower substrates. These findings indicate that spontaneous vegetation significantly enhances rainfall retention on green roofs compared to bare substrates and performs similarly to designed plant communities. However, rainfall retention by spontaneous vegetation is contingent upon factors critical for rainfall retention, such as substrate depth and rainfall patterns, and will likely differ in other climates.

Finally, in Chapter 6, I gathered data from presence/absence surveys of spontaneous vegetation for 192 green roofs around the world to investigate how green roof design characteristics (including age, surface area, substrate depth, and elevation), pre-existing vegetation, accessibility, maintenance, irrigation, landscape vegetation cover and local climate, shape spontaneous plant communities. Using regression analyses, I evaluated the impact of these variables on species richness. Additionally, I applied a Hierarchical Modelling of Species Communities (HMSC) approach to determine how these factors influence the dispersal and establishment of spontaneous species, focusing on their specific traits. The results indicate that seasonal variation affects the composition of spontaneous communities due to its effects on both dispersal and establishment of spontaneous plant species. Dispersal traits of spontaneous vegetation on green roofs were predominantly influenced by the vegetation cover in the surrounding landscape. Conversely, the establishment of spontaneous plant species was primarily determined by climatic conditions, though green roof design features (such as roof height, accessibility, and maintenance intensity) also shaped spontaneous plant communities. Spontaneous species richness was higher during spring and winter, and in both deeper green roof substrates and older roofs. These findings can help inform the design and maintenance of green roofs to achieve specific ecological goals or aesthetic preferences. This study also highlights the interplay between green roof design choices, maintenance practices, landscape and climate context, and the development of spontaneous vegetation communities.

By examining the ecology and functionality of spontaneous vegetation on green roofs this thesis revealed several key findings:

- Spontaneous species display diverse water use and drought response strategies, with fast growing species using more water but exhibiting greater drought stress under water deficit.
- The composition and richness of spontaneous green roof vegetation are significantly influenced by vegetation cover (*Sedum mexicanum*) and water availability (irrigation).
- Spontaneous species can enhance rainfall retention, performing comparably to traditional green roof plantings.
- Globally, spontaneous plant communities on green roofs are shaped by a multitude of factors, including roof design, local climate conditions, and the surrounding landscape.

Overall, this research suggests that spontaneous vegetation could contribute substantial benefits to green roofs due to their ability to establish on shallow substrates and provide functionality in terms of rainfall retention, habitat provisioning, and building cooling. The insights drawn from this research can be used to guide green roof design to support spontaneous plant communities or apply more appropriate maintenance and irrigation regimes to designed plant communities on green roofs. Embracing spontaneous vegetation cover on green roofs could offer a cost-effective solution, potentially making the benefits of green roofs more accessible and equitable across different urban settings.

Declaration

This is to certify that:

1. the thesis comprises only my original work towards the Doctor of Philosophy, except where indicated in the preface;
2. due acknowledgement has been made in the text to all other material used; and
3. the thesis is fewer than 100,000 words, exclusive of tables, maps, bibliographies and appendices.

Signed,

Dean Schrieke

Preface

This thesis consists of an introduction (Chapter 1), literature review (Chapter 2), three experimental chapters (Chapter 3 to 5), a data chapter (Chapter 6) and a synthesis (Chapter 7). Chapters 2 to 5 have been published in peer reviewed journals (details below). Chapter 6 contains unpublished material not submitted for publication. All material was principally (>70%) authored by me, and I conducted all laboratory work and data analyses referred to in this thesis. My supervisory committee, Associate Prof. Claire Farrell and Prof. Nicholas Williams, provided essential guidance and feedback. Coauthors on published material (Chapters 2, 3, 4 and 5) provided feedback. My research was supported by an Australian Government Research Training Program Scholarship. I also received support from the City of Melbourne Green our Rooftop Postgraduate Scholarship 2019-21 (GOR0392019), Hort Innovation Researching the Benefits of Demonstration Green Roofs Across Australia project (GC16002), Maurice and Helen Wood Memorial Scholarship 2019, Dr Betty Elliott Horticulture Scholarship 2019, Frank Keenan Trust Fund Scholarship 2021, and the School of Agriculture, Food and Ecosystem Sciences Travel Award 2023.

Chapter 1: Introduction (Unpublished material not submitted for publication)

Chapter 2: Socio-ecological dimensions of spontaneous plants on green roofs (Published by *Frontiers in Sustainable Cities* on 13 December 2021)

Schrieke, D., Lönnqvist, J., Blecken, G.-T., Williams, N.S.G. & Farrell, C. (2021) Socio-Ecological Dimensions of Spontaneous Plants on Green Roofs. *Frontiers in Sustainable Cities*, 3. DOI: 10.3389/frsc.2021.777128

Chapter 3: Trait-based green roof plant selection: Water use and drought response of nine common spontaneous plants (Published by *Urban Forestry and Urban Greening* on 5 October 2021)

Schrieke, D. & Farrell, C. (2021) Trait-based green roof plant selection: Water use and drought response of nine common spontaneous plants. *Urban Forestry & Urban Greening*, 65, 127368. DOI: 10.1016/j.ufug.2021.127368

Chapter 4: Response of spontaneous plant communities to Sedum mexicanum cover and water availability in green roof microcosms (Published by *land* on 16 June 2023)

Schrieke, D., Williams, N.S.G. & Farrell, C. (2023) Response of Spontaneous Plant Communities to Sedum mexicanum Cover and Water Availability in Green Roof Microcosms. *Land*, 12, 1239. DOI: 10.3390/land12061239

Chapter 5: Evaluating the effectiveness of spontaneous vegetation for stormwater mitigation on green roofs (Published by *Science of the Total Environment* on 19 July 2023)

Schrieke, D., Szota, C., Williams, N.S.G. & Farrell, C. (2023) Evaluating the effectiveness of spontaneous vegetation for stormwater mitigation on green roofs. *Science of The Total Environment*, 898, 165643. DOI: 10.1016/j.scitotenv.2023.165643

Chapter 6: Global patters and drivers of spontaneous vegetation on urban green roofs (Unpublished material not submitted for publication)

Chapter 7: Synthesis (Unpublished material not submitted for publication)

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To my sub-committee chair, Professor Steve Livesley, thank you for your diligent oversight and wise counsel that brought clarity and direction when it was most needed.

I'd like to thank the Burnley Nursery crew for their hard work and technical expertise in support of my research. Their ability to facilitate rigorous science with limited resources has been a cornerstone of my research's success.

To my fellow Burnley PhD colleagues, thank you for your friendship and support. Your readiness to assist in manual labour, engage in meaningful discussions, and share your experiences has been a continual source of inspiration and a much-appreciated avenue for venting and idea exchange.

Finally, I wish to express my deepest gratitude to my friends and family. Your patience, encouragement, and faith in me have been fundamental to my perseverance over these four years. I am deeply thankful for your presence in my life, and I couldn't have reached this milestone without you.

This thesis stands as a testament to the collective support and guidance of each of you and I am immensely grateful for your contributions to this phase of my life.

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Chapter 1 : Introduction

This introductory chapter presents a short overview of green roofs and spontaneous vegetation and defines the research objectives and structure of this thesis. Chapter 2 delivers a more comprehensive analysis of the socio-ecological aspects of spontaneous vegetation on green roofs, as published in *Frontiers in Sustainable Cities* (2021).

Urban green infrastructure and green roofs

Urban green infrastructure (UGI) encompasses the integration of plants and ecosystems into urban settings to sustain natural functions (Andersson et al., 2019). Celebrated for its multifaceted benefits, UGI has been shown to enhance building energy efficiency, regulate climate, and improve air and water quality, alongside managing stormwater, supporting biodiversity, and providing spaces that cater for recreation and psychological restoration (Tzoulas et al., 2007). In dense urban areas with limited open space, rooftops present a significant opportunity for the implementation of UGI. The adoption of green roofs, UGI designed to support rooftop vegetation, can offer a range of advantages to city dwellers (Manso et al., 2021). Nevertheless, the initial and ongoing costs of green roofs are considerable (Bianchini & Hewage, 2012) and their benefits often skew towards affluent neighbourhoods (Sharma et al., 2018). Additionally, green roofs may inadvertently exacerbate social inequality by inflating property values and housing costs, potentially displacing disadvantaged communities (Ichihara & Cohen, 2011). Affordable designs are needed to extend the benefits of green roofs more widely and ensure access to communities most in need.

From ancient practices to modern applications

Green roofs blend architecture and ecology, with a long history embedded in ancient European civilisations (Loveday, 2006). The rudimentary application of soil and vegetation as roofing materials can be traced back to the hanging gardens of Babylon and the sod roofs of

Scandinavian Viking settlements, providing thermal insulation and a sustainable use of local resources (Jim, 2017). Throughout the ages, the incorporation of greenery into architectural design has morphed to cater to the evolving needs of society. The industrial revolution and subsequent urbanisation in the 19th and 20th centuries resurrected the use of green roofs in response to escalating environmental and spatial challenges in Germany’s cities (Köhler, 2003). Modern-day green roofs have evolved from these historical precedents into multifunctional urban green spaces (Figure 1). Enhanced by technological and horticultural advancements, today's green roof systems manifest in varied forms across cities globally, and act as spaces for

Figure 1.1 Green roofs adorn urban landscapes worldwide, symbolising the expansive reach of this sustainable practice in global green infrastructure. Featured locations, clockwise from top left: Ludwigsburg, Germany (Christine Thuring); Texas A&M University, USA (Bruce Dvorak); Chiba University, Japan (Ayako Nagase); Hanover, Germany (Chiara Catalano); Umeå, Sweden (Joel Lönnqvist); Auckland, New Zealand (Robyn Simcock).

urban agriculture (Whittinghill & Rowe, 2012), recreation (Williams et al., 2019), and biodiversity conservation (Williams et al., 2014).

Green roof types, technical aspects, and policy frameworks

Modern green roofs are typically constructed with a lightweight, engineered substrate situated above a filtration fabric, underlain by a drainage system (sometimes with a water retention layer) that sits above a root-resistant layer and waterproofing membrane (Figure 2) (Ampim et al., 2010). Green roof substrates consist of a diverse array of materials. The major components are mostly natural minerals, such as sand, lava rock, and expanded aggregates of shale, clay, and slate (Rowe et al., 2006). Recycled materials, derived from crushed construction waste like bricks, tiles, and concrete, alongside conditioned subsoil, may also be used as alternatives to mineral components (Ishimatsu & Ito, 2013). The inclusion of stabilised organic matter, such as coir (fibrous coconut husk) or compost is often used to increase water availability (Farrell, Ang, & Rayner, 2013; Farrell et al., 2012). The specific proportions of these materials are designed

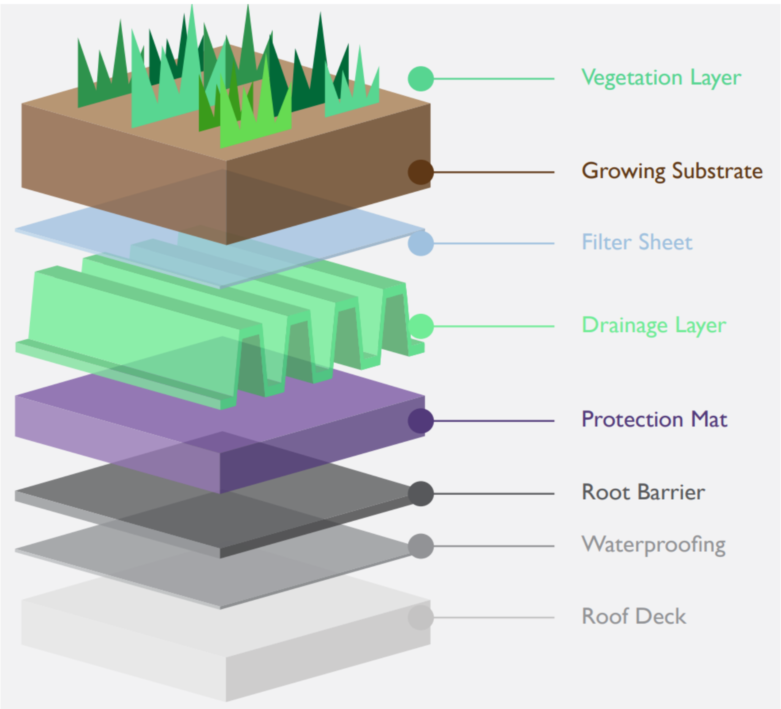

Figure 1.2 Layers of a typical green roof construction. Sourced from the City of Melbourne 'Growing Green Guide' (2014)

according to the intended plant species and green roof design criteria, and it is typically recommended that organic matter is no more than 20% of the substrate mix (FLL, 2008).

Green roofs are often categorised into two main types: extensive and intensive, each with unique design, functionality, and constraints (FLL, 2008). Extensive green roofs are distinguished by their shallow (<15 cm) and freely draining substrates and are typically planted with low-maintenance vegetation, such as drought-tolerant and shallow rooted *Sedum* species (Snodgrass & Snodgrass, 2006). Whereas intensive green roofs are planted with a more diverse array of plant species, potentially including trees, and consequently require deeper (>15 cm) substrates and considerably more structural support (Oberndorfer et al., 2007). Further, semi-intensive green roofs merge characteristics of both types, utilising moderate-depth (15 – 20 cm) substrates to facilitate a broader plant palette than extensive roofs while avoiding the structural demands of intensive systems (Dunnett & Kingsbury, 2008).

Green roofs are gaining global traction as cities adopt policies to enhance urban ecology and sustainability. Since the founding of the German Landscape Research, Development & Construction Society (FLL) in 1975, the standardisation of green roof design has gained momentum, encompassing everything from structural engineering to the selection of vegetation. Although FLL's guidelines are internationally recognised, regional adaptations have emerged, like Melbourne Australia's "Growing Green Guide," which provides a framework for designing, constructing, and maintaining green roofs, walls, and facades (City of Melbourne, 2014). Additionally, the City of Melbourne enforces sustainability metrics in its urban planning, occasionally mandating green roofs on new developments (Bush et al., 2021). Similar green roof policies and guidelines are being adopted in cities globally, balancing information dissemination, advocacy, regulatory intervention, and financial incentives to foster implementation (Zhang et al., 2022).

Economic barriers to implementation

Throughout their lifecycle, green roofs offer combined benefits for both society and ecology (Bianchini & Hewage, 2012). Yet, the broader application of green roofs is hindered by financial demands, complexities involved in modifying existing buildings to accommodate them (Ziogou et al., 2018), and ongoing input demands, such as irrigation in hot and dry climates (Ascione et al., 2013; Williams et al., 2021). The effectiveness of green roofs in delivering ecosystem services is dependent on the health and extent of vegetation coverage (Poë et al., 2015; Speak et al., 2013; Stovin et al., 2015), and guidelines emphasise the need for near-complete coverage a year after installation (FLL, 2008). Nevertheless, the success of vegetation on shallow substrates typical of extensive green roofs is often limited, affecting plant longevity and vigour (Durhman et al., 2007; Eksi & Rowe, 2019; Rayner et al., 2016; Williams et al., 2021). Although deeper substrates on ‘intensive’ green roofs can enhance plant health and increase longevity (Olly et al., 2011), they come with greater structural and maintenance requirements and are less suited to retrofitting on existing structures, leading to their less frequent use compared to extensive green roofs (Shafique et al., 2018).

Green roof functionality

Green roofs can be multifunctional, addressing challenges in cities related to urban heat islands (Santamouris, 2014), altered hydrological cycles (Stovin et al., 2012), diminishing biodiversity (Wang et al., 2017), and mental health (Lee et al., 2015). In densely built environments characterised by large amounts of impermeable surfaces, the capability of green roofs to mitigate stormwater runoff is a crucial aspect of their implementation (Carter & Jackson, 2007). Impervious surfaces directly contribute to large volumes of stormwater runoff and elevated peak flow rates, amplifying flood risk and reducing the quality of downstream water bodies (Walsh et al., 2005). By capturing and retaining rainfall within substrates for subsequent evapotranspiration by plants, green roofs can play a significant role in reducing volume and peak flow rates of stormwater (Stovin et al., 2012; Viola et al., 2017). The efficacy of green roofs in retaining rainfall varies, ranging from no retention to 100% retention, with an average efficacy reported at 62% (Zhang et al., 2021). This variability is due to the type and depth of substrate, the species and density of vegetation, roof design, and prevailing weather conditions such as temperature, wind, humidity and rainfall intensity and duration, as well as the duration of preceding dry periods (Czemiel Berndtsson, 2010). Vegetation cover can increase stormwater retention on green roofs, as vegetation transpires water stored in substrates between rainfall events, thereby replenishing the substrate water holding capacity for subsequent rainfall (Poë et al., 2015; Wolf & Lundholm, 2008).

Vegetation cover on green roofs and spontaneous vegetation

While selecting plant species with higher water use has been shown to increase rainfall retention on green roofs (Farrell, Szota, et al., 2013; Kemp et al., 2019; Szota et al., 2017), the limited water storage capacity of shallow substrates can result in significant plant stress, and poor plant growth and survival, especially in hot and dry climates (Durhman et al., 2007; Rayner et al., 2016; Williams et al., 2021). Due to their drought tolerance, succulent plants like *Sedum* spp. are commonly chosen for extensive green roofs (Oberndorfer et al., 2007; Snodgrass & Snodgrass, 2006); however, their low water usage limits their impact on enhancing rainfall retention (Dunnett et al., 2008; Wolf & Lundholm, 2008). Researchers have identified granite outcrop plant species native to Australia that can maintain high water use when water is available and exhibit drought tolerance when water becomes deficient and linked these characteristics to their traits to enhance the selection process for vegetation suitable for green roofs (Farrell, Szota, et al., 2013).

In addition to stormwater mitigation, the establishment of healthy vegetation cover on green roofs is pivotal for other socio-ecological benefits including providing habitat for plants (Madre et al., 2014) and animals (Gonsalves et al., 2021), and improving mental health through attention restoration (Lee et al., 2015). As climate projections foresee an increase in extreme heat events and unpredictable rainfall patterns in urban areas (IPCC, 2018; McCarthy et al., 2010), the survival of planted species other than *Sedum* on unirrigated extensive green roofs, particularly in hotter and drier conditions, is increasingly uncertain (Guo et al., 2021; Rayner et al., 2016). When left without maintenance, green roofs can become colonised by spontaneous vegetation or 'weeds' (Catalano et al., 2016; Madre et al., 2014; Vanstockem et al., 2019). Sometimes, this is the desired design outcome. For example, green roof designs that emulate brownfield habitats, referred to as 'brown roofs", utilise construction debris to create low-maintenance ecosystems that support urban wildlife like the Black Redstart *Phoenicurus ochruros* and Lapwing *Vanellus vanellus* (Grant, 2006). Brown roofs are designed to attract spontaneous vegetation cover and their cost-effectiveness lies in their minimal maintenance and inputs, as they rely on self-regenerating plants and recycled substrate materials. Brown roofs provide biodiversity in cities as they can foster conservation-worthy spontaneous flora and serve as refuges for rare arthropods, like ground-level brownfields (Kadas, 2006).

Spontaneous plant species assemblages on green roofs are influenced by the roof's age and design characteristics, the characteristics of the nearby environment, and local weather patterns (Madre et al., 2014; Vanstockem et al., 2019; Vidaller et al., 2023). Specifically, Madre et al. (2014) found that substrate depth was a significant factor in the diversity of spontaneous vegetation on 115 green roofs in northern France (maritime climate), with greater substrate depths having greater taxonomic and functional spontaneous species richness. Additionally, factors such as the size of the green roof, its elevation, and the intensity of maintenance were shown to be influential, favouring spontaneous species that are suited to warm and dry conditions. Likewise, in a study on 129 roofs in Flanders and Brussels, Belgium (temperate maritime climate), Vanstockem et al. (2019) showed that the functional traits of spontaneous plant species on green roofs were influenced by potential habitat in the surrounding landscape and substrate depth, with greater landscape habitat and substrate depth supporting greater functional diversity of spontaneous vegetation communities. They also found that biotic factors such as the presence of planted species decreased the functional diversity and abundance of spontaneous species. Green roof age also plays a significant role in shaping spontaneous vegetation communities. For example, plant communities on 15 unmanaged green roofs (16 cm substrate depth) in Hannover, Germany, were shown to shift from an initially sown community dominated by competitive species to spontaneous assemblages marked by stress-resilient traits over a 30-year period (Catalano et al., 2016).

Plant interactions can oscillate between competition and facilitation as influenced by water availability (Bertness & Callaway, 1994; Holmgren et al., 1997). Due to their low moisture-holding substrates and exposure to the elements, green roofs are prone to rapid water depletion (Ampim et al., 2010; Farrell et al., 2016), with high evaporation rates exacerbated by rooftop conditions (Rayner et al., 2016). In arid regions, irrigation is critical for establishing green roof vegetation (Williams et al., 2021), with evidence suggesting it also boosts the diversity and abundance of spontaneous plants (Köhler, 2006). Greater water availability on green roofs located in higher rainfall areas in Scandinavia increases spontaneous plant cover (Lönnqvist et al., 2021). Unlike slow-growing and drought-resistant *Sedum* species commonly planted on green roofs, spontaneous plant communities are often characterised by competitive and ruderal traits (Vanstockem et al., 2019) indicative of fast growth and short life cycles (Grime, 1977). Species that exhibit rapid growth likely consume more water compared to their slower-growing counterparts (Reich, 2014), a characteristic that might enhance the water retention capabilities of green roofs during rainfall events (Farrell et al., 2013).

The presence and density of vegetation already established on green roofs likely inhibits or fosters the growth of spontaneously arriving species by altering the access to "safe sites" (Harper et al., 1961) for germination and growth. However, this impact is not uniform. Vanstockem et al. (2019) found that increased functional diversity among pre-existing green roof plants led to reduced spontaneous plant coverage, contrasting with Van Mechelen et al. (2015) , who observed a positive correlation between pre-established species richness and the richness of spontaneous species. Meanwhile, Nagase and Dunnett (2013) consistently noted a detrimental effect on the prevalence of spontaneous species with higher densities of pre-existing vegetation. These findings imply that the coverage and density of existing vegetation may play a more significant role than species richness in constraining the spread of spontaneous flora on green roofs.

As discussed, the presence of spontaneous vegetation on green roofs may contribute to their overall functionality due to the importance of vegetation cover and diversity (Lundholm, 2015; Nagase & Koyama, 2020; Poë et al., 2015; Wang et al., 2017), however these benefits are not yet clearly established.

Research objectives and thesis outline

The global phenomenon of spontaneous colonisation of green roofs by plants highlights the need to develop a deeper understanding of the potential impact of this vegetation type on green roof functionality, and the trends that shape spontaneous species communities. The objectives of this thesis are to evaluate 1) the potential tolerance of spontaneous green roofs species to hot and dry conditions (water use and drought response strategies); 2) how spontaneous plant communities respond to existing vegetation cover and water availability on green roofs; 3) the potential of spontaneous vegetation to contribute to stormwater mitigation on green roofs; and 4) how green roof design characteristics, surrounding landscape vegetation cover and climate shape spontaneous vegetation communities on green roofs. In so doing, this thesis will address the following questions:

1. Can spontaneous vegetation cover help expand green roofs into areas that are funding or space limited, or does the inherent ‘weediness’ of this vegetation type make it an unwelcome addition to urban landscapes? (Chapter 2 – published mini-review)
2. What are the water use and drought resistance strategies of spontaneous green roof plants? Are their traits, such as relative growth rate and leaf size, correlated with their drought tolerance and water consumption, and is there a trade-off between water use efficiency and drought survival? (Chapter 3)
3. What impact does the presence of existing vegetation cover (*Sedum mexicanum*) and water availability (irrigation) on a green roof have on the growth, abundance, traits, and diversity of spontaneous plant species on extensive green roofs? (Chapter 4)
4. Can spontaneous vegetation cover contribute to stormwater management on green roofs, and how do substrate depth and rainfall patterns affect rainfall retention and spontaneous plant community diversity and composition? (Chapter 5)
5. How do factors such as roof design, accessibility, maintenance, irrigation, vegetation cover in the surrounding landscape, season, and local climate shape the species richness and functional traits of spontaneous vegetation on green roofs worldwide? (Chapter 6)

This thesis provides an analysis of the potential for spontaneous vegetation to contribute to green roof function and an understanding of how spontaneous plant communities vary according to green roof design, climate, and surrounding landscapes (Figure 2, overleaf). Chapter 1 (this chapter) introduces green roof systems, their roles, and the challenges they face, setting the stage for the research questions addressed in the thesis. Chapter 2 reviews existing peer-reviewed literature around the socio-ecological dimensions of spontaneous vegetation on green roofs. Chapter 3 describes a glasshouse experiment that examines the drought response and water-use of nine common spontaneous green roof plant species.

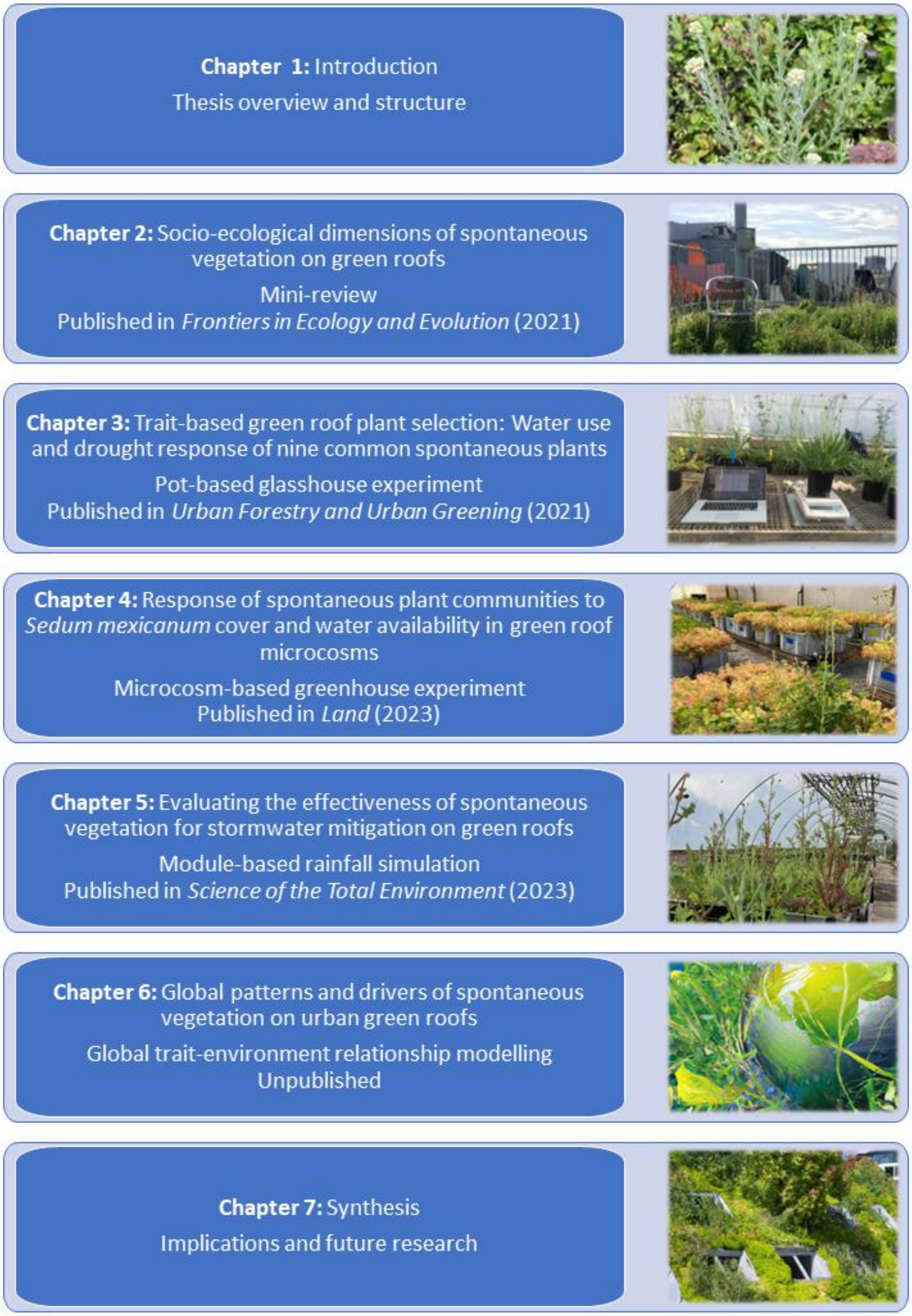

Figure 1.3 Thesis structure, chapter titles and publication details.

Chapter 4 is a green roof module experiment conducted in a greenhouse which investigates how spontaneous plant communities on green roofs are affected by existing vegetation cover (*Sedum mexicanum*) and water availability (irrigation). Chapter 5 uses a polytunnel based rainfall simulation to evaluate stormwater mitigation by spontaneous vegetation cover on green roofs and determines whether rainfall retention is influenced by substrate depth and rainfall regime. Chapter 6 provides a global perspective, analysing data from 192 green roofs worldwide to explore how local conditions and green roof design affect spontaneous species richness and traits. The thesis concludes with Chapter 7, synthesising findings from the previous chapters, discussing their implications for green roof design and maintenance, and suggesting directions for future research.

Chapter overview

Chapters 2 to 5 are research articles previously published and formatted according to the University of Melbourne's guidelines for graduate research. These papers, while independent, contain some overlap in introductory background and identification of research gaps to maintain their integrity as separate entities. Chapter 6 presents an unpublished study of how spontaneous green roof vegetation is influenced by green roof design attributes, vegetation cover in the surrounding landscape, and local climate conditions. Finally, Chapter 7 synthesises the findings from Chapters 2 through 6, addresses the research questions, considers implications for green roof design and management, and discusses the methodological limitations while proposing directions for future research.

Chapter 2 utilises an analysis of existing literature on spontaneous green roof vegetation, examining its ecological and social implications. The chapter integrates these findings to evaluate the role such vegetation could play in enhancing green roof functionality and making the benefits of green roof more accessible.

Chapter 3 presents findings from an eight-week glasshouse water-deficit experiment that investigated the water use and drought tolerance of nine spontaneous green roof species under well-watered (WW) and water-deficit (WD) conditions. These species were subjected to either well-watered or water-deficit conditions, with the water-deficit group receiving limited water until reaching a soil water content (SWC) threshold of 15%, then being re-watered to capacity, a cycle that continued until day 51 when further watering was ceased. Prior to the water-deficit experiment, baseline biomass measurements were taken, and upon reaching the 10% SWC, plants were harvested for final biomass and leaf relative water content (RWC) to assess plant water status and drought response.

Chapter 4 presents the outcomes of a 10-month investigative study on the impact of varying coverages of *Sedum mexicanum*, from 0 to 100%, on the emergence and growth of spontaneous species in green roof microcosms, under well-watered and water-deficit conditions. It evaluates the abundance and community biomass of 14 spontaneously occurring species, along with their specific leaf area (SLA), leaf dry matter content (LDMC), and relative growth rate (RGR), as well as species and functional richness, to understand how *S. mexicanum* coverage shapes the spontaneous plant community's structure.

Chapter 5 outlines results of a 100-day rainfall simulation study on 14 plant species that spontaneously colonise green roofs. This study aimed to elucidate the contribution of spontaneous vegetation to stormwater management on green roofs. Modules for the experiment were prepared with either a shallow (7 cm) or deep (14 cm) layer of substrate that was left bare or sown with a community of spontaneous species, which achieved near-total coverage before the rainfall simulations began. The simulations consisted of "dry" and "wet" rainfall phases modelled after historical climate data from Melbourne, Australia. The "dry" phase mimicked the pattern and amount of the driest recorded rainfall period, while the "wet" phase involved rainfall amounts derived from the 90th, 95th, and 99th percentiles of historical data. Over 17 rainfall events, the study measured rainfall retention, evapotranspiration, the delay before runoff began, and soil water content. Vegetation cover, along with species and functional diversity, was recorded at the end of each rainfall phase, and biomass was measured after the wet phase.

Chapter 6 details the outcomes of a global analysis of spontaneous vegetation communities on 192 green roofs. The objective of this chapter was to discern how the composition of these communities is influenced by various factors, including green roof design elements such as age, size, substrate depth, and elevation, along with management practices such as maintenance and irrigation, and the presence of surrounding vegetation within 200 and 1000 metre radii, in addition to seasonal and climatic conditions. Utilising regression analyses, the chapter evaluates the impact of these variables on species richness and employs Hierarchical Modelling of Species Communities (HMSC) to understand their influence on the dispersal and establishment of spontaneous species, based on their traits.

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Chapter 2 : Socio-ecological dimensions of spontaneous plants on green roofs

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Abstract

Green roofs have the potential to provide socio-ecological services in urban settings that lack vegetation and open space. However, implementation of green roofs is limited by high construction and maintenance costs. Consequently, green roof projects often disproportionately benefit wealthy communities and can further marginalise disadvantaged communities by increasing property values and housing costs. Vegetation cover on green roofs is crucial to their provisioning of socio-ecological services. Evidence suggests that green roof plantings change over time, especially with limited maintenance, and are replaced with spontaneous 'weedy' species. This is often perceived as a failure of the original green roof design intent and spontaneous species are usually removed. However, where good coverage is achieved, spontaneous vegetation could provide beneficial services such as stormwater mitigation, habitat provision and climate regulation. While social norms about 'weediness' may limit the desirability of some spontaneous species, research suggests that their acceptability on green roofs increases with coverage. As spontaneous species can establish on green roofs without irrigation and fertiliser, reduced input costs could help facilitate adoption particularly in markets without an established green roof industry. Construction costs may also be reduced in hot and dry climates where deeper substrates are necessary to ensure plant survival, as many spontaneous species are able to colonise shallow substrates and can regenerate from seed. If implemented based on socio-ecological need, green roofs with spontaneous vegetation coverage may apply less pressure to property values and housing costs than conventionally planted green roofs, increasing the resilience of urban communities while limiting gentrification.

Introduction

Urbanisation is an ongoing global process with serious impacts on socio-ecological processes. Urban development seals soils with impervious materials, initiates habitat loss and fragmentation and modifies natural hydrology and climate (Grimm et al., 2008). Vegetation can alleviate some of these impacts, yet disadvantaged communities are often disproportionately green space poor (Barbosa et al., 2007; Zhang et al., 2008; Dai, 2011; Wolch et al., 2014). Maintaining and expanding urban green space is therefore a significant issue facing city planners and policymakers globally. Engineered 'blue-green infrastructure' (BGI), also referred to as 'nature-based solutions', such as green roofs, can mitigate flooding in built up catchments and prevent damage to waterways (Stovin et al., 2012; Viola et al., 2017), provide habitat for urban biodiversity (Wang et al., 2017), reduce urban heat island effects (Santamouris, 2014) and provide psychological benefits such as attention restoration (Lee et al., 2015). The importance of urban BGI was further illustrated by recent COVID-19 lockdowns that limited mobility and highlighted the importance of localised green space (Ugolini et al., 2020). On the whole of lifecycle scale, combined social-ecological benefits of green roofs represent a low-risk amendment with short-term net return on investment (Bianchini and Hewage, 2012). However, significant barriers to widespread adoption of green roofs include high costs associated with installation and maintenance (Shafique et al., 2018), difficulty retrofitting existing rooftops (Ziogou et al., 2018) and input demands such as irrigation in hot and/or dry climates (Williams et al., 2010; Ascione et al., 2013).

Vegetation cover on green roofs is crucial to their provisioning of socio-ecological services (Speak et al., 2013). Achieving close to 80% vegetation cover 12 months post installation is an objective of extensive green roofs (FLL, 2008; Dvorak and Volder, 2010) and bare patches are considered a failure. However, the relatively shallow substrates of extensive green roofs limit plant growth and survival (Durhman et al., 2007; Eksi and Rowe, 2019). Increased substrate depths of ‘intensive’ green roofs can improve plant health and survival (Olly et al., 2011), but incur higher engineering and maintenance costs and are less able to be retrofitted on existing buildings (Bianchini and Hewage, 2012), hence extensive green roofs are much more common (Shafique et al., 2018). Several studies (see Table 2.1, overleaf) show that, when left unmanaged, spontaneous vegetation can completely replace original green roof plantings over time. Unmanaged green roofs with spontaneous vegetation coverage could be considered an ‘informal green space’, a term proposed by Rupprecht et al. (2015) to classify unmanaged urban ecosystems with a history of anthropogenic disturbance that are at least partly occupied by spontaneous vegetation. Informal green space has long been a focus of urban ecology research (Sukopp, 2008) and recent studies focus on its potential to support ecosystem health (Kim et al., 2018), plant and animal biodiversity (Gardiner et al., 2013) including rare and endangered species (Kowarik, 2011; Bonthoux et al., 2014), and facilitate nature experiences for urban dwellers (Threlfall and Kendal, 2018).

Increasingly, cities undergoing densification are implementing strategies to encourage and facilitate green roof adoption (Shafique et al., 2018). Paradoxically, greening strategies can increase housing costs and property values (Ashley et al., 2018; Hamann et al., 2020), leading to gentrification and displacement of disadvantaged communities (Wolch et al., 2014). Installation of green roofs can increase rental prices in surrounding areas (Ichihara and Cohen, 2011) and the high cost of green roof construction and ongoing maintenance can mean that these projects do not benefit disadvantaged communities (Sharma et al., 2018). To avoid gentrifying processes and democratise the benefits of green infrastructure such as green roofs, a ‘just green enough’ (Curran and Hamilton, 2012; Wolch et al., 2014) approach conceives greening projects based on socio-ecological need rather than normative design or species conservation outcomes. This strategy prioritises installation of low maintenance green infrastructure in smaller and underutilised sites, compared to large-scale projects that are concentrated geographically and can kick-start gentrification processes (Schauman and Salisbury, 1998; Wolch et al., 2014). Should spontaneous vegetation provide functionality to green roofs like that of planted vegetation, it might embody a novel ‘just green enough’ nature-based solution. However, research on the potential for ‘just green enough’ or other informal urban greening approaches to avoid gentrification is still in its infancy (Rupprecht and Byrne, 2017) and has not yet been explored for elevated landscapes such as green roofs. In this mini-review we discuss the socio-ecological dimensions of spontaneous vegetation on green roofs (Table 2.2, overleaf) and whether spontaneous vegetation cover could help expand green roofs into areas that are funding or space limited, or whether their inherent ‘weediness’ may make them an unwelcome addition to urban landscapes.

Table 2.1 Vegetation coverage and species richness of spontaneous green roof plants recorded in global surveys. For more than half of the surveys, spontaneous species provided more than 50% of the vegetation cover and more than 50% of species richness, regardless of maintenance regime or substrate depth. Older unmanaged green roofs typically had higher spontaneous species cover.

Study	**Location**	**Climate**	**Season**	**Roof age (years)**	**Substrate depth (mm)**	**Maintenance regime**	**Spontaneous cover %**	**Spontaneous richness %**
Deng and Jim (2017)	Hong Kong, China	Oceanic monsoon	Year-round	1-4	50-100	No maintenance	80-95%	100%
Dunnett et al. (2008)	Sheffield	Temperate	Summer	4	100-200	High maintenance	2.5% of biomass	70%
Lönnqvist et al. (2021)	Kiruna, Sweden	Subarctic	Summer	2	63	Low maintenance	5%	28%
Lönnqvist et al. (2021)	Luleå, Sweden	Subarctic	Summer	4	26	Low maintenance	17%	28%
Lönnqvist et al. (2021)	Umeå, Sweden	Humid continental/subarctic	Summer	2	67	Regular fertilising and irrigation during drought	2%	74%
Thuring and Dunnett (2019)	Stuttgart (three sites)	Warm-temperate	Summer	~20	80-100	Very low maintenance	60%	-
Bates, Sadler & Mackay (2013)	Birmingham	Temperate	Year-round	1-2	40-120	Low maintenance	-	59-66%
Bevilacqua et al. (2015)	Lleida, Spain	Dry Mediterranean Continental	Year-round	4-5	80	Minimal maintenance	6-61%	50%
Catalano et al. (2016)	Hannover, Germany	Warm-temperate, fully humid	Summer-Autumn	30	50-250	No additional maintenance following installation	90% +	93-94%
Köhler et al. (2006)	Berlin, Germany	Temperate oceanic	Spring-Summer-Autumn	1-19	100	No additional maintenance following installation	1-35%	5-36%,
Köhler et al. (2006)	Berlin, Germany	Temperate oceanic	Spring-Summer-Autumn	15	100	No additional maintenance following installation	17-61%	17-76%
Madre et al. (2014)	Paris, France – 115 sites	Western European oceanic	Summer	1-42	20-600	Variable	-	41%
Olly, Bates, Sadler & Mackay (2011)	Birmingham	Temperate	Summer-Autumn	1	100-150	No maintenance	-	62%

*Cover of spontaneous species and their total contribution to species richness were estimated from published data presented for the time of survey. All surveys were conducted in colder temperate and subarctic climates, except for studies in Hong Kong (Oceanic monsoon), Lleida (Dry Mediterranean/Continental) and Paris (Western European Oceanic).

Table 2.2 Potential trade-offs between spontaneous green roof vegetation traits and their social and ecological function. Colours represent perceived beneficial (green) and unfavourable (red) outcomes.

Spontaneous green roof vegetation traits	Social function	Ecological function	Trade-off
Prolonged flowering continuity[1]	Cue to care[5], ecological beauty[6], high preference[7]	Support butterfly biodiversity[1], floral resource for pollinators[8]	No clear trade-off
High biodiversity[2]	Biodiverse vegetation preferred[4], acceptance increases when residents informed of ecological function[9]	Habitat for rare insects and spiders[10], increased GR functionality[11,12,13]	Perceived messiness of naturalistic plantings[9]
Fast growth/ annual lifecycle[3]	Accumulation of organic matter when plants senesce perceived as 'messy'[9]	High transpiration[3] may increase stormwater mitigation and cooling	Accumulation of organic matter when annual plants senesce provides arthropod habitat[18]
Gaps in vegetation[4]	Significant negative impact on green roof aesthetic[4]	Gaps provide safe sites for plant colonisation[15]	Loss of transpiration and canopy cooling when vegetation senesces[16]
Low maintenance	Reduction to green roof costs, overcoming a significant deterrent to adoption[4]	No fertiliser, herbicide, or pesticide application	No clear trade-off

[1](Wang et al., 2017), [2](Madre et al., 2014), [3](Schrieke and Farrell, 2021), [4](Vanstockem et al., 2019), [5](Nassauer et al., 2009), [6](Sutton, 2014), [7](Lee et al., 2014), [8](Bretagnolle and Gaba, 2015), [9](Southon et al., 2017), [10](Kadas, 2006), [11](Dunnett et al., 2008), [12](Farrell et al., 2012), [13](Kemp et al., 2019), [14](Kyrö et al., 2020), [15](Harper et al., 1961), [16](Speak et al., 2013)

Ecological dimensions of spontaneous green roofs

Environmental filters such as habitat transformation and fragmentation, and human preferences shape urban vegetation communities by selecting against certain species (Williams et al., 2009). Plant traits of spontaneous species, such as woodiness, height, and seed mass, appear to increase along gradients of urbanisation, yet other traits have mixed responses associated with localised factors (Williams et al., 2015). On green roofs, factors such as substrate depth and roof age determine spontaneous plant diversity, composition, and traits (Madre et al., 2014). The species composition of spontaneous green roof vegetation also changes with competition with and/or facilitation by established plants (Miller et al., 2014; Ksiazek-Mikenas and Köhler, 2018; Thuring and Dunnett, 2019) and the frequency of green roof maintenance (Madre et al., 2014; Catalano et al., 2016). Shallow green roof substrates appear to have greater cover and diversity of spontaneous species than deeper substrates (Lönnqvist et al., 2021), presumably due to increased availability of bare areas or 'safe sites' for colonisation by spontaneous plants (Harper et al., 1961). Maintenance and resource input is greater initially following green roof installation, and spontaneous vegetation assemblages are dominated by 'ruderal' (sensu Grime, 1977) species (Köhler, 2006; Dunnett et al., 2008; Van Mechelen et al., 2015; Catalano et al., 2016; Ksiazek-Mikenas and Köhler, 2018). These ruderal species grow fast and can complete their life cycles before drought occurs, allowing them to set seed and germinate rapidly in response to rainfall (Bevilacqua et al., 2015). However, as green roofs age, and in the absence of routine maintenance, ruderal species tend to disappear (Bates et al., 2013) and are replaced by more stress tolerant species which can tolerate hotter and drier conditions (Madre et al., 2014; Catalano et al., 2016; Ksiazek-Mikenas and Köhler, 2018). Yet the influence of spontaneous vegetation on green roof functionality, compared to commonly planted green roof species, is less clear.

Spontaneous green roof communities can have high biodiversity, with species richness becoming greater than the original plantings if left unmanaged (see Table 1). Spontaneous vegetation can also provide habitat for invertebrates (Kadas, 2006; Robinson and Lundholm, 2012) and floral resources for pollinators (Bretagnolle and Gaba, 2015). Where these communities replace Sedum green roof vegetation, they can support greater butterfly diversity due to increased flowering continuity over the year and the presence of flowers with short corollas that are accessible to a wide range of species (Wang et al., 2017). Green roofs have also been specifically designed to promote biodiversity and habitat provision (Grant, 2006; Ishimatsu and Ito, 2013; Benvenuti, 2014). Early examples were designed to mimic 'brownfield' habitats such as gravel piles (known to also host spontaneous plant species) for declining birds such as black redstart *Phoenicurus ochruros* and lapwing *Vanellus vanellus* (Grant 2006). These roofs used construction rubble as substrates and spontaneous plant species were left to colonise them. Some spontaneous plant species of conservation interest appeared on these roofs; however, initial coverage of spontaneous vegetation did not meet expectations and researchers eventually reseeded the roof with a locally sourced wildflower seed mix (Grant, 2006). Rare spiders and insects hosted by ground level brownfield sites were also found on these green roofs (Kadas, 2006).

Rapid urbanisation increases stormwater runoff in urban areas, polluting and damaging receiving waterways (Walsh et al., 2005). The negative health impacts associated with stormwater runoff and flooding have been shown to disproportionally affect disadvantaged communities (Patz et al., 2005). Green roofs can reduce the volume and peak flow of runoff by retaining water and releasing it to the atmosphere via evapotranspiration, mitigating downstream flooding and other socio-ecological harm (Getter, 2006). Stormwater mitigation by green roofs is influenced by a range of factors, however substrate type and depth are the primary determinants of water retention (Czemiel Berndtsson, 2010; Zhang et al., 2019), though vegetation increases rainfall retention through interception by plant canopies and evapotranspiration (Zhang et al., 2018; Zhang et al., 2019). Research suggests that green roof plantings with high functional diversity incorporating species with higher water use provide greater stormwater retention than commonly used monocultures of Sedum species which generally have low water use (Dunnett et al., 2008a; Farrell et al., 2012; Kemp et al., 2019). However, the role of spontaneous vegetation on green roof hydrological performance is unclear (Robinson and Lundholm, 2012). As spontaneous green roofs are likely to be more diverse than many sedum-based roofs and have also been shown to become more diverse if left unmanaged (see Table 1), they may provide greater stormwater retention. Spontaneous vegetation may improve stormwater retention on green roofs through increased functional diversity (Cook-Patton and Bauerle, 2012), high transpiration (Schrieke and Farrell, 2021) and maintenance of vegetation cover on green roofs where the original plants have died (Dunnett et al., 2008). Highly managed green roofs have also been shown to reduce runoff quality as they act as nutrient sources (Buffam and Mitchell, 2015) due to fertiliser use (Li and Babcock, 2014). As spontaneous vegetation can thrive with limited or no fertiliser, this type of green roof is less likely to produce poor quality water runoff.

Sociological dimensions of spontaneous green roofs

To our knowledge, there is no research that specifically appraises the sociological dimensions of spontaneous vegetation on green roofs. Further, studies that have evaluated the psychological dimensions of green roof vegetation caution against generalising outcomes of ground-level social research to the context of green roofs (Williams et al., 2019). Human landscape and plant preferences are highly complex and influenced by cultural norms at neighbourhood (Nassauer et al., 2009) and individual scales (Fernandez-Canero et al., 2013; Brun et al., 2018; Nagase and Koyama, 2020). Aesthetics are an important element of landscape preference; however, preference studies of green roof vegetation appear to have inconsistent findings and may vary with context. For example, while office workers in Toronto and Chicago considered green roofs planted with native prairie meadows untidy and out of place in the urban context, spontaneous vegetation was viewed with interest and curiosity (Loder, 2014). In contrast, Australian office workers preferred diverse, taller, green, and flowering vegetation on green roofs; traits associated with meadow-type vegetation (Lee et al., 2014). A similar survey conducted in Chiba, Japan, found preference for turfed green roofs (Nagase and Koyama, 2020). In all these preference studies, participants were presented with images of green roofs, or experienced these roofs directly. Whether perceptions of green roofs change when vegetation is inaccessible, not viewed closely or fully concealed is unclear.

Spontaneous vegetation can be perceived negatively due to its unpredictability, lack of human control and perception of ‘weediness’ that challenges the static ecosystem view of green roofs (Lundholm, 2016) (Table 2). When landscapes lack easily recognisable designed elements, or ‘cues to care’ (Nassauer et al., 2009), residents can experience feelings of social and physical isolation, hopelessness, and diminished social capital (Mair et al., 2012). As spontaneous plants replace original green roof plantings where maintenance is infrequent, this could be perceived as a lack of care and may reduce their acceptance. However, spontaneous vegetation on green roofs often has high floristic diversity (Catalano et al., 2016; Kratschmer et al., 2018) which may improve their acceptance as flowers can be perceived as a ‘cue to care’ (Nassauer et al., 2009). Flowers were also shown in the study with Australian office workers to increase preference, regardless of the vegetation type (Lee et al., 2014). Additionally, as spontaneous vegetation on green roofs is framed within the substrate area, this may communicate a ‘cue to care’ (Nassauer et al., 2009). Moreover, in the case of wild or naturalistic biodiverse roofs, people can appreciate ‘ecological beauty’ when they understand their purpose (Jungels et al., 2013; Sutton, 2014). For example, Southon et al. (2017) showed improved acceptance for perennial meadows that undergo winter senescence after residents were informed about their benefits for pollinators. When the biodiversity benefits of green roof meadows were better understood, these types of roofs were perceived as more ’natural’ and therefore preferable to Sedum species monocultures (Loder, 2014). Therefore, it is possible that perceptions of spontaneous vegetation on green roofs would improve if people were informed of the potential benefits to biodiversity and stormwater retention.

Finally, weed ‘conspicuousness’ on green roofs may not matter when there is good cover, as gaps have been shown to have greater effects on aesthetics than weediness (Vanstockem et al., 2018).

Spontaneous green roofs in practice

To maintain designed plantings on green roofs, weeding of spontaneous vegetation is recommended (FLL, 2008). The risk of annual spontaneous species damaging water proofing membranes is limited by their shallow and non-invasive root systems. However, spontaneous green roofs would still require periodic inspection and maintenance to identify and remove woody spontaneous species to avoid membrane penetration or blocking of drains (Archibold and Wagner, 2007). Controlled disturbance, such as the cutting of the vegetation to mimic grazing, could also prevent competitive species from dominating and optimise species diversity. There are concerns spontaneous green roof vegetation could result in these plants spreading beyond the roof (Lundholm, 2015) as the distance travelled by wind dispersed seeds increases with release height, improving their ability to colonise surrounding urban landscapes. Green roof designers are therefore encouraged to plant native species in areas of conservation value (Williams et al., 2010). However, a large-scale study in France found that spontaneous vegetation that colonised green roofs had greater native species richness (86%) than the initial plantings (30%) and included rare and endangered species (Madre et al., 2014). The urban landscapes that surround green roofs are likely already populated by the typically cosmopolitan species that commonly colonise green roofs (Lundholm and Marlin, 2006). Indeed, the composition of spontaneous green roof vegetation often reflects that of the surrounding environment (Madre et al., 2014; Catalano et al., 2016). Consequently, the risk of invasion by spontaneous green roof species in these landscapes is likely to be limited and potentially lower than species used in horticulture, which is consistently identified as the source of many invasive plants (Dodd et al., 2015; van Kleunen et al., 2018). However, where green roofs are near conservation areas increased monitoring for invasive species is warranted.

Spontaneous green roofs may provide a nature based ‘just green enough’ (Curran and Hamilton, 2012) solution that improves the health and wellbeing of residents while limiting associated green gentrification. Incorporating spontaneous vegetation on green roofs could reduce high initial costs associated with installation, and ongoing costs associated with plant replacement and maintenance. As spontaneous species colonise and persist on green roofs with shallow substrates (Madre et al., 2014), spontaneous green roofs could also alleviate engineering costs associated with increased weight loading and deeper substrates. Furthermore, locating these roofs in inaccessible locations or in areas where they are not overlooked could improve their acceptance. Together, these factors could facilitate adoption of spontaneous green roofs across cities and improve access to socio-ecological services in areas where urban greening is overlooked. However, there are a range of potential positive and negative functional outcomes related to spontaneous vegetation traits on green roofs (Table 2). For example, spontaneous green roofs still require maintenance and costs would be incurred for annual inspections of roofing membranes and drainage, and the removal of woody plants to prevent damage to waterproofing membranes. Relying completely on spontaneous vegetation for good plant cover could also have drawbacks, particularly on tall buildings where height could limit propagules reaching the roof. If no or very few propagules reach the substrate, the roofs will be left with low cover and low diversity potentially leading to erosion of the substrate and reduced energy and stormwater performance. Additionally, as spontaneous vegetation can take time to establish (see Catalano et al., 2016) there may be periods of time with little to no vegetation present. In this case, direct sowing with common green roof spontaneous species could provide initial vegetation cover.

Conclusion

In a rapidly urbanising world, the socio-ecological benefits of spontaneous vegetation on green roofs may outweigh other considerations associated with ‘weediness’ or aesthetic preferences. Maintenance and input costs could be significantly reduced, and this may alleviate ‘green gentrification' and associated displacement of vulnerable communities by large green infrastructure projects. While the desirability of spontaneous vegetation may be limited by social and cultural norms, research suggests that their acceptability on green roofs is likely to increase with plant coverage and 'cues to care' (Nassauer, 2003) such as boundaries, neat edges, and flowers. Negative perceptions of 'weediness' may reduce the acceptability of spontaneous green roofs in highly visible and accessible locations, although this could be reduced through education of their benefits. In inaccessible or less visible locations, the 'weedy' perception of spontaneous vegetation may not matter, broadening opportunities for implementation. We suggest that lightweight green roofs with shallow substrates that facilitate spontaneous colonisation could deliver socio-ecological benefits at a lower cost than conventional extensive green roofs. These roofs could be delivered as part of a 'just green enough' (Wolch et al., 2014) strategy, based on socio-ecological need rather than normative design or conservation outcomes.

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Chapter 3 : Trait-based green roof plant selection: Water use and drought response of nine common spontaneous species

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Abstract

Plant health and cover are critical components of stormwater mitigation on green roofs. Green roof plants can be selected from analogous habitats (e.g., rocky outcrops) and/or by using plant traits associated with survival (e.g., succulence). Plants selected for stormwater mitigation should have high transpiration to replenish substrate storage capacity following rainfall, which is likely associated with 'fast' traits such as faster growth rate or higher leaf area. However, 'slow' traits such as slower growth rate or smaller biomass can help plants survive dry periods. Without routine maintenance, green roof plant communities are often replaced by 'spontaneous' vegetation. As spontaneous species can survive green roof conditions, they may contribute to stormwater mitigation and understanding how their traits relate to drought and water use strategies may help improve green roof plant selection. Therefore, we conducted an eight-week glasshouse experiment to determine the water use and drought response of nine spontaneous species commonly found on green roofs under well-watered (WW) and water-deficit (WD) conditions. Higher transpiration under WW conditions was related to 'fast' traits including greater biomass, leaf area and relative growth rate. There was a trade-off between water use under WW conditions and drought resistance under WD. While 'fast' species reduced transpiration by 57-72% and biomass by up to 50 % under WD, this was insufficient to maintain leaf water status (leaf RWC <90%) and avoid drought stress. Whereas 'slow' species with less biomass used less water under both WW and WD conditions, maintained their leaf water status and resisted drought stress. Diverse water use and drought responses of the nine spontaneous species reflects fluctuating

conditions on green roofs that likely favour different strategies over time. While spontaneous species may not be desirable, they are likely to provide similar stormwater mitigation to planted species where good plant cover is achieved.

Introduction

Green roofs are engineered systems designed to facilitate vegetation growth on building rooftops. Yet the green roof environment can limit plant growth and survival due to high wind and irradiance, exposure to temperature fluctuations and shallow substrates that limit water availability and restrict plant rooting volume (Dunnett et al., 2008; Lundholm et al., 2015). These limitations, and the absence of regular maintenance, can result in plant failure and overtime the original designed green roof plant community is often replaced by weedy or 'spontaneous' vegetation that colonises bare substrates and grows and reproduces without human intervention (Catalano et al., 2016; Madre et al., 2014; Wolf and Lundholm, 2008). While the presence of spontaneous species may be perceived as a failure in terms of design and aesthetics (Lundholm, 2016; Vanstockem et al., 2019), their ability to survive and achieve good plant coverage (Catalano et al., 2016; Madre et al., 2014) under tough conditions may mean that these species could provide benefits such as cooling and stormwater mitigation. Further, as these species are suited to green roof conditions, there is potential to evaluate and use their traits to guide future plant selection of more desirable species.

Although green roofs may be installed for many reasons, stormwater mitigation is a key driver of their adoption globally, to reduce the risk of flooding in built up catchments and damage to waterways (Stovin et al., 2012; Viola et al., 2017). Green roofs reduce stormwater runoff by retaining rainfall in growing media or substrate and releasing it to the atmosphere via evapotranspiration (Monterusso et al., 2004). Plant transpiration helps to replenish the retention capacity of green roof substrates (Poë et al., 2015); however, species need to tolerate periods of water-deficit between rain events to survive (Farrell et al., 2013). Therefore, appropriate plant selection is critical to maximise both stormwater mitigation and plant survival on green roofs (Szota et al., 2017). Spontaneous species could contribute to stormwater mitigation, especially where they have good roof coverage. Therefore, determining how spontaneous green roof species use water and resist drought stress could help us understand what drives their success on green roofs and whether they can contribute to stormwater mitigation. This information could also assist green roof plant selection and improve roof management.

Plant selection for green roofs often prioritises species from analogous ground-level habitats (habitat template approach) such as rocky ecosystems (Lundholm, 2006) or by selecting species with traits suitable for green roof environments (trait approach). Habitat template approaches have been used by researchers globally to identify species suitable for green roofs (Nagase and Tashiro-Ishii, 2018; Sutton et al., 2012; Van Mechelen et al., 2014) or to identify regional vegetation types from which to source suitable species (Caneva et al., 2015; Williams et al., 2010). However, studies suggest that habitat template approaches alone may fail (Walker and Lundholm, 2018) as plants from the same habitat can have different strategies and may not be equally drought tolerant (Du et al., 2018b; Farrell et al., 2013). This has led to increasing support for trait-based plant selection for green roofs (Du et al., 2018b; Farrell et al., 2013; Ksiazek-Mikenas and Köhler, 2018; Lundholm et al., 2014; Rayner et al., 2016).

Researchers have identified morphological traits such as high leaf succulence in both non-succulent species and true succulents (Farrell et al., 2012; Rayner et al., 2016), greater root allocation (high root mass fraction) (Farrell et al. 2013) and low leaf area (Lundholm et al., 2014) as indicative of drought tolerance and advantageous for stormwater retention on green roofs. Trait-based approaches therefore typically select succulent species, such as *Sedum* sp., due to their high drought resistance and shallow rooting depth (Durhman et al., 2006; Monterusso et al., 2005; VanWoert et al., 2005). However, while *Sedum* species have high survival, their low water use is not conducive to rainfall retention on green roofs (Dunnett et al., 2008a; Farrell et al., 2012; Kemp et al., 2019). Species with high water use when water is available and the capability to avoid drought stress by maintaining leaf water status or down-regulating water use under water-deficit have been identified in green roof experiments, although generally there is a trade-off between these strategies (Du et al., 2018b; Farrell et al., 2013).

In addition to individual traits, trait-based frameworks that capture trade-offs in acquiring, processing and conserving resources could be useful to evaluate plant suitability for green roofs. The ‘fast-slow’ plant economic spectrum (Reich, 2014) contrasts species that rapidly acquire and process resources (‘fast’) with species that slowly acquire and conserve resources (‘slow’). A species position on the fast-slow spectrum, relative to other species, can be quantified by growth rate and uptake of resources, for example plant water use. According to this spectrum, plants with faster growth rates should acquire water and other limiting resources more rapidly than slower growing species. To date, growth rate has not been used as a trait for evaluating green roof plants, however studies have shown that water use of green roof plants generally increases with plant biomass (Du et al., 2018b; Farrell et al., 2013).

We determined the growth rate, morphological traits, water use strategies and drought response (leaf relative water content; RWC) of nine common green roof spontaneous species. We hypothesised that species with ‘fast’ traits such as high relative growth rate (RGR) and leaf area would have greater water use than species with ‘slow’ traits. We also anticipated a trade-off between water use under well-watered conditions and drought response under water-deficit, with plants with higher water use under well-watered conditions having lower RWC under water-deficit.

Materials and Methods

Species selection and plant establishment

Nine spontaneous species that are commonly found on green roofs (Table 3.1, overleaf) were selected for our experiment based on a survey of 115 green roofs in northern France (Madre et al., 2014). These are common cosmopolitan species across Europe and are also commonly found on green roofs in Melbourne (Schrieke D., unpublished data). This study was chosen due to the large number of green roofs surveyed and similarity between the Mediterranean-type climates in northern France and Melbourne, Victoria, where the glasshouse experiment was conducted. Seeds of the nine species was collected from sites across metropolitan Melbourne in August (winter) 2016 and grown as seedlings in a temperature-controlled (21 - 26 °C) glasshouse (located at Burnley Campus, the University of Melbourne, Australia). In October (spring) 2016, individual seedlings were transplanted into 1.9 L black plastic pots (i.e., one seedling per pot) filled with 2 kg of a scoria-based green roof substrate (60 % scoria <8 mm scoria including fines; 20 % 7 mm scoria aggregate and 20 % composted coir; Farrell et al., 2012) and 5 g of slow release fertiliser (Osmocote® Exact; NPK 15:9:12) applied to the surface of each pot. Plants were watered once daily prior to the start of the water-deficit experiment.

Experimental design

The water-deficit experiment ran for 61 days between November 2016 to February 2017. Pots were arranged in the glasshouse in a complete randomised block design and blocked for plant biomass to ensure plants of the same species in each block were the same size. Six replicate plants of each species (one plant per pot) per block were randomly allocated to either well-watered (WW) or water-deficit (WD) treatments. Every second day, WW plants were hand-watered to pot capacity. Whereas WD plants received 30% of the water used by their WW equivalent since the previous watering (by weight), until a critical soil water content (SWC) threshold of 15% was reached. When this threshold was reached, plants were re-watered to pot capacity and then the

WD treatment resumed. The time taken to reach 15% SWC varied among the species due to differences in their transpiration rates (3 – 20 days). This process was repeated until day 51 of the experiment when the WD treatment was re-watered to pot capacity and then allowed to dry down without any further water addition. The decision to initiate dry down at day 51 of the experiment was taken to avoid species completing their lifecycles and allow sufficient time for species to adjust physiological and morphological traits to low water availability (Farrell et al., 2013). During the final dry-down, when WD pots reached 10% SWC, leaf relative water content (RWC) was measured to determine plant water status and plants were harvested for biomass measurements. The time taken to reach 10% SWC varied among the species due to differences in their transpiration rates (3 – 22 days). Twelve pots (six per treatment) containing bare substrate were used during the experiment to determine evaporation and enable calculation of transpiration.

Table 3.1 Species information and plant type for the nine spontaneous species used in the glasshouse experiment to evaluate their transpiration and drought response strategies.

Species	Family	Common Name	Plant Type
Euphorbia maculata	Euphorbiaceae	Spotted Spurge	Herbaceous annual
Euphorbia peplus	Euphorbiaceae	Petty Spurge	Herbaceous annual
Lolium perenne	Poaceae	Perennial Rye-Grass	Evergreen annual grass
Malva neglecta	Malvaceae	Common Mallow	Herbaceous annual
Plantago lanceolata	Plantaginaceae	English Plantain	Perennial herb
Polycarpon tetraphyllum	Caryophyllaceae	Four-leaf Allseed	Herbaceous annual
Rumex acetosa	Polygonaceae	Common Sorrel	Perennial herb
Trifolium repens	Fabaceae	White Clover	Herbaceous annual
Solanum nigrum	Solanaceae	Black Nightshade	Herbaceous annual/perennial shrub

Growth and biomass measurements

Before the water-deficit experiment, six plants of each species (one from each block) were harvested to determine leaf mass, total leaf area and total biomass. Fresh biomass weight was also used to correct pot weights for soil water content. Leaves were stripped from stems and leaf area was measured using an area meter (Li3100, LiCor, Lincoln, NE, USA). Samples were oven dried at 70°C until weight was constant to determine dry weights. Specific leaf area (SLA, m^2 kg^{-1} leaf) was calculated as the one-sided leaf area, divided by its oven-dry mass.

When WD plants reached the 10% SWC threshold, both pairs of WW and WD plants in the same block were harvested to determine leaf mass, total leaf area and total biomass. Samples were oven dried at 70°C until weight was constant to determine dry weights. Relative growth rate (RGR) was calculated as per Hoffmann and Poorter (2002) as RGR = $(\ln W_2 - \ln W_1)/(t_2 - t_1)$, where $\ln W_1$ was the natural logarithm-transformed mean of the initial harvest whole plant dry mass (g) and $\ln W_2$ was the natural logarithm-transformed mean of the final harvest whole plant dry mass (g).

Soil water content and transpiration

Soil water content (SWC) was determined from pot weights before and after each watering and corrected for plant weight. Plant weight was estimated as per Farrell et al. (2012) as *initial mean fresh weight* + *daily biomass gain*, where daily biomass gain = (*final fresh weight – initial fresh weight*)/*number of days in experiment*. Soil water content (SWC) was calculated as (*corrected pot weight* - *substrate dry weight*)/*substrate dry weight*. Substrate dry weight was determined by drying substrate from 12 substrate-only pots in an oven at 105 °C until their weight remained constant. Evaporation was determined from total water loss of substrate only pots between each watering. Daily transpiration (E) was determined by subtracting evaporation from total water lost from planted treatments (one plant per pot) at each weighing event. Species differences in mean E between treatments was calculated for mean WD as a percentage of mean WW E.

Leaf relative water content

Leaf relative water content (RWC) was measured to determine plant water status for WW and WD plants at the end of the experiment. We chose leaf RWC as a measure of plant water status and drought stress due to technical limitations in measuring leaf water potential of soft, herbaceous, and succulent tissues using a pressure chamber (Boyer and Kramer, 1995; Kirkham, 2014). Leaf RWC is also easily measured and has been used as a drought indicator in similar green roof studies (Farrell et al., 2013). Leaf RWC was determined per Wright (1977) by removing one youngest fully expanded leaf from each plant in each of the six replicates of each treatment at solar noon. The leaf was re-cut under deionised water to prevent cavitation, dried using tissue paper, then weighed immediately to obtain the fresh weight. Once weighed, the leaf was rehydrated via the petiole in deionised water at room temperature (24 °C) in a dark cupboard for four hours (Wright, 1977). Care was taken to avoid submerging leaves to reduce apoplastic water influx and oversaturation (Arndt et al., 2015). Samples were then removed, dried with tissue, and weighed again to obtain the turgid weight before being oven dried at 80°C until constant weight (dry weight). Leaf relative water content (RWC) was calculated as (*fresh weight – dry weight*)/(*turgid weight – dry weight*). Loss of leaf RWC in WD plants relative to WW plants was used to classify drought stress using Hsiao (1973)'s framework, where mild drought stress = 10 % loss, moderate = 10 – 20 % loss, severe = 20 – 50 % loss and desiccation >50 % loss of RWC.

Data analyses

Data were checked prior to analysis to ensure univariate normality. Plant biomass data was natural logarithm transformed to avoid bias when calculating growth rate (Hoffmann and Poorter, 2002). All figures and tables show untransformed values. One-way ANOVA was used to analyse differences in traits, leaf RWC and transpiration among species within each watering treatment and within species between watering treatments. Two-way ANOVA was not used as we were not interested in interactions between species and watering treatments. Simple linear regression was used to examine relationships between growth and morphological traits and between traits and physiological response (transpiration and leaf RWC). All statistical analyses were performed in R (R Core Team, 2016).

Results

Transpiration and leaf relative water content

Mean transpiration of the nine spontaneous green roof species was 89.7 g H_2O pot^{-1} day^{-1}. Both *Lolium perenne* and *Trifolium repens* had the highest transpiration rate under well-watered (WW) conditions, transpiring approximately 152 g of water per day (Table 3.2, overleaf). *Euphorbia maculata* (6.9 g H_2O pot^{-1} day^{-1}) had the lowest rate of transpiration under WW, followed by *Euphorbia peplus* (38.8 g H_2O pot^{-1} day^{-1}).

Under WD, *L. perenne* (98.1 g H_2O pot^{-1} day^{-1}) maintained the highest transpiration rate, and *E. maculata* (8.3 g H_2O pot^{-1} day^{-1}) and *E. peplus* (22 g H_2O pot^{-1} day^{-1}) maintained the lowest transpiration. All species except *E. maculata* and *Malva neglecta* significantly reduced their transpiration under WD when compared with WW conditions. For the other seven species, reductions in transpiration between WW and WD conditions ranged between 28 (*Solanum nigrum*) and 46 % (*T. repens*), with an average reduction of 35 % across all seven species.

Leaf relative water content (RWC) under WW conditions was > 90 % for all species. Under WD, *E. maculata* and *E. peplus* had the highest RWC of all species (> 90 %), indicating mild drought stress. The other seven species did not maintain leaf water status; *M. neglecta*, *R. acetosa*, *P. lanceolata* and *Polycarpon tetraphyllum* had severe drought stress (20 – 50 % loss of RWC) and *L. perenne* exhibited desiccation (> 50 % loss) (Hsiao 1973).

Table 3.2 Mean (± SE, n=6) transpiration, leaf relative water content and relative growth rate under well-watered (WW) and water-deficit (WD) conditions for the nine common spontaneous green roof species evaluated in the glasshouse experiment. Bolded P-values indicate significant differences between WW and WD treatments within each species (P-value <0.05). Different letters indicate significant differences between species within WW or WD treatments (all P-values <0.001).

	Transpiration (g H_2O pot^{-1} d^{-1})			Leaf relative water content (%)			Relative growth rate (mg g^{-1} d^{-1})		
Species	WW	WD	*P*	WW	WD	*P*	WW	WD	*P*
E. maculata	7.0 ^{i} (4.1)	8.3 ^{i} (3.4)	0.547	98.1 ^{a} (0.4)	96.7 ^{ab} (0.7)	0.139	133 ^{g} (11.4)	112 ^{h} (13.7)	**0.016**
E. peplus	38.8 ^{gh} (14.6)	22.0 ^{hi} (5.8)	**0.026**	95.0 ^{abcd} (0.7)	90.4 ^{abcd} (2.2)	0.091	101 ^{g} (40.3)	50 ^{h} (34.5)	**0.039**
L. perenne	152.3 ^{a} (3.9)	98.1 ^{abc} (1.6)	**0.002**	97.9 ^{a} (1.1)	49.9 ^{f} (3.4)	**<0.001**	396 ^{a} (47.5)	389 ^{ab} (32.2)	0.775
M. neglecta	47.2 ^{fgh} (11.3)	46.3 ^{fgh} (7.2)	0.869	94.7 ^{abcd} (1.8)	75.3 ^{de} (6.1)	**0.028**	253 ^{ef} (37.1)	254 ^{fg} (17.0)	0.972
P. lanceolata	142.4 ^{a} (10.1)	89.7 ^{bcd} (10.5)	**<0.001**	97.6 ^{a} (0.5)	62.2 ^{ef} (8.9)	**0.011**	381 ^{abc} (29.2)	332 ^{bcd} (36.4)	**0.028**
P. tetraphyllum	70.4 ^{def} (9.4)	55.5 ^{efg} (9.4)	**0.021**	95.8 ^{abc} (0.3)	60.6 ^{ef} (8.5)	**0.009**	247 ^{f} (18.7)	208 ^{g} (39.5)	0.058
R. acetosa	113.2 ^{b} (23.2)	66.2 ^{def} (4.7)	**0.001**	94.6 ^{abcd} (0.7)	75.7 ^{cde} (4.7)	**0.011**	383 ^{abc} (39.8)	324 ^{cd} (19.7)	**0.008**
S. nigrum	78.5 ^{cde} (10)	56.4 ^{efg} (4.5)	**0.001**	95.7 ^{abc} (1.1)	54.8 ^{f} (3.2)	**<0.001**	330 ^{bcd} (5.5)	307 ^{def} (15.0)	**0.005**
T. repens	152.2 ^{a} (10.3)	86.5 ^{cd} (7.9)	**<0.001**	89.7 ^{abcd} (1.2)	53.5 ^{f} (5.3)	**0.001**	365 ^{abcd} (13.8)	317 ^{de} (19.9)	**0.001**

Plant traits (relative growth rate, biomass, leaf area and specific leaf area)

Relative growth rate (Table 3.3, overleaf) under WW conditions ranged from 101 (*E. peplus*) to 396 mg g^{-1} day $^{-1}$ (*L. perenne*). Under WW conditions, the fastest growing species (*L. perenne*; 396 mg g^{-1} day $^{-1}$) grew almost 300 % faster than the slowest growing species (*E. peplus*; 101 mg g^{-1} day $^{-1}$). Under WD, relative growth rate declined significantly, from seven (*S. nigrum*) to 50 % (*E. peplus*) for all species except *L. perenne*, *M. neglecta* and *P. tetraphyllum*.

Biomass under WW differed significantly among the nine common spontaneous green roof species (Table 3, overleaf). *Lolium perenne* had the greatest biomass (59.4 g); more than twenty times greater than the smallest species *E. peplus* (2.95 g). All species except *L. perenne*, *M. neglecta* and *P. tetraphyllum* significantly reduced their biomass under WD. Reductions in biomass between WW and WD conditions ranged from 18 (*E. maculata*) to 47 % (*R. acetosa*), with an average reduction in biomass of 34 %.

Total leaf area under WW conditions ranged between 134 cm^2 (*E. maculata*) and 1584 cm^2 (*R. acetosa*). Under WD conditions all species except *L. perenne* and *P. tetraphyllum* significantly reduced their total leaf area. Reductions in total leaf area ranged from 39 (*E. maculata*) to 78 % (*T. repens*), with an average reduction in total leaf area of 61 %.

Specific leaf area (SLA) under WW conditions ranged between 12.3 (*L. perenne*) and 33.9 m^2 kg^{-1} leaf (*E. peplus*). Under WD conditions all species other than *E. peplus*, *L. perenne* and *P. tetraphyllum* significantly reduced their SLA under WD. Reductions in SLA ranged from 28 (*E.* maculata) to 47 % (*T.* repens).

Table 3.3 Mean (± SE, n=6) total dry mass, leaf area, leaf area ratio (LAR) and specific leaf area (SLA) under well-watered (WW) and water-deficit (WD) conditions for the nine common spontaneous green roof species evaluated in the glasshouse experiment. Bolded P-values indicate significant differences between WW and WD treatments within species (P-value <0.05). Different letters indicate significant differences between species within WW or WD treatments (all P-values <0.001).

	Total dry mass (g)			Total leaf area (cm^2)			Specific leaf area (m^2 kg^{-1} leaf)		
Species	WW	WD	*P*	WW	WD	*P*	WW	WD	*P*
E. maculata	3.8 ^{h} (.2)	3.1 ^{h} (.2)	**0.019**	133.7 ^{c} (35.7)	81.1 ^{b} (16.9)	**0.009**	13.4 ^{efg} (1.1)	9.8 ^{fg} (.8)	**0.024**
E. peplus	2.9 ^{i} (.4)	1.7 ^{i} (.3)	**0.038**	254.1 ^{bc} (40.1)	93.1 ^{b} (22.6)	**<0.001**	33.9 ^{a} (.7)	28.3 ^{ab} (4.5)	0.273
L. perenne	59.4 ^{a} (9.8)	53.1 ^{ab} (6.2)	0.599	440.0 ^{bc} (313)	263.1 ^{ab} (252)	0.306	12.3 ^{fg} (.7)	8.6 ^{fg} (2.1)	0.150
M. neglecta	13.7 ^{efg} (1.9)	13.2 ^{efg} (.9)	0.823	454.3 ^{bc} (117.9)	210.4 ^{ab} (30.4)	**0.001**	24.7 ^{abcd} (1.0)	14.7 ^{def} (1.1)	**<0.001**
P. lanceolata	49.0 ^{abc} (6.7)	30.4 ^{cde} (4.2)	**0.045**	1424.7 ^{a} (350)	561.6 ^{a} (368)	**0.002**	14.1 ^{efg} (1.3)	9.1 ^{fg} (.8)	**0.011**
P. tetraphyllum	12.2 ^{efg} (2.0)	8.9 ^{fg} (1.9)	0.154	214.7 ^{bc} (32.5)	195.6 ^{ab} (21.4)	0.833	14.6 ^{def} (1.0)	11.3 ^{fg} (1.1)	0.058
R. acetosa	50.4 ^{ab} (6.3)	26.8 ^{def} (2.2)	**0.012**	1584.0 ^{a} (543)	498.0 ^{a} (293)	**0.002**	26.3 ^{ab} (1.1)	15.6 ^{cdef} (2.7)	**0.010**
S. nigrum	28.3 ^{de} (.63)	22.7 ^{def} (1.4)	**0.008**	666.7 ^{b} (74.3)	226.9 ^{ab} (103.8)	**<0.001**	25.0 ^{abc} (.46)	15.5 ^{cdef} (1.5)	**0.002**
T. repens	40.1 ^{bcd} (2.2)	25.2 ^{def} (4.3)	**<0.001**	1347.0 ^{a} (305)	298.8 ^{ab} (131.1)	**<0.001**	22.9 ^{bcde} (1.2)	13.1 ^{efg} (1.1)	**<0.001**

Relationships between transpiration, leaf relative water content and plant traits

Transpiration under WW conditions was positively related to growth rate, biomass, and total leaf area. Under WW conditions, species with greater transpiration had higher RGR (R^2=0.78; p=<0.001; Figure 3.1 A), total biomass (R^2=0.83; *p*=<0.001; Figure 3.1 B) and leaf area (LA) (R^2=0.43; *p*=0.033; Figure 3.1 C) than those with lower transpiration. There was no relationship between transpiration and specific leaf area (SLA) under WW conditions (R^2=-0.08; *p*=0.530; Figure 1 D).

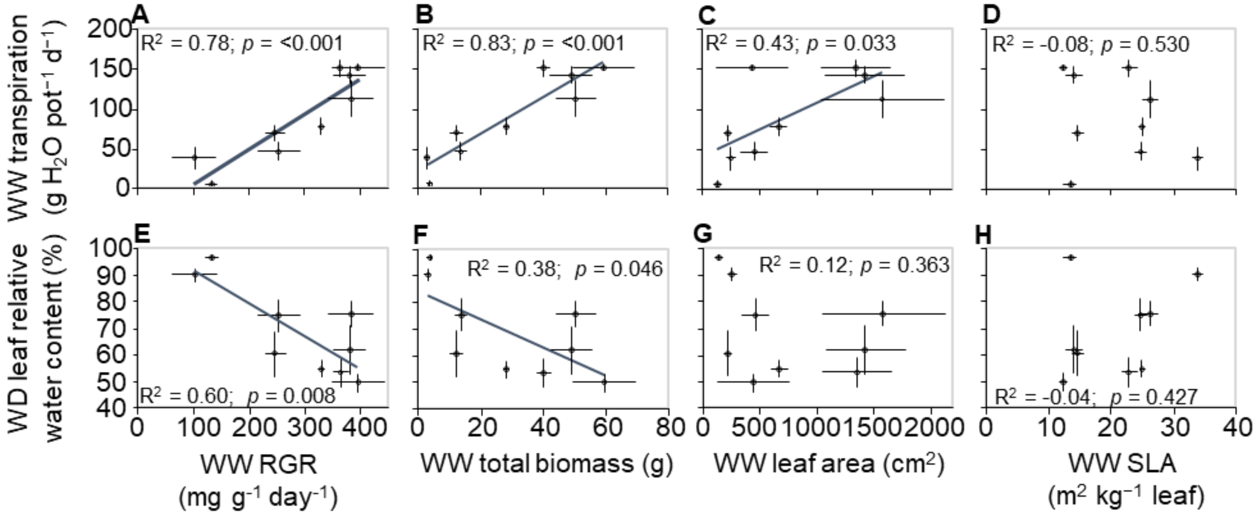

Figure 3.1 Relationships between transpiration and A) relative growth rate (RGR), B) total biomass, C) leaf area and D) specific leaf area (SLA) under well-watered (WW) conditions, and relationships between leaf relative water content under water-deficit (WD) conditions and E) RGR, F) total biomass, G) leaf area and H) SLA under WW for the nine common spontaneous green roof species evaluated in the glasshouse experiment.

Leaf relative water content (RWC) under WD was negatively correlated to growth rate and biomass under WW conditions. Under WD conditions, species with greater leaf RWC had lower relative growth rate (RGR) (R^2=0.60; p=0.008; Figure 3.1 E) and biomass (R^2=0.38; p=0.046; Figure 3.1 F). There was no significant relationship between leaf RWC under WD conditions and leaf area (R^2=0.12; p=0.36; Figure 3.1 G) or SLA (R^2=-0.04; p=0.427; Figure 3.1 H) under WW conditions.

Relationships between transpiration under well-watered and water-deficit conditions

Transpiration under WD conditions was positively related to transpiration under WW, i.e. species with greater transpiration under WD conditions had greater transpiration under WW conditions (R^2=0.94; *p*=<0.001; Figure 3.2 A).

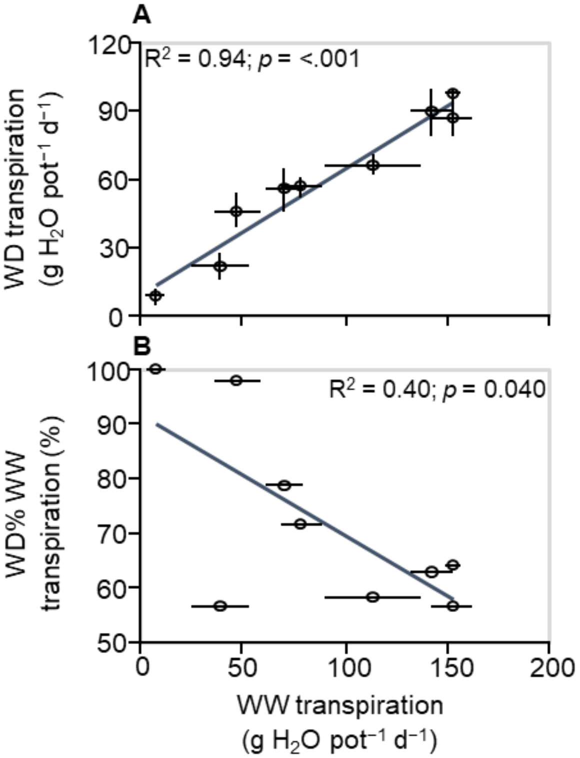

Figure 3.2 Relationships between transpiration under well-watered (WW) conditions and A) water-deficit (WD) transpiration and B) WD transpiration as a percentage of WW transpiration (WD% WW) for the nine common spontaneous green roof species evaluated in the glasshouse experiment.

The percentage of transpiration under WD relative to WW conditions was positively related to transpiration under WW conditions (R^2=0.40; *p*=0.040; Figure 3.2 B). Species with greater transpiration under WW conditions downregulated their transpiration under WD to a greater degree than those with lower transpiration under WW conditions.

Relationships between transpiration and leaf RWC

Transpiration under WW conditions was negatively related to leaf relative water content under WD; species with greater transpiration under WW conditions had lower leaf RWC under WD conditions (R^2=0.58; *p*=0.010; Figure 3.3 A, overleaf). Although species that had greater transpiration under WW reduced their transpiration to a greater extent under WD, there was no significant relationship between transpiration under WD expressed as a percentage of WW transpiration (WD % WW) and leaf RWC under WD (R^2=0.04; *p*=0.282; Figure 3.3 B).

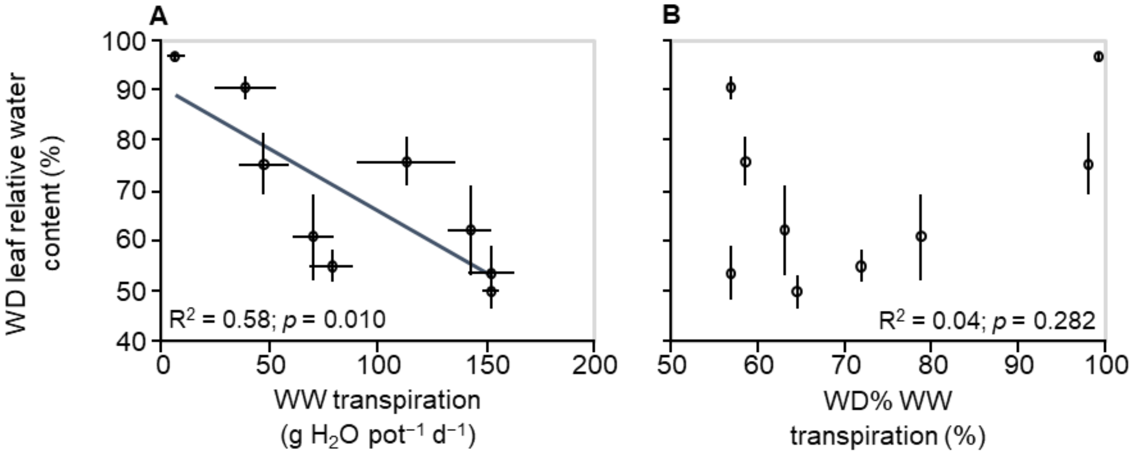

Figure 3.3 Relationships between leaf relative water content (RWC) under water-deficit (WD) conditions and A transpiration under well-watered (WW) conditions and B) WD transpiration as a percentage of transpiration under WW (WD% WW) for the nine common spontaneous evaluated in the glasshouse experiment.

Discussion

Long term studies of green roofs show that spontaneously colonising species eventually replace original designed plantings in the absence of maintenance. However, due to the success of spontaneous species in colonising green roofs, these species may contribute to stormwater mitigation and understanding how their traits relate with water use and drought response may help improve plant selection for green roofs. Therefore, we conducted an eight-week glasshouse experiment with nine species that commonly colonise green roofs to determine their water use and drought response strategies and relate these with their morphological traits. We hypothesised that species with 'fast' traits such as high relative growth rate (RGR) and leaf area would have greater water use than species with 'slow' traits. We also anticipated a trade-off between water use under WW conditions and drought tolerance under WD.

Species with 'fast' traits have greater water use than species with 'slow' traits

Greater transpiration under WW conditions was associated with 'fast' traits such as greater biomass, leaf area and RGR in the nine spontaneous species evaluated in our experiment. Vegetation surveys of green roofs have shown that species with 'fast' traits in our study, such as *Lolium perenne*, *Trifolium repens* and *Solanum nigrum*, are found on newly installed green roofs (Archibold and Wagner, 2007; Dunnett et al., 2008b; Köhler, 2006; Van Mechelen et al., 2015); whereas species with 'slow' traits, such as *Euphorbia peplus* and *E. maculata*, become increasingly dominant as green roofs age (Catalano et al., 2016). Fast traits are generally advantageous in resource-rich environments (Davis et al., 2000; Grime, 1974, 1977; Gross et al., 2008; Reich, 2014) and the dominance of 'fast' species on newly established green roofs reflects their higher fertility and the use of supplementary water for plant establishment (Buffam and Mitchell, 2015). Species with greater transpiration are desirable on a green roof as they will replenish substrate storage capacity for rainfall retention (Farrell et al., 2013).

The highest transpiring spontaneous species in our study (*L. perenne*) transpired more water than reported in other green roof plant selection experiments which quantified water use. For example, the daily water use on a pot basis of *L. perenne* was greater than 14 out of 20 shrub species evaluated by Du et al. (2018b) and 19 % greater than the highest transpiring species (*Isotoma axillaris*) evaluated by Farrell et al. (2013). In our study the lowest transpiring species (*E. maculata*), also had the same daily water use as the *Sedum* species (*Sedum pachyphyllum*) used for comparison in Farrell et al. (2013)'s study.

Trade-off between water use under well-watered conditions and drought resistance under water-deficit conditions

While 'fast' species in our study were able to reduce their transpiration by 57-72% under water-deficit (WD), this was insufficient to maintain their leaf water status and avoid drought stress (leaf RWC <70%; Table 3.4, overleaf). Significant reductions in transpiration under drought conditions in the species with 'fast' traits in our study likely arise from higher stomatal sensitivity (Jarvis and McNaughton, 1986) that can help plants avoid drought stress over short periods of water-deficit (Chaves et al., 2002). This response is consistent with a 'fast' resource use strategy (Reich, 2014), where species with 'fast' traits dedicate considerable resources to reproduction (Grime, 1977; Nicotra and Davidson, 2010). While this strategy will likely lead to plant death if drought conditions are severe, the capacity of these species to mature quickly and set seed may mean species with 'fast' traits can recolonise the roof following periods of water-deficit when water availability increases (Bevilacqua et al., 2015) On older green roofs, the seed bank can contain more than 80 % spontaneous species with a higher proportion of species with 'fast' traits than in the established vegetation (Vanstockem et al., 2018). Indeed, all spontaneous species with 'fast' traits in our study had begun to set seed prior to the end of the experiment (pers. obs.). In this sense it may not be critical that annual species with 'fast' traits tolerate water-deficit on a green roof if they can avoid it via seed dormancy and return when water availability increases. In temperate and

Mediterranean climates, increased water availability often coincides with reduced evaporative demand and hence the time when stormwater mitigation is most desirable (Razzaghmanesh and Beecham, 2014).

Table 3.4 Synthesis of key results categorising the nine common spontaneous green roof species evaluated in the glasshouse experiment according to: (1) transpiration under well-watered conditions, (2) reduction in transpiration between well-watered and water-deficit conditions and (3) water status (leaf relative water content; RWC) under water-deficit at harvest. Adapted from Farrell et al. (2013).

Characteristic	Category 1	Category 2	Category 3
Transpiration when well-watered	**High transpiration (>70 g H_2O pot^{-1} d^{-1})** *S. nigrum* *L. perenne* *T. repens* *P. lanceolata* *R. acetosa*	**Moderate transpiration (30-50 g H_2O pot^{-1} d^{-1})** *E. peplus* *M. neglecta* *P. tetraphyllum*	**Low transpiration (<20 g H_2O pot^{-1} d^{-1})** *E. maculata*
Reduction in transpiration between well-watered and water-deficit conditions	**High reduction (>40 %)** *E. peplus* *R. acetosa* *T. repens*	**Moderate reduction (20 – 40 %)** *L. perenne* *P. lanceolata* *P. tetraphyllum* *S. nigrum*	**Low reduction (<20 %)** *E. maculata* *M. neglecta*
Leaf relative water content (%) under water-deficit	**High leaf relative water content (>90%)** *E. maculata* *E. peplus*	**Moderate leaf relative water content (70 – 90 %)** *M. neglecta* *R. acetosa*	**Low leaf relative water content (<70 %)** *S. nigrum* *L. perenne* *T. repens* *P. lanceolata* *P. tetraphyllum*

Species with ‘slow’ traits such as lower biomass, leaf area and RGR under WW conditions used less water under both WW and WD conditions. Low biomass and leaf area have been shown to confer a competitive advantage on green roofs with low resources by decreasing plant vulnerability to drought stress (Nagase and Dunnett, 2010). Hence, on older green roofs without maintenance, spontaneous species with ‘slow’ traits are more abundant that species with ‘fast’ traits (Bates et al., 2013; Ksiazek-Mikenas and Köhler, 2018; Thuring and Dunnett, 2019). Due to lower transpiration, species with ‘slow’ traits may be more likely to tolerate periods of water-deficit yet are unlikely to provide optimal stormwater mitigation on green roofs. However, Szota et al. (2017) showed that low water-using species which were able to avoid drought stress could still achieve high (66-81 %) rainfall retention on green roofs in Melbourne's Mediterranean-type climate. Hence, older green roofs which are not maintained may still provide significant stormwater mitigation if vegetation cover of spontaneous species with 'slow' traits is high.

Species with 'fast' traits generally had greater trait plasticity between watering treatments. This is consistent with the literature, where faster growing invasive species generally have more phenotypic plasticity than co-occurring non-invasive species with slower growth (Bossdorf et al., 2005; Davidson et al., 2011; Lacey et al., 2021). One exception was *L. perenne*, which reduced transpiration by approximately 36 % but did not significantly reduce its biomass, leaf area, or growth rate under WD conditions. As perennial grasses like *L. perenne* are capable of rapid recovery from drought (Florence et al., 1998), *L. perenne* may have maintained growth under WD (Poorter et al., 2012), resulting in similar traits between treatments.

There was no relationship between specific leaf area (SLA) and RGR or between SLA and transpiration in our study. This is in contrast with other studies which have shown positive relationships between SLA and RGR (Hunt and Cornelissen, 1997; Reich et al., 1999; Villar et al., 2005) and reduced SLA has been related to greater water-use efficiency in Mediterranean vegetation (Ackerly, 2004). For this reason, low SLA has been used to select non-succulent plants for Mediterranean green roofs (Van Mechelen et al., 2014). However, we found no relationship between SLA and leaf water status in our study. This reflects two studies that evaluated Australian native plants for green roofs and showed no relationship between SLA and drought tolerance for 12 rocky outcrop species (Farrell et al., 2013), and 20 shrub species from different climates of origin (Du et al., 2018). This suggests that relationships between SLA, water use and drought response may be species or life-form specific, and SLA should not be used as a single trait to select green roof plants.

Different drought response strategies in species with ‘slow’ traits

The two slowest species were both Euphorbias (*E. maculata* and *E. peplus*), yet these species had different strategies to maintain leaf RWC under WD. *E. maculata* maintained water use in both treatments, whereas *E. peplus* significantly reduced transpiration under WD. This reflects the study by Farrell et al. (2013) that showed that species which can either maintain low water use or down-regulate water use can both maintain leaf water status under water-deficit. Differences in water use under WD likely reflect differences in photosynthetic pathways; *E. maculata* has a C^4 and *E. peplus* C^3 photosynthesis pathway (Batanouny et al., 1991; Kalapos et al., 1997). Lower water use in *E. maculata* reflects greater water use efficiency associated with the C^4 pathway (Osmond et al., 1982) and C^4 *Euphorbia* species occur in hot and arid regions, whereas C^3 Euphorbias are native to regions with higher moisture availability (Pearcy, 1975). This result highlights the need to consider multiple traits in unison when considering the suitability of taxonomically related species for planting on a green roof.

Implications for spontaneous green roofs

The diverse water-use and drought response strategies of the nine spontaneous species we evaluated reflects the dynamism of green roof environments (Williams et al., 2010), where fluctuating conditions likely favour different strategies through time (Chesson, 2000). Hence, as green roofs age, spontaneous green roof plant assemblages have been shown to reach somewhat of an equilibrium among different functional types (Catalano et al., 2016; Köhler, 2006). In naturally occurring annual plant communities, increased functional diversity has been shown to reduce inter-species competition (Dovrat et al., 2019) and this may increase green roof stormwater mitigation because of greater spatial and temporal variation in resource partitioning (Lundholm, 2015). Therefore, the diversity of water-use and drought response strategies exhibited by the spontaneous green roof species in this study could provide temporal stability in stormwater capture on green roofs, despite their shorter lifespan.

Our experiment considered plant species in isolation and not as assemblages. Further research is necessary to determine how interactions between spontaneous green roof species influences stormwater retention and recruitment dynamics at the community level. Additionally, spontaneous species may be problematic when they do not fit the green roof’s original design intent. However, limitations in the capacity to retrofit many existing buildings with intensive, deep substrate green roofs necessary for many non-succulent species, may mean that the practical benefits of using spontaneous species to colonise shallow green roofs outweigh other considerations.

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Chapter 4 : Response of spontaneous plant communities to *Sedum mexicanum* cover and water availability in green roof microcosms.

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Abstract

Lack of maintenance can lead to ‘weedy’ spontaneous vegetation on green roofs. Aspects of green roof design, including substrate depth and roof height, have been shown to influence the composition of spontaneous vegetation. In drier climates, *Sedum* species are often planted on shallow substrate ‘extensive’ green roofs and irrigated during summer to maintain cover. However, the response of spontaneous vegetation to *Sedum* cover and water availability is unclear. Understanding this relationship could help minimise maintenance and maintain *Sedum* vegetation cover. We hypothesised that increasing *Sedum* (*Sedum mexicanum*) cover and reduced water availability would reduce the abundance, biomass, species and functional richness, and the community weighted mean specific leaf area (SLA; CWM by abundance) of spontaneous plant communities. We conducted a 10-month experiment in green roof microcosms planted with *S. mexicanum* (0, 25, 50, 75 and 100% total cover), subjected to a well-watered or water-deficit irrigation treatment, and sown with a mix of 14 plant species that commonly occur as spontaneous on green roofs. We measured spontaneous species abundance, community biomass, and functional traits (specific leaf area, leaf dry matter content, and relative growth rate), and calculated species and functional richness. Increasing *S. mexicanum* cover reduced spontaneous species abundance and species and functional richness but did not affect community biomass. Species richness was affected by the interaction of *S. mexicanum* cover and watering treatment and was greatest in well-watered microcosms with 0% *S. mexicanum* cover. Increased water availability increased spontaneous plant biomass but did not affect functional richness. The SLA of spontaneous communities was affected by the interaction of *S. mexicanum* cover and

watering and was significantly greater in well-watered treatments where *S. mexicanum* cover was <100%. Therefore, maximising *Sedum* cover and limiting water availability on green roofs will likely limit the abundance, biomass, and diversity of spontaneous vegetation. Conversely, for green roofs where substrate is left to be naturally colonised, increasing water availability could encourage establishment and increase functional richness of spontaneous vegetation.

Introduction

On extensive green roofs, good vegetation coverage can enhance green roof functionality and the provision of ecosystem services, such as thermal insulation [1,2], stormwater mitigation [3,4], habitat provision [5,6] and improved mental health and wellbeing [7-9]. However, fluctuating temperatures, high evaporation, wind exposure, and shallow (<20 cm) substrate depths on extensive green roofs can limit plant growth and survival [10,11]. Green roof practitioners therefore often select plant species with traits thought to improve plant survival in extreme environments (i.e., trait approach) [12,13], or that originate from natural habitats analogous to green roofs (i.e., habitat template approach) [14]. Succulent species from the genus *Sedum* are commonly planted on extensive green roofs due to their low-growing habit, shallow root system, high leaf succulence, water use efficiency and drought tolerance [15-17]. In semi-arid Mediterranean climates, research demonstrates that *Sedum* species, including *Sedum album*, *S. sediforme*, and *S. sexangulare*, can be successful on green roofs when planted as seedlings [18], whereas their growth capacity is diminished when they are seeded [19]. Yet, without routine maintenance, green roof plantings are often replaced by spontaneous vegetation [6,20], a process encouraged on biodiverse green roofs [21,22]. Spontaneous plants exist on green roofs without human intervention, suggesting a level of short-term adaptation to the green roof environment. However, the longevity of such adaptations under more extreme conditions remains an open question. Nonetheless, understanding how green roof conditions affect their growth and establishment could help inform green roof design, plant selection, and maintenance.

Existing green roof vegetation influences the success of spontaneously colonising species. Increasing vegetation cover and planting density limits the availability of bare substrate gaps that may otherwise provide microsites suitable for germination and establishment of spontaneous species (i.e., ‘safe sites’ [23]). However, the influence of established green roof vegetation on the coverage, species richness, and functional diversity of spontaneously colonising species, is inconsistent. For example, [24] showed greater functional diversity of existing green roof vegetation decreased spontaneous vegetation cover, whereas [25] showed a positive relationship between existing plant species richness and spontaneous species richness. Notably, [26] demonstrated that varying densities of existing plant species had a consistent negative effect on the abundance of spontaneous species. These results suggest that existing plant coverage and density may be more important than species richness in limiting spontaneous plants on green roofs.

Water availability can shift the nature of competitive/facilitative interactions between existing vegetation and spontaneous species [27,28]. Extensive green roofs can quickly become water limited, owing to freely draining substrates with low water retention [29,30] and high evaporative demand on rooftops [31]. Supplementary irrigation is often essential to establish vegetation on extensive green roofs, particularly in hot and dry climates [32,33]. Although irrigation promotes the health and survival of existing green roof vegetation, studies have also shown that irrigation during establishment increases spontaneous plant cover and richness on green roofs [34]. Greater water availability on green roofs located in higher rainfall areas in Scandinavia also increases spontaneous plant cover [35]. While lower water availability may limit spontaneous plant biomass and richness, the ‘stress-gradient’ hypothesis [36,37] suggests existing plant cover may facilitate spontaneous plant coverage under these conditions. On green roofs this was shown where *Sedum album* impeded the growth of neighbouring herbaceous perennials (*Agastache rupestris* and *Asclepias verticillate*) when water availability was high but facilitated their growth in hotter and drier conditions [38].

Competitive and facilitative effects of *Sedum* cover on green roofs are also likely to differ according to growth and resource use strategies of spontaneous plant species. Due to niche trade-offs, colonising spontaneous species that have different growth and resource use strategies to existing *Sedum* cover are likely to be more successful than those with functionally analogous traits [39]. *Sedum* species are typically stress tolerant, having high leaf succulence and CAM (Crassulacean Acid Metabolism) or facultative CAM/C3 photosynthesis [40] and static, conservative water use strategies [12,41]. Therefore, spontaneous species with resource acquisitive traits such as fast growth, high specific leaf area and high water use strategies [42] should be more successful on green roofs with high *Sedum* cover. This is consistent with [43] who showed most species colonising green roof plots planted with *Sedum* mats in Malmö, Sweden was fast growing 'ruderal' [44] species such as *Erophila verna*, *Poa alpina* and *Cerastium pumilum*. However, the effects of *Sedum* cover on the traits of spontaneous green roof plant assemblages have not been investigated.

Functional traits, or features that indirectly impact growth, reproduction, and survival [45] of spontaneous green roof vegetation should reflect the green roof environment where they establish. Specific leaf area (SLA) is a key functional trait in plant ecology as it relates with plant fitness, growth, and photosynthesis [46]. Studies have shown that SLA is lower in less productive habitats [47] and typically in-creases with greater precipitation and soil moisture [48]. Lower SLA indicates an increased investment in leaf structural tissue that helps maintain leaf turgor under drought stress [49] and has been related to greater water-use efficiency in Mediterranean vegetation [50]. For this reason, low values of SLA have been used to select non-succulent plants for Mediterranean green roofs [13]. Studies have shown positive relationships between water use and SLA [12,51-52] and higher SLA has been related to increased aboveground biomass and canopy density in experimental green roof mixtures [54].

Extensive green roofs are commonly planted with *Sedum* spp. and provided supplemental irrigation during establishment or during summer months in hot and dry climates [32-33]. However, the influence of these factors on spontaneous plant species growth, abundance, traits and both species and functional richness is unclear. Understanding these factors could help predict and manage spontaneous community composition and inform green roof design, plant selection and maintenance to either minimise or enhance spontaneous vegetation cover and diversity. Therefore, we conducted a green roof microcosm experiment to determine how *Sedum* (*Sedum mexicanum*) cover and water availability influence the growth, abundance, traits and species and functional richness of fourteen common spontaneous green roof plant species. We hypothesised that greater *S. mexicanum* cover and lower water availability would reduce spontaneous green roof plant community biomass, abundance and species and functional richness and reduce the community weighted mean (CWM; by abundance) SLA.

Materials and methods

Species selection and seed collection

We selected 14 globally cosmopolitan plant species that spontaneously occur on green roofs in Australia and across Europe (Table 4.1, overleaf; Schrieke et al., unpublished). Seeds of the fourteen species were collected from green roofs and green roof habitat analogues located across metropolitan Melbourne, Australia in August-September (winter-spring) 2019. Fully mature seeds, indicated by dehiscence, brown colouration or hardness, were harvested, and stored in brown paper bags. Subsequent processing in the lab involved the removal of excess plant material, chaff, and debris to minimise the risk of disease and pests. The seeds were then stored at a consistent room temperature of approximately 20 to 22°C within the same brown paper bags for a period of roughly six months. This period of storage ensured that the commencement of our experiment, marked by the removal of seeds from storage, aligned with their typical germination period.

Seed germination

To determine germination capacity (see Appendix 1.1), five replicates per species, each with 25 sterilised seed (submerged in 3% active chlorine solution for 90 to 120 seconds then rinsed with distilled water) were placed evenly on 3 mm thick 1% agar solution (non-nutrient enriched) in sterilised petri dishes and sealed with parafilm in June 2020. Petri dishes were placed in a growth cabinet (PGX −250, Ningbo Saifu Experimental Instrument Co., Ltd) with an alternating temperature regime of 20/10°C (12/12h light/dark photoperiod) and checked for germination every day for the first two weeks and then every other day for an additional three weeks. Germination was defined by emergence of the radicle through the seed coat. At the end of the germination trial, ungerminated seed was cut lengthways with a scalpel and examined under a dissecting microscope to determine viability. Seed was considered potentially viable if the embryo was intact and endosperm appeared white, turgid, and solid, and non-viable if the embryo appeared damaged, detached, discoloured and/or shrinkage was visible. No ungerminated viable seed were detected. Percentage germination was calculated as = (number of germinated seed / total number of seed sown) x 100.

Table 4.1 Information on the fourteen spontaneous species utilised in the green roof microcosm experiment, along with the respective countries where each species was identified on a green roof.

Species	Family	Common name	Country
Epilobium parviflorum	Onagraceae	Hoary willowherb	Australia, United Kingdom, France, Switzerland, Belgium,
Euphorbia maculata	Euphorbiaceae	Spotted spurge	Australia, France, Belgium
Euphorbia peplus	Euphorbiaceae	Petty spurge	Australia, France, Belgium, New Zealand
Helichrysum luteoalbum	Asteraceae	Jersey cudweed	Australia, United Kingdom, Germany
Malva neglecta	Malvaceae	Common mallow	Australia, Germany
Nepeta cataria	Lamiaceae	Catnip	Australia, Germany
Polycarpon tetraphyllum	Caryophyllaceae	Four-leaf allseed	Australia, France, Sweden, United Kingdom
Portulaca oleracea	Portulacaceae	Common purslane	Australia, France
Rumex crispus	Polygonaceae	Curly dock	Australia, France
Solanum nigrum	Solanaceae	Black nightshade	Australia, France
Sonchus oleraceus	Asteraceae	Common sowthistle	Australia, France, Sweden, Switzerland, New Zealand, United Kingdom
Stellaria media	Caryophyllaceae	Chickweed	Australia, France, United Kingdom
Taraxacum officinale	Asteraceae	Dandelion	Australia, Belgium, Germany, New Zealand, Switzerland, United Kingdom
Trifolium repens	Fabaceae	White clover	Australia, Belgium, France, Switzerland, United Kingdom

Relative growth rate

The relative growth rate (RGR) of the 14 species used in the microcosm experiment was quantified as a metric in our assessment of functional diversity within the vegetation communities. Relative growth rate (see Appendix 1.1) was determined on individual plants sown into pots and grown in a glasshouse at the Burnley Nursery, The University of Melbourne (37°49'42.9"S 145°01'13.8"E) from October (spring) to December (summer) 2019. Ten seeds of each species were sown into 1.9 L (155 x 150 mm) pots (25 pots per species) filled with seed raising mix (10% washed coarse sand, 10% sieved coir peat, 80% medium pine bark) and thinned to the most central germinant. Once four 'true leaves' fully emerged, seedlings were blocked into numbered pairs by biomass (i.e., plants of similar size). One seedling per pair was randomly selected and harvested to determine initial shoot dry weight after oven drying whole plant mass at 70 °C for two days. Remaining seedlings were grown on until flowering (approximately three to four weeks), at which point plants were harvested to determine whole plant dry weight after oven drying at 70 °C for two days. Relative growth rate was calculated from these measurements per [53] as = $(\ln W2 - \ln W1)/(t2 - t1)$, where ln W1 is the natural logarithm-transformed mean of the initial harvest whole plant dry mass (g) and ln W2 is the natural logarithm-transformed mean of the final harvest whole plant dry mass (g).

Experimental design

The 10-month green roof microcosm experiment ran from 24 November 2020 (spring) to 20 September (spring) 2021. Sixty green roof microcosms (HDPE boxes, 55 x 35 x 20 cm) were filled with 15 cm green roof substrate (60% scoria <8 mm, 20% 7 mm scoria, and 20% coir; [12]). This substrate possesses a water retention capacity of 46% and exhibits a bulk density measuring 1.26 g/cm^3 [12]. Microcosms were arranged in a complete randomised block design in a fully enclosed poly-tunnel at the Burnley Nursery, the University of Melbourne (Figure 4.1, overleaf). Other than rainfall and wind, modules were exposed to ambient conditions (see Appendix 1.2). Controlled slow-release fertiliser (Osmocote® Pro, Everris Australia Pty Ltd.: 15 N:1.3 P:10 K) was added to the substrate surface of each microcosm (30 g m^2) after filling with substrate to replicate a newly established green roof. Cuttings of *Sedum mexicanum* were then placed evenly across the soil surface and left to establish for two months until 100% coverage was achieved. Irrigation was applied for one minute twice daily (3.30 L d^{-1} $microcosm^{-1}$) with an automatic irrigation system consisting of six shrubblers® 360° adjustable flow spikes (Antelco Pty Ltd., 33 L h-1 flow rate) evenly spaced within each microcosm to ensure even watering. This regime is designed to mirror a summer 'establishment' watering pattern for *Sedum* on green roofs, thereby promoting the rapid growth of the planted S *mexicanum*.

Figure 4.1 Clockwise from top left, images showing green roof microcosms shortly after sowing of spontaneous species community and just before harvest.

Upon reaching a full (100%) surface coverage of *S. mexicanum*, each microcosm was assigned to one of five coverage treatment categories: 0, 25, 50, 75, or 100% (10 microcosms per cover treatment). These treatments represent different proportions of the module covered by *S. mexicanum*. In the 0% coverage treatment, all *S. mexicanum* biomass, both above and below ground, was completely removed from the microcosm. For the 25, 50 and 75% coverage treatments, a defined area of *S. mexicanum* biomass was selectively removed from the microcosm's centre using rectangular templates. The removed area ranged from complete *S. mexicanum* absence (0% coverage) to a minimal central gap (75% coverage), while the remaining periphery was left with a consistent 100% *S. mexicanum* coverage. This approach ensured the distinct variations in *S. mexicanum* coverage across different treatments, while keeping the *S. mexicanum* density in the remaining areas constant. The 10 microcosms in each coverage treatment were then assigned one of two watering treatments: well-watered (WW) or water deficit (WD), with five replicates of each cover x watering treatment. Well-watered microcosms were irrigated twice daily for one minute (3.30 L d^{-1} $microcosm^{-1}$) to saturate the substrate profile. Whereas WD microcosms received 50% water of WW microcosms, applied once daily (i.e., 1.65 L d^{-1} $microcosm^{-1}$). Temperature (°C) and relative humidity (RH) within the poly-tunnel were recorded at 30-minute intervals using an iButton® Hygrochron Temperature/Humidity Logger (DS1923, Maxim Integrated Products™) and daily averaged (18°C, 68% RH; see Appendix 1.2).

Seed sowing in microcosms

Sixty seed mixes (one per microcosm) of the 14 spontaneous green roof plant species were made based on each species seed mass and percent germination, so that each species had the same potential germination (i.e., species with low germination rate had a higher ratio by weight of seed in mixtures), with a final sowing rate equivalent to one germinant per 5 cm^2. Seed mass (see Appendix 1.3) was measured as the weight of seed after removing all accessories and drying in an oven at 80 °C for three days [56]. Seed mixes were individually blended into 100 ml fine sand to assist spreading and sown evenly across each microcosm surface (24 November 2020; spring) leaving a 5 cm buffer unsown around the perimeter of the microcosm to limit edge effects.

Spontaneous species abundance, biomass, and trait measures

Vegetation surveys were conducted to count and identify spontaneous species at roughly month intervals from 3rd March 2021 (summer) until the end of the experiment (20 September 2021; spring). Following the final species survey, each spontaneous plant species found in microcosms was harvested and divided into leaves and stems. Leaf area was measured per [55] by randomly selecting, stripping, and weighing two fully expanded leaves from each individual plant within each microcosm, then photo-graphed from a height of 20 cm (2nd generation Apple iPhone SE, Apple Inc) and imported into Image J to measure leaf area [56]. All samples were then oven dried at 70 °C until weight was constant to determine aboveground species and community biomass, and leaf mass fraction. Leaf dry matter content was calculated as leaf dry mass (g) divided by leaf fresh weight (g). Specific leaf area (SLA, m^2 kg^{-1} leaf) was calculated as the one-sided leaf area, divided by oven dry mass.

Data analyses

Data were checked prior to analysis to ensure univariate normality; no transformations were necessary. Species richness, functional richness, and community-level weighted means of specific leaf area (by abundance; CWM) were calculated using the FD package [57] in R 4.1.1 [58]. Functional richness, defined as the amount of functional space filled by the community, was determined by coordinating and linking trait values (specific leaf area, leaf dry matter content, and relative growth rate). We included 'block' as a random factor in our analyses to account for any potential variation between blocks. One-way ANOVA was used to identify significant differences in species abundance between watering treatments within each *S. mexicanum* cover treatment, accounting for the block effect. Two-way ANOVA was used to identify interactions between *S. mexicanum* cover and watering treatments for spontaneous species community biomass (total microcosm biomass), species richness and CWM SLA, again with 'block' as a random factor. Tukey's HSD was used for post hoc tests. We examined the residuals from our final models to ensure they meet the assumption of normality and homoscedasticity. All statistical analyses were performed in R 4.1.1 [58].

Results

Species abundance

Total abundance of spontaneous vegetation was significantly affected by *Sedum mexicanum* cover (P<0.001) but there was no effect of watering (P=0.22) and no interaction between treatments (P=0.69; Figure 4.2). Microcosms with 0% *S. mexicanum* cover had the greatest mean total abundance (32 ± 10), followed by those with 25% (18.6 ± 7.5) and 50% *S. mexicanum* cover (16 ± 4.2). Microcosms with 75% (7 ± 3.6) and 100% (4.2± 1.8) *S. mexicanum* cover had significantly lower mean total abundance than microcosms with 0% cover.

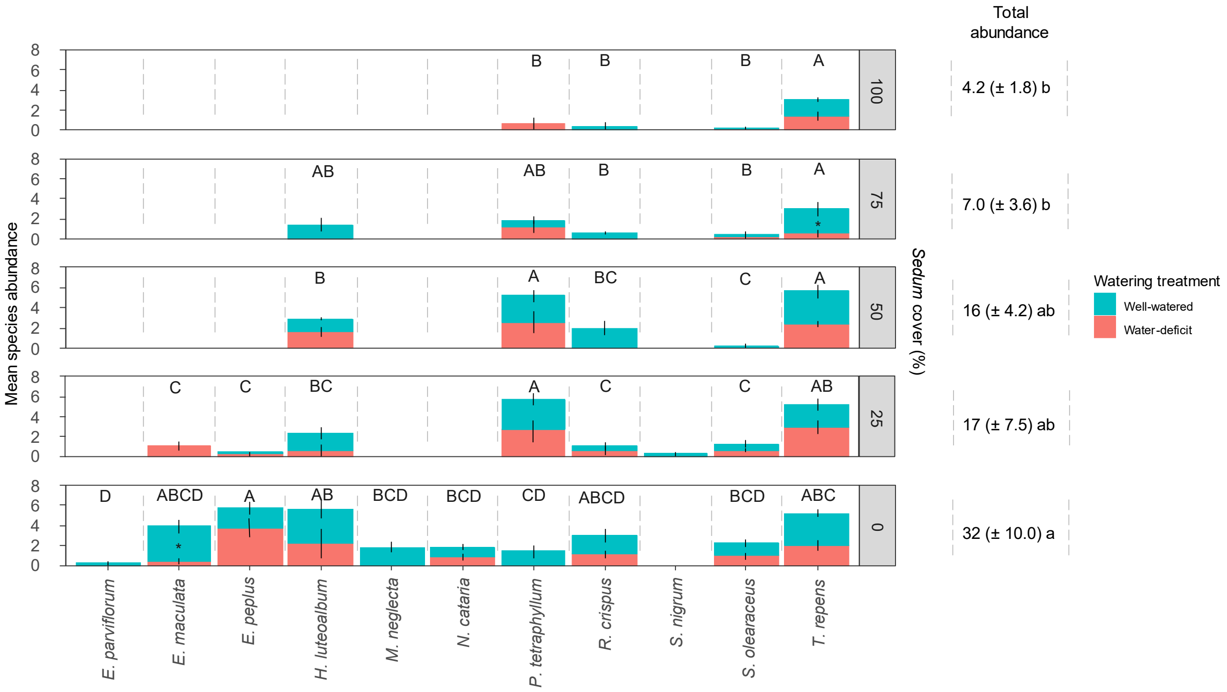

Figure 4.2 Mean abundance of spontaneous species present in green roof microcosms at the end of the experiment. Asterisks indicate significant (P≤0.05) differences in species abundance between watering treatment within Sedum cover class (two-way ANOVA). Dissimilar letters indicate significant differences between species abundance within Sedum *cover class (Tukey's post-hoc test; P≤0.05).*

In the 0% *S. mexicanum* cover treatment with the greatest abundance of spontaneous species, Euphorbia peplus was the most abundant species (well-watered; WW 2.6 ± 0.6; water deficit; WD 4.2 ± 1.6). However, this species was absent in microcosms with 50, 75 and 100% *S. mexicanum* cover, regardless of watering treatment. Similarly, *Euphorbia* *maculata* was highly abundant in WW microcosms with 0% *S. mexicanum* cover (3.6 ± 0.6) but was absent in microcosms with 50, 75 and 100% *S. mexicanum* cover, regardless of watering treatment.

When present, the abundance of *P. tetraphyllum*, *R. crispus*, and *S. oleraceus* was not significantly different in any of the *S. mexicanum* cover or watering treatments. Total abundance *of Trifolium repens* did not change significantly with *S. mexicanum* cover but in 75% *S. mexicanum* cover ($P<0.05$) the abundance of *T. repens* was greater in WW microcosms. Despite having the same theoretical germination capacity, *Portulaca oleracea*, *Stellaria media* and *Taraxacum officinale* were absent from all microcosms. Several species, including *Nepeta cataria*, *Malva neglecta* and *Epilobium parviflorum* were only present at 0% *S. mexicanum* cover.

3.2. Biomass and species richness of spontaneous plant communities

Overall, total biomass of the spontaneous plant community was not significantly affected by *S. mexicanum* cover ($P=0.11$) but was affected by watering treatment, with increased total biomass in WW microcosms ($P<0.001$; Fig 4.3, overleaf). Mean total biomass of the spontaneous plant community in WW microcosms (121.41 g) was 160% greater than in WD microcosms (46.61 g). In all treatments, *Trifolium repens* accounted for >90% of the total biomass (see Appendix 1.4).

Species richness of spontaneous plant communities was significantly affected by *S. mexicanum* cover ($P<0.001$), watering treatment ($P=0.003$) and the interaction between *S. mexicanum* cover and watering treatment ($P=0.03$; Fig. 4.3). Species richness was greatest in microcosms with 0% *S. mexicanum* cover and within this cover class WW microcosms had 52% greater species richness (7.6 ± 0.6) than WD microcosms (5.0 ± 0.5). Species richness in WD microcosms with 0% *S. mexicanum* cover was greater than in microcosms with 75 and 100% *S. mexicanum* cover, regardless of watering treatment. At greater levels of

S. mexicanum cover (25, 50, 75 or 100%), species richness was not significantly different between WW and WD microcosms.

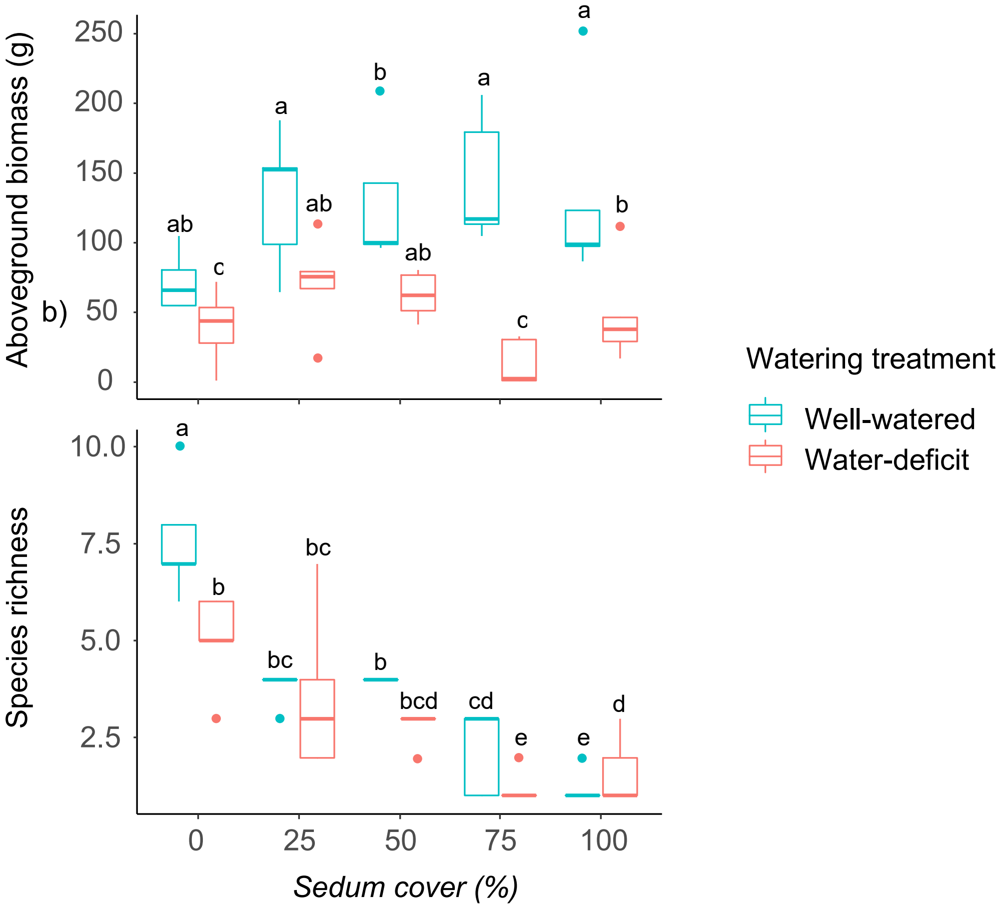

Figure 4.3 a) Aboveground biomass (g) of the spontaneous species community and b) spontaneous community species richness in green roof microcosms at the end of the experiment. Dissimilar letters indicate significant differences between watering treatment and Sedum cover class (Tukey's post-hoc test; P≤0.05).

Spontaneous plant community leaf traits and functional richness

Community weighted mean (by abundance; CWM) specific leaf area (SLA) of the spontaneous species community was significantly affected by *S. mexicanum* cover (P<0.001), watering treatment (P<0.003) and the interaction between *S. mexicanum* cover and watering treatment (P=0.001; Figure 4.4, overleaf). Community weighted mean SLA was greater in WW than WD microcosms in all *S. mexicanum* cover treatments with less than 100% cover.

Functional richness was significantly affected by *S. mexicanum* cover (P<0.001) but there was no significant effect of watering treatment (P=0.31) and no interaction between treatments (P=0.23). Functional richness was greatest at 0% *S. mexicanum* cover, followed by 25% cover. There were no significant differences in Functional richness among 50, 75 and 100% *S. mexicanum* cover.

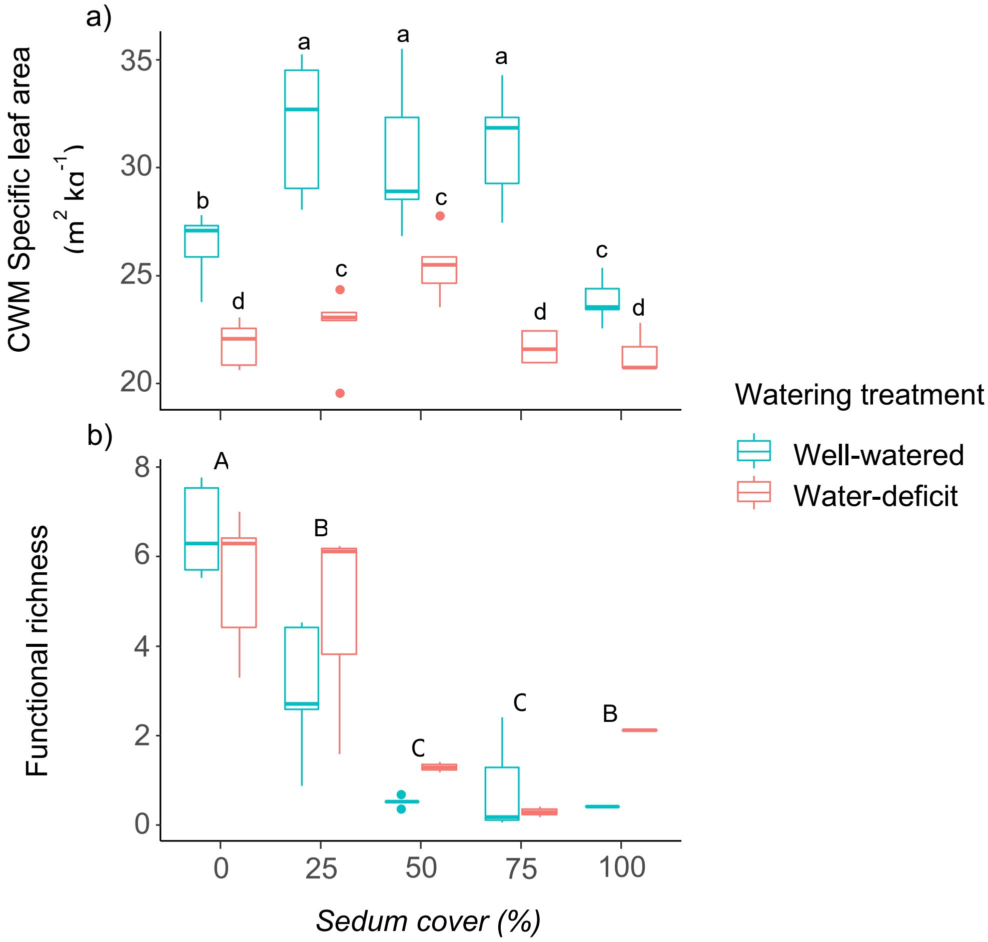

Figure 4.4 a) Abundance weighted community mean (CWM) specific leaf area (m^2 kg^{-1}) and b) functional richness of spontaneous vegetation in green roof microcosms at the end of the experiment. Dissimilar lowercase letters indicate significant differences between watering treatment and Sedum cover class (Tukey's post-hoc test; P≤0.05). Dissimilar capital letters indicate significant (P<0.001) differences between Sedum cover class (two-way ANOVA).

Discussion

We hypothesised that increasing *Sedum* (*S. mexicanum*) cover and lower water availability would reduce the abundance, biomass and species and functional richness of spontaneous green roof plant communities. We also hypothesised that increasing *S. mexicanum* cover and lower water availability would decrease the specific area (SLA; CWM by abundance) of spontaneous green roof plant communities. Increasing *S. mexicanum* cover reduced abundance and functional richness, whereas decreased water availability decreased biomass of spontaneous communities. However, species richness and SLA of spontaneous communities was influenced by an interaction between *S. mexicanum* cover and watering treatment.

Spontaneous community abundance and biomass

Consistent with our hypothesis, spontaneous species abundance declined with increasing *S. mexicanum* cover. We suggested that *S. mexicanum* cover would reduce the availability of microsites suitable for germination and establishment of spontaneous species (i.e., 'safe sites' [23]) and it is likely that the *S. mexicanum* used in our experiment physically prevented seed from reaching the substrate surface and limited light for germination. However, contrary to our hypothesis, abundance of spontaneous species was not influenced by water availability. We expected lower water availability would reduce the abundance of spontaneous species, as establishment irrigation increases spontaneous plant cover and richness on green roofs in Berlin [34] and greater water availability on Scandinavian green roofs due to higher rainfall increases spontaneous plant cover [35]. However, *S. mexicanum* cover may have improved water availability in the water deficit treatment by 'mulching' substrate and reducing evaporation. This is consistent with other pot-based green roof experiments. For example, [61] showed pots planted with *Sedum* acre and *S. reflexum* held more moisture than those with more upright species including *S. kamtschaticum* 'Ellacombianum', *S. scoparium*, *Coreopsis lanceolata* or unvegetated control pots under identical watering regimes, due to greater shading at the substrate surface reducing evaporation. [62] also showed that pots planted with *S. acre* lost significantly less water than 13 other plant species under an 'intermediate' (watered to field capacity every 11 days) watering regime, due to *S. acre*'s conservative water use strategy and shading of the substrate surface. In addition to mulching reducing the loss of water from water-deficit microcosms, the lack of an effect of watering on species abundance may also have been due to increased competition in well-watered microcosms [63], reducing the benefit of greater water availability for some species [36,37].

Contrary to our hypothesis, biomass of the spontaneous plant communities was not significantly affected by increasing *S. mexicanum* cover, but was affected by water availability, with greater biomass in well-watered microcosms. In all treatments, *Trifolium repens* accounted for >90% of spontaneous plant biomass and likely masked differences in biomass amongst cover treatments due to its ability to grow well, regardless of *S. mexicanum* cover. The dominance of *T. repens* may have potentially exerted competitive pressures on other spontaneous species, thereby curtailing their germination and subsequent growth. The low organic matter content of the green roof substrate used in our study [62] likely gave the nitrogen fixing *T. repens* [64] a competitive advantage over other species. Additionally, the leaves of *T. repens* have long petioles, reducing the competitive effect of *S. mexicanum* cover on light availability for photosynthesis. Competition between *S. mexicanum* and *T. repens* was also likely reduced by the ability of *T. repens* to root at nodes across the microcosm surface and its greater rooting depth (up to 20 cm) [66] than *S. mexicanum* (<5 cm) [67]. While *T. repens* growth has been shown to be limited by water availability in pot experiments with green roof substrates [42], this was not the case in our water deficit microcosms with *S. mexicanum* cover. Potentially, the deeper roots of T. repens were able to access water that infiltrated deeper into the substrate profile of microcosms, beyond the shallow substrate depth typically utilised by *Sedum* species [67] like *S. mexicanum*.

Spontaneous community species and functional richness

Species richness of spontaneous communities in microcosms was influenced by the interaction between *S. mexicanum* cover and watering, with greater species richness in well-watered microcosms with no (0%) *S. mexicanum* cover. It is likely that increased water availability and the lack of *S. mexicanum* cover maximised the availability of 'safe sites' in our experiment [23]. However, species richness was not significantly different between well-watered and water deficit microcosms with 25, 50, 75 and 100% *S. mexicanum* cover. This may reflect differences in competition and facilitation, with greater *S. mexicanum* cover increasing competition and limiting species richness in well-watered microcosms, whereas in water deficit microcosms greater *S. mexicanum* cover facilitated species richness. This is consistent with other green roof studies looking at the effects of *S. mexicanum* cover on other plants. For example, when water availability was high on a 13 cm deep green roof in Medford, Massachusetts, *Sedum* album reduced the growth of neighbouring herbaceous perennials (*Agastache rupestris* and *Asclepias verticillate*), whereas it facilitated their growth in hotter and drier conditions [40]. Species richness was also influenced by differences in longevity and germination of the spontaneous plant species sown into microcosms. *Taraxacum officinale* did not germinate in any of the microcosms and both *Nepeta cataria* and *Malva neglecta* did not grow beyond the seedling stage in the 10-month experiment; whereas *Portulaca oleracea* and *Stellaria media* completed their life cycle and set seed prior to the end of the experiment.

Functional richness of the spontaneous plant community was significantly affected by *S. mexicanum* cover but not water availability in our experiment and microcosms with 0% *S. mexicanum* cover had the greatest functional richness. This may be due to 'limiting similarity' [68], whereby the spontaneous species which are most functionally like the *S. mexicanum* are less likely to establish and grow due to niche overlap [69,70]. For example, two species that failed to germinate and grow when *S. mexicanum* coverage was greater than 25% were *Euphorbia maculata* and *Euphorbia peplus*, both species are relatively slow growing species that exhibit conservative water use [42] and facultative CAM/C3 photosynthesis [71]. The presence of *S. mexicanum*, which has similar conservative water use and a facultative CAM/C3 photosynthetic pathway as *E. maculata* and *E. peplus*, may have impacted the germination and growth of *E. maculata* and *E. peplus* through resource limitation, increased competition, and alterations in the microenvironment [72,73]. This is likely the reason for the absence of *E. maculata* and *E. peplus* in microcosms with >25% *S. mexicanum* cover.

Spontaneous community specific leaf area

We also hypothesised that increasing *S. mexicanum* cover and lower water availability would decrease the specific area (SLA; CWM by abundance) of spontaneous green roof plant communities, as low SLA is associated with less productive habitats [74]. Spontaneous plant community SLA was lower in water deficit than well-watered microcosms with less than 100% *S. mexicanum* cover. The lower SLA for spontaneous communities in water deficit microcosms reflects greater investment in leaf structural tissue which is likely to improve leaf turgor under drought stress [50] and is consistent with research showing lower SLA in drier habitats [48,51]. Greater SLA in well-watered microcosms with 25, 50 and 75% *S. mexicanum* cover may also suggest that *S. mexicanum* cover increased soil moisture content and facilitated the spontaneous plant community [62,75,76]. At 100% *S. mexicanum* cover there was no difference in CWM SLA between well-watered and water deficit microcosms, but this likely reflects the dominance of *T. repens*, which has a relatively high SLA, in both watering treatments. Vegetation surveys of established green roofs show that fast growing species with traits such as high SLA are generally found on newly installed green roofs [25,34,77,78]; whereas slower growing, stress tolerant species, such as *E. peplus*, become increasingly abundant as green roofs age [20]. This indicates that the traits of spontaneous green roof communities are likely to change over time, which is something we could not deter-mine in our 10-month experiment.

Conclusions

This research contributes valuable insights into the interplay between plant species management, water availability, and the subsequent impacts on biodiversity and functionality of green roof systems. It has shown that active management strategies like manipulation of *Sedum mexicanum* cover and water availability can significantly influence spontaneous plant community characteristics, adding a new dimension to green roof maintenance and design practices. For example, our experiment indicates that spontaneous species biomass, abundance, and richness can be limited by maintaining at least 25% *S. mexicanum* cover and minimising water availability to what is needed to maintain this plant cover. However, our findings also indicate that some species (e.g., *T. repens*) can become dominant on green roofs regardless of existing plant coverage (i.e., *S. mexicanum* cover) or water availability. Therefore, if green roof practitioners wish to preserve the design of planted vegetation, periodic maintenance measures like hand-weeding may still be necessary. Furthermore, our research provides insights that could be critical for urban biodiversity conservation efforts. For example, where green roof substrates are left to be colonised by spontaneous species, such as on green roofs designed for biodiversity conservation in London [19], our experiment shows that spontaneous plant species abundance, richness and functional diversity will be improved with irrigation on bare substrates or with patchy *S. mexicanum* cover. Our study also highlights the need for continued research in this field. As our experiment ran for 10 months, longer-term studies are necessary to better understand the influence of green roof characteristics, such as *S. mexicanum* cover and water availability, on the development of spontaneous green roof plant assemblages.

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Chapter 5 : Evaluating the Effectiveness of Spontaneous Vegetation for Stormwater Mitigation on Green Roofs

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Abstract

Green roofs can reduce stormwater runoff in urban areas by capturing rainfall. The extent of this capture is partially influenced by vegetation type and cover, which can be manipulated to optimise run-off reduction. However, in the absence of routine maintenance, planted green roof vegetation is often replaced by ‘weedy’ spontaneous species with unknown rainfall retention qualities. To better understand the role of spontaneous vegetation in green roof stormwater mitigation, we undertook a 100-day rainfall simulation involving 14 plant species that occur spontaneously on green roofs in Mediterranean-type climates. Green roof modules were filled with either 7 cm (shallow) or 14 cm (deep) substrate. The substrate was either left bare or sown with the spontaneous species community, which established approximately 100% cover prior to the beginning of the rainfall simulation. During the simulation, modules were subjected to a "dry" and then a "wet" rainfall phase, each based on historical climate records from Melbourne, Australia. The "dry" treatment replicated the timing and depth of the driest rainfall period on record, while the "wet" treatment applied rainfall depths randomly selected from the 90th, 95th, and 99th percentiles of recorded rainfall. Rainfall retention, evapotranspiration, time to initiation of runoff and soil water content was measured for 17 rainfall events. Spontaneous vegetation cover and both species and functional diversity were measured at the end of each rainfall phase, and biomass was measured at the end of the wet phase. During the dry phase, modules with spontaneous vegetation cover retained 88% of applied rainfall regardless of substrate depth and had 6% greater retention than bare substrate. During the wet phase, deep substrate modules with spontaneous vegetation cover had 30% greater retention than other treatment combinations. At the end of the wet phase, spontaneous vegetation in deep substrate had 42% greater biomass, 19% greater coverage

and more than twofold greater functional richness than in shallow substrate. These findings demonstrate that spontaneous vegetation can increase stormwater retention on green roofs relative to bare substrate and have similar retention performance to commonly utilised species. However, the extent to which stormwater mitigation on green roofs is enhanced by spontaneous vegetation is dependent on factors that are more important for rainfall retention, such as substrate depth and rainfall patterns.

1. **Introduction**

Nature-based solutions, such as green roofs, are often implemented to address the negative impacts of stormwater runoff that is associated with high surface imperviousness in cities (Zheng et al., 2021). Impervious surfaces increase the volume of stormwater runoff and peak flow rates, increasing flood risk and degrading receiving waterways (Walsh et al., 2005). Green roofs can intercept and store rainfall in substrates before it is evapotranspired, reducing stormwater runoff volumes, and delaying and reducing peak flow rates (Stovin et al., 2012; Viola et al., 2017). On a per-event basis, rainfall retention performance of green roofs ranges from 0 – 100%, with an average of 62% (Zhang et al., 2021). Variation in rainfall retention is attributed to substrate type and depth, vegetation type and cover, roof geometry, and climatic conditions such as air temperature, wind speed, humidity, rainfall intensity and duration and antecedent dry weather periods (Czemiel Berndtsson, 2010).

Vegetation can increase rainfall retention on green roofs by transpiring water stored in the substrate between rainfall events and replenishing substrate storage capacity (Poë et al., 2015; Wolf and Lundholm, 2008). Although planting species with high water use can increase rainfall retention (Farrell et al., 2013; Kemp et al., 2019; Nagase and Dunnett, 2012), shallow substrates have limited water storage which can lead to severe plant drought stress and poor growth and survival, particularly in hot and dry climates (Durhman et al., 2007; Eksi and Rowe, 2019; Rayner et al., 2016; Williams et al., 2021). Drought tolerant succulents, such as some *Sedum* spp., are often planted on shallow green roofs (Oberndorfer et al., 2007; Snodgrass and Snodgrass, 2006) but they have low water-use which limits their ability to restore substrate water storage between rainfall events and therefore improve rainfall retention (Dunnett et al., 2008a; Wolf and Lundholm, 2008).

Climate change is anticipated to increase extreme heat events in many cities, as well as increasing rainfall variability (McCarthy et al., 2010; IPCC, 2018). Species other than *Sedum* are increasingly likely to fail on unirrigated extensive green roofs, particularly in hot and dry climates (Guo et al., 2021; Rayner et al., 2016). Providing irrigation and increasing substrate depth (Olly et al., 2011) to support a greater plant diversity on green roofs increases engineering and maintenance costs. Increased expense may inhibit the retrofitting of green roofs to older buildings or their adoption in lower socio-economic areas, such as cities in economic decline or those in the global south, where the ecosystem service benefits provided by green roofs may be most needed (Schrieke et al., 2021). Therefore, an alternative cost-effective approach is necessary to maintain plant cover and maximise rainfall retention on green roofs.

In the absence of routine maintenance, green roofs are often colonised by ‘weedy’ spontaneous vegetation which can become dominant (Catalano et al., 2016; Madre et al., 2014; Vanstockem et al., 2019). Spontaneous vegetation cover is encouraged on ‘brown’ biodiversity green roofs (Grant, 2006; Ishimatsu and Ito, 2013) and has been shown to provide habitat for rare invertebrates (Williams et al., 2014) and resources for pollinators (Wang et al., 2017). As green roof vegetation type has been shown to influence rainfall retention, alongside planting characteristics such as canopy size and structure, cover and density, and leaf morphology (Lundholm et al., 2010; Nagase and Dunnett, 2012), spontaneous vegetation could contribute to mitigating stormwater runoff.

The composition of spontaneous green roof vegetation is affected by substrate depth and climate, with deep substrates promoting greater species richness, functional richness, and canopy cover (Lönnqvist et al., 2021a; Madre et al., 2014; Vanstockem et al., 2019), and higher rainfall areas promoting greater species richness and plant cover (Lönnqvist et al., 2021b). Vegetation surveys conducted on 129 extensive green roofs in northern Belgium show that in contrast to slow growing and stress tolerant *Sedum* communities, spontaneous vegetation communities can have competitive and ruderal trait signatures (Vanstockem et al., 2019) that are associated with faster growth and shorter lifecycles (Grime, 1977). Faster growing spontaneous species have been shown to use more water than slower growing species in glasshouse pot experiments (Schrieke and Farrell, 2021) which may improve green roof rainfall retention (Farrell et al., 2013). However, while fast growing spontaneous vegetation may be a viable alternative to commonly planted *Sedum* spp., their effect on rainfall retention is unclear.

In the absence of routine maintenance, green roofs are often colonised by ‘weedy’ spontaneous vegetation, however the influence of this vegetation on green roof stormwater mitigation is unclear. To better understand the role of spontaneous vegetation in stormwater mitigation on green roofs, we undertook a 100-day rainfall simulation experiment involving 14 plant species that commonly occur spontaneously on green roofs in Mediterranean-type climates. We evaluated how substrate depth and rainfall regime influenced rainfall retention and spontaneous species biomass, cover and species and functional richness. We hypothesised that modules with spontaneous vegetation cover would have greater rainfall retention and time to initiation of rainfall, and this effect would be greatest in modules with deeper substrate as there would be greater spontaneous vegetation cover.

2. **Materials and methods**

2.1 Experimental design

Sixteen green roof modules (1.15 x 1.15 m) were arranged in a randomised block design beneath an open-ended poly-tunnel (L 28 m, W 5 m, H 2.5 m) at the Burnley campus of The University of Melbourne (-37.828664611676245, 145.02022500312387). A weather station (ATMOS 41, Meter Group Inc. USA) was installed in the middle of the poly-tunnel to measure air temperature, relative humidity, wind speed and solar radiation. The data logger recorded readings every second and data was averaged to a 15-minute resolution. During the experiment, mean temperature ranged from 7.4 – 31.3 ºC, minimum temperature ranged from 1.4 - 20.4 ºC, mean relative humidity ranged from 6 – 29% and mean vapor pressure deficit ranged from 0.99 - 3.95 kPa. Crop factors, a measure of the crop's water demand relative to a standard reference crop, were calculated for each treatment by summing evapotranspiration (ET) and reference evapotranspiration (ETo) for each event, and then determining the crop factor as the ratio of total ET to total ETo across the treatment's duration. Crop factors varied between 0.78 and 1.03 across the experiment (Table 5.1). To simulate rainfall events, the poly-tunnel was fitted with an overhead irrigation system using pressure regulated drippers on a 10 cm grid, positioned 1.3 m above each module, providing 45.7 mm h^{-1} (±0.12 mm h^{-1}) rainfall to each module. This rate reflects the 1% annual exceedance probability for Melbourne (48.6 mm h^{-1} for 1 h duration; Australian Bureau of Meteorology, 2022).

Table 5.1 Calculated crop factors calculated for treatment combinations in the rainfall experiment.

Rainfall	**Substrate depth**	**Vegetation cover**	**Crop factor**
Dry	Deep	N	0.81
Dry	Deep	Y	1.03
Dry	Shallow	N	0.78
Dry	Shallow	Y	0.89
Wet	Deep	N	0.82
Wet	Deep	Y	1.00
Wet	Shallow	N	0.80
Wet	Shallow	Y	0.83

Green roof modules consisted of a plastic base (Nally megabin®) topped with a steel frame that supports a black high-density polyethylene plastic tray (1.15 x 1.15 x 0.30 m; 396 L) with a single rectangular drainage outlet (10 x 15 cm). A drainage layer was installed in the tray base (VersiDrain® 25P; water storage capacity 6.1 L m^{-2}; equivalent to 8.1 mm) and covered by geotextile fabric (Elmich A14) before modules were filled with a lightweight, porous volcanic rock (scoria) based green roof substrate (60% scoria <8 mm, 20% 7 mm scoria, and 20% coir) (Farrell et al., 2013). Half (eight) of the modules were filled to a depth of 7 cm (shallow), and half to a depth of 14 cm (deep). Prior to the experiment, substrate was tested for air-filled porosity (13.8%), bulk density (1.26 g cm^{-3}) and water holding capacity (45.9%) as per the Australian Standard for Potting Mixes (AS 3743-2003; Standards Australia, 2003). These properties meet the FLL guidelines used to assess the suitability of green roof substrates (FLL, 2008). A controlled slow-release fertiliser (Osmocote® Pro, Everris Australia Pty Ltd.: 15 N:1.3 P:10 K) was added to the substrate surface of each module (30 g m^{-2}) and each substrate depth treatment was then allocated one of two vegetation treatments; a) bare substrate or b) spontaneous vegetation cover.

2.2 Seed sowing and spontaneous plant establishment

Modules with spontaneous vegetation cover were sown with a seed mix of 14 plant species that occur spontaneously on green roofs in Mediterranean type climates (Table 5.2, overleaf). Seeds of the fourteen species were collected from green roofs and green roof habitat analogues located across metropolitan Melbourne, Australia in August-September (winter-spring) 2019. Eight mixes (one per ‘vegetation cover’ module) of the 14 spontaneous green roof plant species were made based on each species seed mass and percent germination. This ensured each species had the same potential germination (i.e., species with low germination rate had a higher ratio by weight of seed in mixtures), with a final sowing rate equivalent to one germinant per 5 cm^2. Seed germination rates were determined previously (Schrieke et al., 2023), and seed mass was measured as the weight of seed after removing all appendages and drying in an oven at 80 °C for three days (Pérez-Harguindeguy et al., 2013). Seed mixes were individually blended into 400 ml fine sand to assist spreading and were sown evenly across the surface of each module (12 April 2021; autumn). Modules were then irrigated with 10 mm 'rainfall' every second day for five months to facilitate establishment and achieve approximately 100% cover. Additional plant species found colonising the modules over this period were removed.

Table 5.2 Species information and plant type of the fourteen spontaneous species selected for the experiment.

Species	**Family**	**Common name**
Epilobium parviflorum	Onagraceae	Hoary willowherb
Euphorbia maculata	Euphorbiaceae	Spotted spurge
Euphorbia peplus	Euphorbiaceae	Petty spurge
Helichrysum luteoalbum	Asteraceae	Jersey cudweed
Malva neglecta	Malvaceae	Common mallow
Nepeta cataria	Lamiaceae	Catnip
Polycarpon tetraphyllum	Caryophyllaceae	Four-leaf allseed
Portulaca oleracea	Portulacaceae	Common purslane
Rumex crispus	Polygonaceae	Curly dock
Solanum nigrum	Solanaceae	Black nightshade
Sonchus oleraceus	Asteraceae	Common sowthistle
Stellaria media	Caryophyllaceae	Chickweed
Taraxacum officinale	Asteraceae	Dandelion
Trifolium repens	Fabaceae	White clover

2.3 Rainfall simulation

The rainfall simulation ran for 100 days from 2nd September (spring) to 10th December (summer) 2021 and included a 'dry' and 'wet' phase to simulate a Mediterranean type of climate (i.e., Melbourne, Australia), with a total of 17 events across the study period (Fig. 5.1, overleaf). In the 'dry' phase (2nd September – 10th October 2021) 65.5 mm of rainfall was applied over 40 days and replicated the rainfall timing and depth of the driest rainfall period on record in Melbourne, Australia (2006; Melbourne Regional Office; site 086071; Australian Bureau of Meteorology) sourced from SILO (Jeffrey et al., 2001). In the 'wet' phase (11th October to 10th December 2021) 212.7 mm of rainfall was applied over 60 days, where rainfall

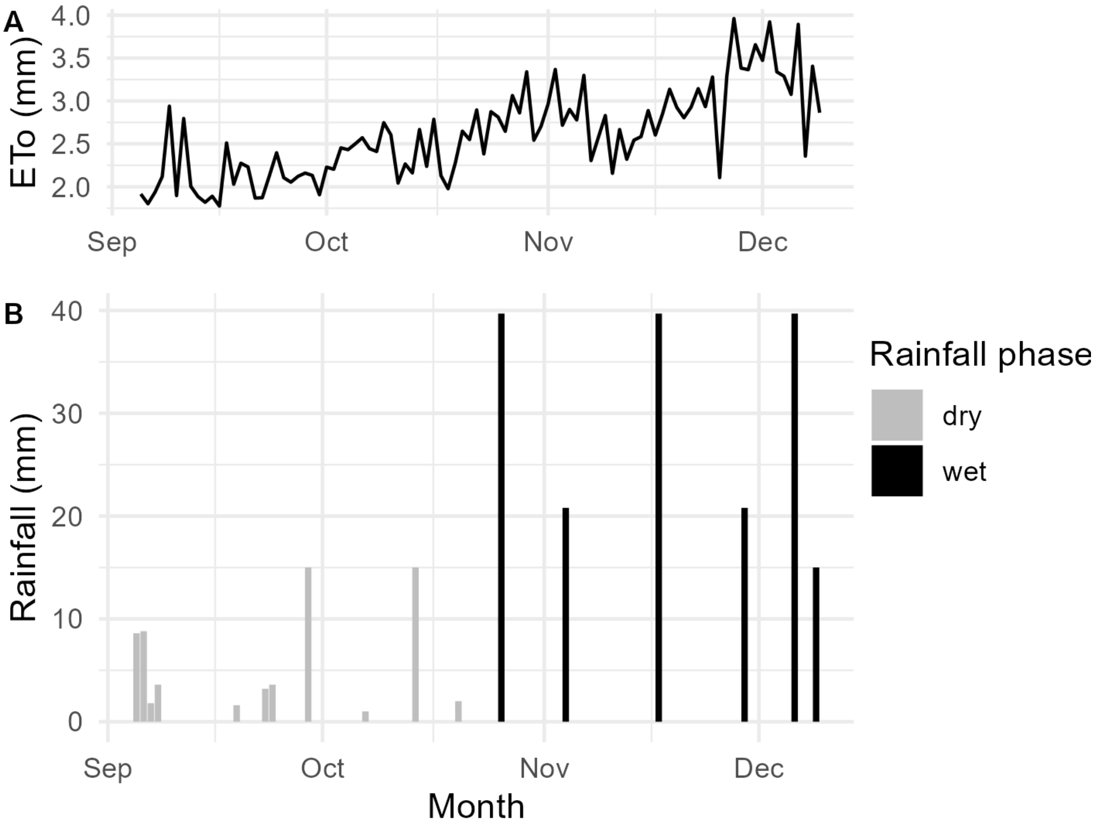

Figure 5.1 Overview of the climatic conditions throughout the study. (A) Daily reference evapotranspiration (ETo) for the duration of the experiment and (B) occurrence and magnitude of simulated rainfall events, differentiated by the phase of rainfall.

depth was based on random selection from the 90th, 95th and 99th percentile rainfall depths (14.4, 20.8 and 39.7 mm) as calculated from six-minute rainfall data for the period January 1, 1988, to December 31, 2007 (Melbourne Regional Office; site 086071; Australian Bureau of Meteorology). As the rainfall simulation apparatus required 30 seconds to reach uniform pressure (approximately 0.5 mm rainfall depth) small (<1 mm) rainfall events during the dry phase were removed and instead these events were added to the nearest rainfall event in the time-series to avoid error.

2.4 Rainfall retention and evapotranspiration

To compare percent rainfall retention and cumulative evapotranspiration (ET) among substrate depth and vegetation cover treatments, we weighed modules using a pallet jack scale with 500 g resolution (TPS-L-1, WEIGH PTY LTD) before and after each simulated rainfall event. Rainfall events were applied at approximately 5:30 pm to limit solar radiation (and ET).

Retention was calculated for each rainfall event ($Retention_n$) per Szota et al (2017b) as:

$Retention_n = M_{after\ n} - M_{before\ n}$	*Equation 1*

where $M_{after\ n}$ is the module mass 14 hours after the rainfall event was applied (to facilitate drainage overnight) and $M_{before\ n}$ is the module mass at 5:30pm before application of rainfall event n. Percent retention was determined as the sum of retention in each module during the experiment, divided by total rainfall applied and multiplied by 100, separated into dry and wet phases.

Evapotranspiration occurring after a rainfall event (ET_n) was calculated per Szota et al (2017b) as:

$ET_n = M_{after\ n} - M_{before\ n+1}$	*Equation 2*

where $M_{after\ n}$ is the module mass 14 hours after the rainfall event was applied (to facilitate drainage overnight) and $M_{before\ n+1}$ is the module mass at 5:30pm before application of the next rainfall event in sequence (n+1). Cumulative ET was determined as the sum of ET (i.e., the total amount of water lost from each module during the experiment, separated into dry and wet phases).

2.5 Time to runoff initiation and soil water content

We measured time to runoff initiation and soil water content (SWC_t) on 26/10/2021 (i.e., dry phase) and 06/12/21 (i.e., wet phase). Time to initiation of runoff was defined as the time (minutes) between the beginning of rainfall application and appearance of consistent runoff from an outlet located on the green roof modules. We calculated soil water content (SWC) before rainfall events from module mass per Szota et al (2017b):

$SWC_t = \frac{M_{tot} - M_{fp} - M_{ds} - M_{ms}}{A_m}$	*Equation 3*

where SWC_t is the soil water content at time t, M_{tot} is the total weight of the module, M_{fp} is the final fresh weight of the plants, M_{ds} is the weight of the dry substrate, M_{ms} is the weight of the module structure and A_m is the area of the module.

2.6 Spontaneous species abundance, richness, and plant cover

Vegetation in the modules was surveyed at the end of the dry phase (October 10, 2021) and at the end of the wet phase (December 12, 2021). Surveys were conducted by dividing modules into 16 evenly sized (27.5 x 27.5 cm) square quadrats (with a 5 cm buffer along the outer edge of modules to limit edge effects). Four quadrats were randomly selected and surveyed, with all species identified and counted to determine species abundance. Species richness was calculated using the FD package (Laliberté et al., 2014) in R 4.1.1 (R Core Team, 2021). At the same time, digital images were captured (iPhone SE 2nd generation, Apple Inc) at a height of 2 m the above modules and analysed using ImageJ to determine % vegetation cover (Abràmoff et al., 2004).

2.7 Spontaneous plant biomass and specific leaf area at the end of the experiment

Aboveground biomass of each species in the modules was harvested from the four randomly selected quadrats used to conduct species surveys at the end of the experiment (i.e., end of the wet phase). Aboveground biomass per species per module was determined by combining quadrat subsample weights and multiplying by four. Total aboveground community biomass per module was determined by combining total aboveground biomass per species per module. Two fully expanded leaves from each plant within treatment combinations were randomly selected, stripped, weighed, photographed (iPhone SE 2nd generation, Apple Inc) from directly above at a distance of 20 cm, then measured using ImageJ (Abràmoff et al., 2004) before being oven dried at 70 °C until constant weight to determine Specific leaf area (SLA, $m^2\,kg^{-1}$ leaf), calculated as the one-sided leaf area, divided by its oven-dry mass. Leaf dry matter content was calculated as leaf dry mass (g) divided by leaf fresh weight (g). To determine root biomass, all substrate was excavated from the four quadrats and washed away from roots which were then patted dry with paper towel and oven dried at 70 °C to a constant weight. Average shoot and root biomass per module was then determined from these measurements. Leaf dry matter content was calculated as leaf dry mass (g) divided by leaf fresh weight (g).

2.8 Spontaneous plant functional richness, community-level weighted mean specific leaf area and relative growth rate

Functional richness and community-level weighted mean specific leaf area (weighted by biomass; CWM) were calculated using the FD package (Laliberté et al., 2014) in R 4.1.1 (R Core Team, 2021). Functional richness refers to the extent of functional space occupied by a given species community. It is determined by coordinating and correlating trait values (i.e., specific leaf area, leaf dry matter content, and relative growth rate), following the approach of Villéger et al. (2008). The relative growth rate of the 14 spontaneous species was assessed in a separate study (Schrieke et. al., 2023).

2.9 Statistical analysis

Data were checked prior to analysis to ensure univariate normality and other than log transforming plant biomass to calculate RGR (Hoffmann and Poorter, 2002), no transformations were necessary. Two-way ANOVA was used to identify any significant effects of vegetation treatment or substrate depth on rainfall retention, cumulative ET, time to initiation of runoff. Two-way ANOVA was also used to determine significant differences between substrate depths, within the spontaneous vegetation treatment for spontaneous species abundance, richness, and plant cover. One-way ANOVA was used to determine significant differences between substrate depths for community biomass, functional richness, and specific leaf area. Tukey’s HSD was used to indicate significant differences among treatments ($P<0.05$). All statistical analyses were performed in R 4.1.1 (R Core Team, 2021).

3. **Results**

3.1 Rainfall retention

Rainfall retention during the dry phase was significantly affected by vegetation (*P*=0.01; Fig. 5.2, A, overleaf) but not by substrate depth (*P*=0.11) or the interaction between vegetation and substrate depth (*P*=0.89). Modules with spontaneous vegetation cover retained 88% of applied rainfall and had 6% greater retention than bare substrate, regardless of substrate depth. During the wet phase, retention was significantly affected by vegetation (*P*<0.001; Fig. 5.2, B, overleaf), substrate depth (*P*<0.001) and the interaction between vegetation and substrate depth (*P*<0.001). Retention was greatest (94% retention) in modules with vegetation cover and 14 cm (deep) substrate, with 30% greater retention than all other treatments. In modules with 7 cm (shallow) substrate, green roof modules with vegetation cover had 7% greater retention (78% retention) than bare modules.

3.2 Cumulative evapotranspiration

Cumulative evapotranspiration (ET) during the dry phase was significantly affected by vegetation (*P*<0.001; Fig. .52, C, overleaf), substrate depth (*P*<0.001) and the interaction between vegetation and substrate depth (*P*<0.01). Modules with vegetation cover and deep substrate had the greatest ET (85 mm); with 16% greater ET than modules with vegetation cover and shallow substrate and 29% greater than modules with bare substrate (both substrate depths). In shallow substrate, modules with vegetation cover had 12% greater ET (73 mm) than modules with bare substrate. During the wet phase, ET was significantly affected by vegetation (*P*<0.001; Fig. 5.2, D, overleaf), substrate depth (*P*<0.001) and the interaction between vegetation and substrate depth (*P*<0.001). Modules with vegetation cover and deep substrate had 23% greater ET (167 mm) than all other treatments.

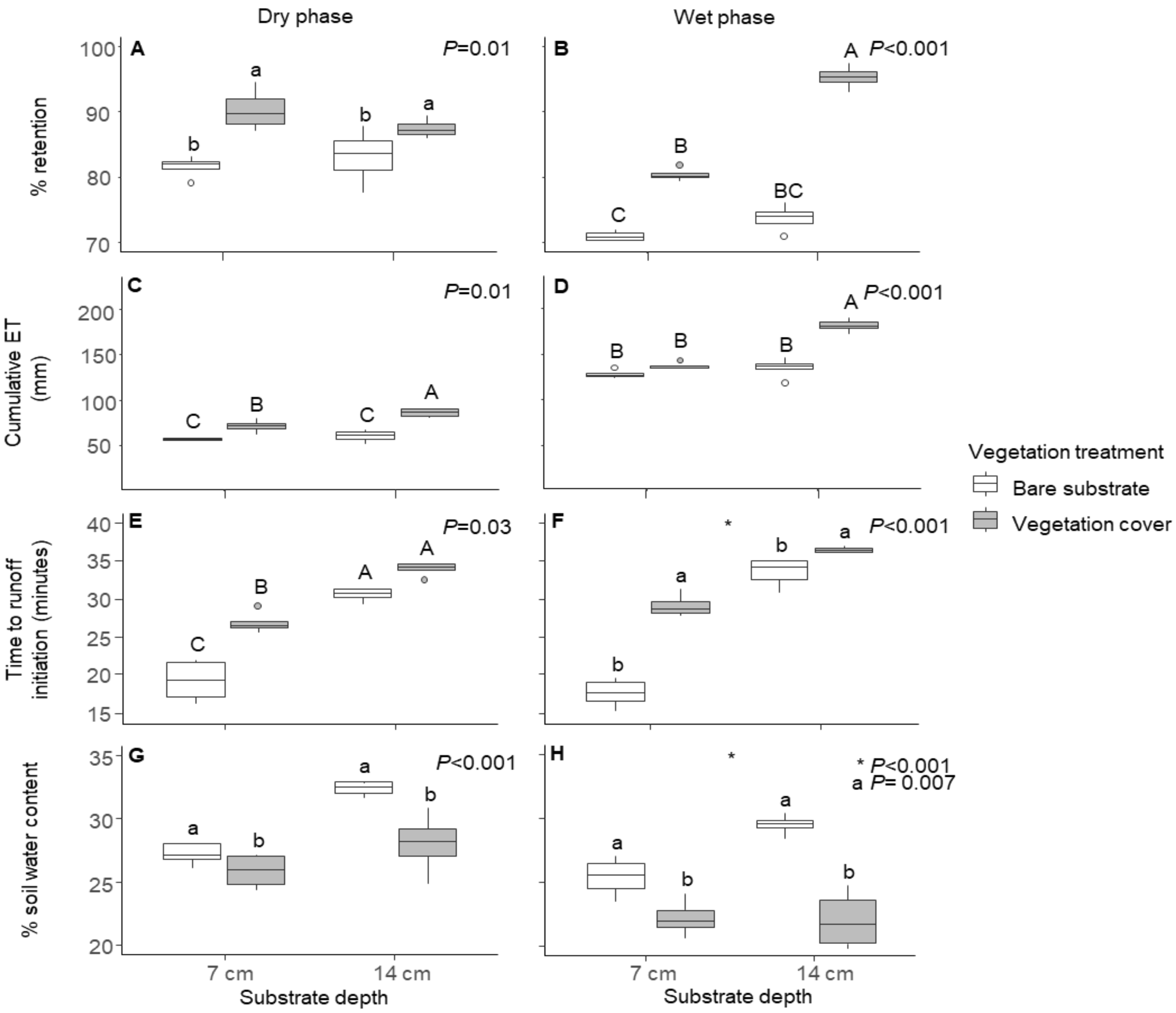

*Figure 5.2 Percent rainfall retention in the dry (A) and wet (B) phase, cumulative evapotranspiration (ET) in the dry (C) and wet (D) phase, time to runoff initiation measured on 26/10/2021 (i.e., dry phase; E) and 06/12/21 (i.e., wet phase; F), and percent soil water content before rainfall application on 26/10/2021 (i.e., dry phase; G) and 06/12/21 (i.e., wet phase; H) in the green roof modules. Different capital letters denote significant differences among mean values between treatment interactions (two-way ANOVA, n = 4). Different lowercase letters denote significant differences among mean values between vegetation treatments (two-way ANOVA, n = 4). * Denote significant differences among means between substrate depths (two-way ANOVA, n = 4, all P<0.01)*

3.3 Time to initiation of runoff and soil water content

Time to initiation of runoff during the dry phase was significantly affected by vegetation (*P*<0.001; Fig. 5.2, E), substrate depth (*P*<0.001) and the interaction between vegetation and substrate depth (*P*=0.03). In deep substrate there was no significant difference in time to runoff initiation in vegetated and bare modules and deep substrates took longer to initiate runoff than shallow substrates. In shallow substrate, vegetation delayed runoff by 28%. During the wet phase, time to initiation of runoff was significantly affected by vegetation treatment (*P*<0.001; Fig. 5.2, F) and substrate depth (*P*<0.001), but there was no significant interaction (*P*=0.31). Modules with vegetation cover took 20% longer to initiate runoff than bare modules, and modules with deep substrate took 28% longer to initiate runoff than modules with shallow substrate.

Soil water content (SWC) during the dry phase was significantly affected by vegetation (*P*<0.001; Fig. 5.2, G) but not by substrate depth (*P*=0.10) or the interaction between vegetation and substrate depth (*P*=0.06). Percent SWC was greatest in modules with bare substrate (30%), 10% greater than in modules with vegetation cover. Percent SWC during the wet phase was affected by vegetation treatment (*P*<0.001; Fig. 5.2, H) and substrate depth (*P*=0.007) but not the interaction between vegetation treatment and substrate depth (*P*=0.07). Percent SWC was 13% greater in modules with bare substrate (26%) than in modules with vegetation cover. Modules with deep substrate had 9% greater SWC (26%) than modules with shallow substrate.

3.4 Spontaneous plant community species richness and vegetation cover

Species richness of the spontaneous plant community was significantly affected by sampling time (i.e., dry, and wet phases; *P*<0.001; Fig. 5.3, A, overleaf) but not substrate depth (*P*=0.13) or the interaction between substrate depth and sampling time (*P*=0.06). Species richness was 30% greater during the dry phase than wet phase, regardless of substrate depth.

Vegetation cover of the spontaneous plant community was significantly affected by substrate depth (*P*<0.001; Fig. 5.3, B, overleaf) and sampling time (*P*<0.001), but not the interaction between substrate depth and sampling time (*P*=0.20). Vegetation cover was 19% greater in modules with deep substrate than shallow substrate, and 18% greater during the dry phase than wet phase.

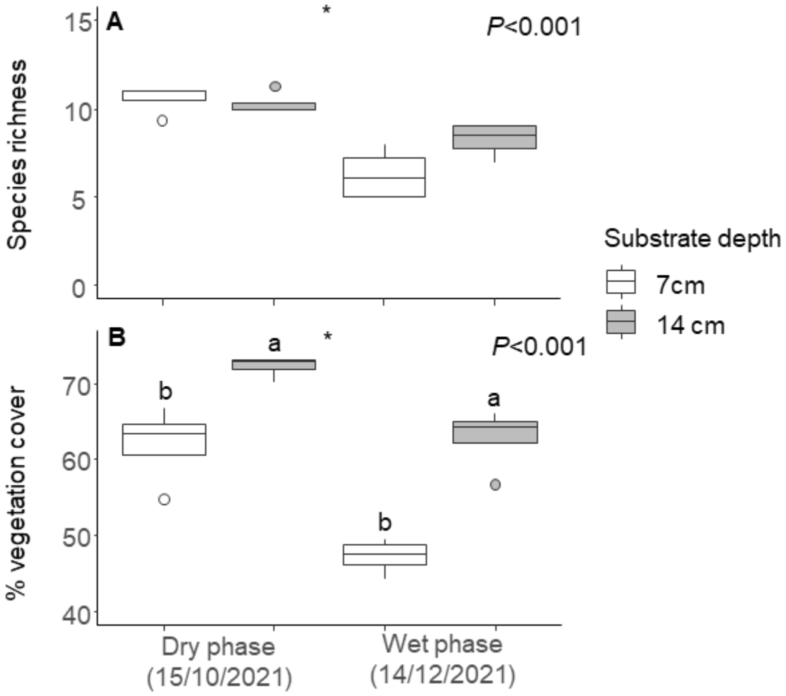

*Figure 5.3 Species richness (i.e., number of species) (A) and % vegetation cover (B) of spontaneous communities at the completion of 'dry' (15/10/2021) and 'wet' (14/12/2021) phase. Different lowercase letters denote significant differences among mean values between substrate depths (two-way ANOVA, n = 4). * Denote significant differences among means between rainfall phase (two-way ANOVA, n = 4).*

3.5 Spontaneous plant community biomass and individual species biomass

Total shoot biomass of spontaneous plants was 42% greater in deep than in shallow substrate (*P*=0.02; Fig. 5.4, A, overleaf). There was no significant difference in total root biomass between substrate depths (*P*=0.73; Fig. 5.4, B, overleaf). Root allocation (root: shoot) was 38% greater in shallow than deep substrate (*P*<0.001; Fig. 5.4, C, overleaf).

In deep substrate, *Helichrysum luteoalbum* (40.26 g), *Polycarpon tetraphyllum* (25.27 g) and *Trifolium repens* (29.02 g) had significantly greater shoot biomass than the other species (*P*<0.05; Fig. 5.5, overleaf). The shoot biomass of *P. tetraphyllum* was >10-fold greater in modules with deep than shallow substrate (P<0.001). *Helichrysum luteoalbum* was not present in modules with shallow substrate. In modules with shallow substrate, *T. repens* had

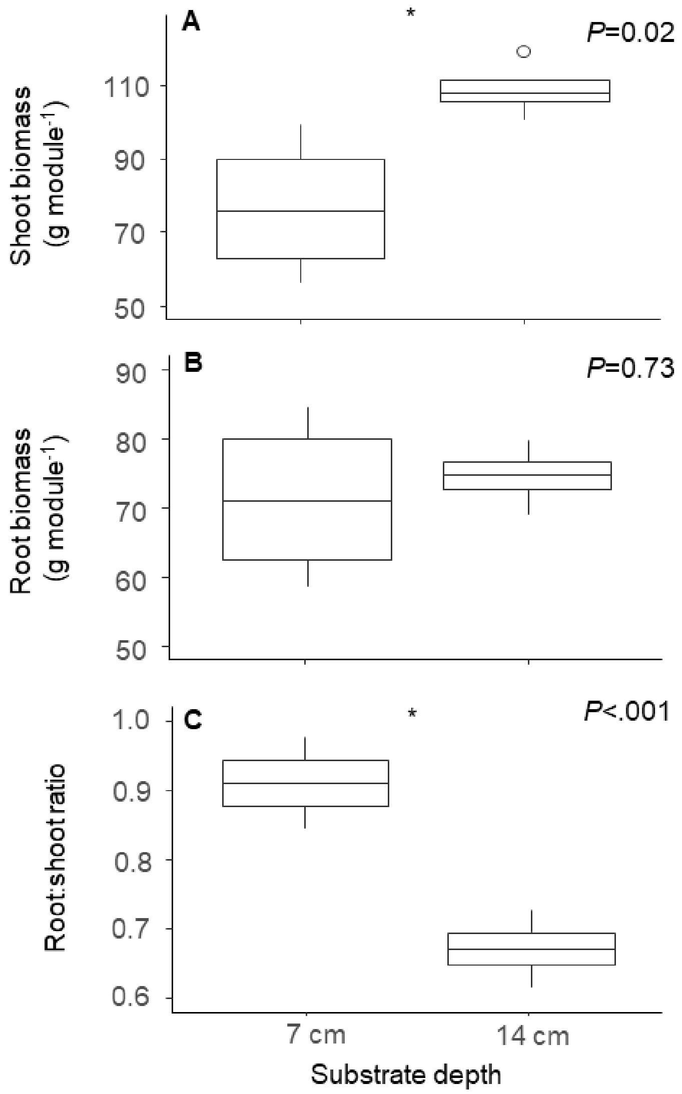

Figure 5.4 Shoot biomass (A), root biomass (B), and root:shoot ratio (C) of the spontaneous vegetation communities present in the green roof modules at the end of the 100-day experiment. Asterisks indicate significant differences among means (one-way ANOVA, n = 4).

the greatest shoot biomass (63.04 g, *P*<0.05), and its biomass was 53% greater than in deep substrate (*P*<0.001). Despite an experimental design that attempted to make sure all species had the same number of individuals, *Euphorbia maculata*, *Euphorbia peplus*, *Portulaca oleracea*, *Sonchus oleraceus*, and *Taraxacum officinale* were absent from all modules at the end of the experiment. In modules with shallow substrate, *Helichrysum luteoalbum* and *Stellaria media* were completely absent at the end of the experiment.

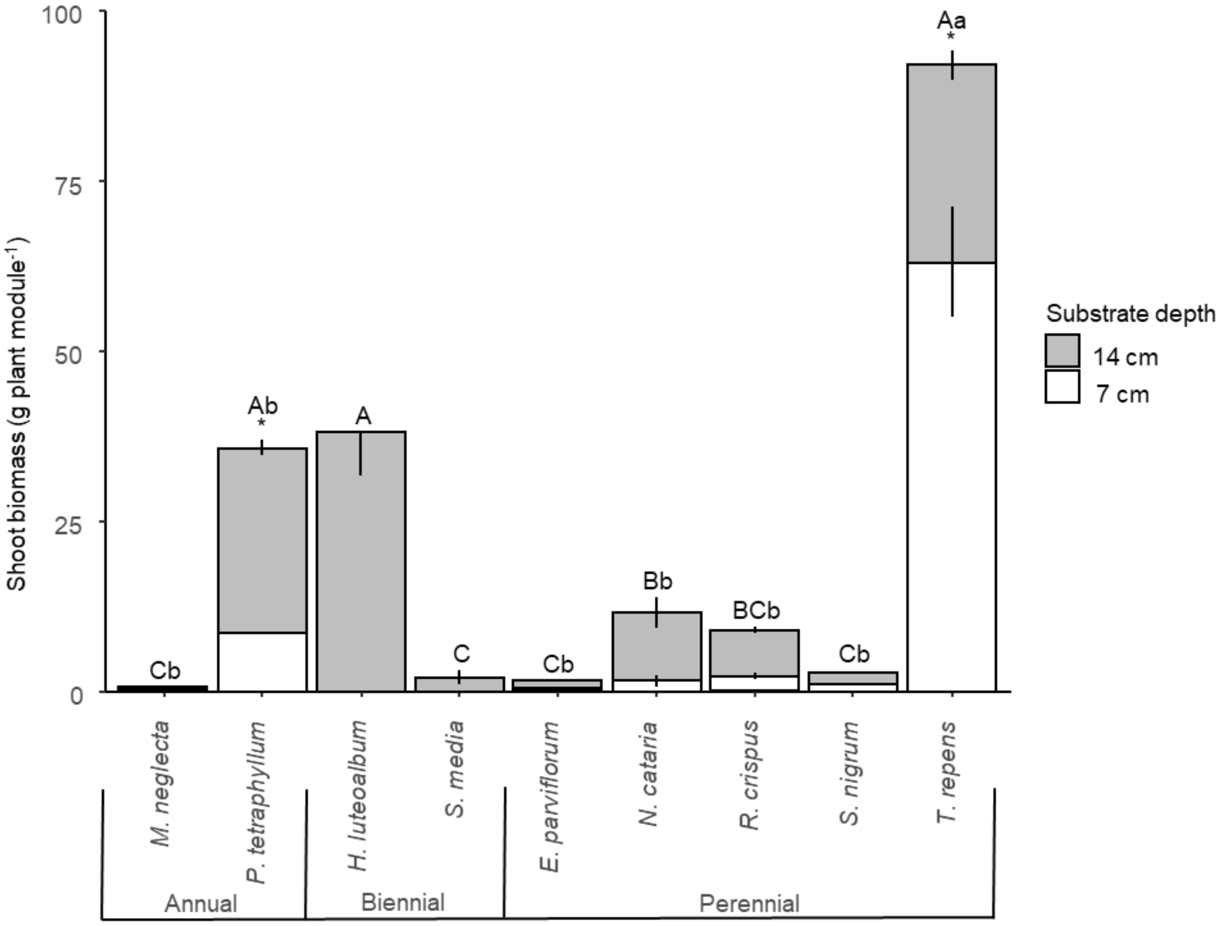

Figure 5.5 Shoot biomass of the spontaneous species present in modules at the end of the 100-day experiment. Asterisks indicate significant differences in shoot biomass between substrate depths (one-way ANOVA, n= 4). Dissimilar letters indicate significant differences in shoot biomass among spontaneous species within substrate depth treatment; capital letters = 14 cm depth, lowercase letters = 7 cm depth (one-way ANOVA and Tukey's post-hoc test; n= 4). All P <0.05.

3.6 Functional richness and specific leaf area (community weighted mean)

Functional richness of the spontaneous plant community was greater in the deep substrate (*P*=0.008; Fig. 5.6 A, overleaf). The community weighted mean (by biomass) of specific leaf area of the spontaneous plant community was 8% greater in modules with shallow than deep substrate (*P*=0.01; Fig. 5.6 B, overleaf).

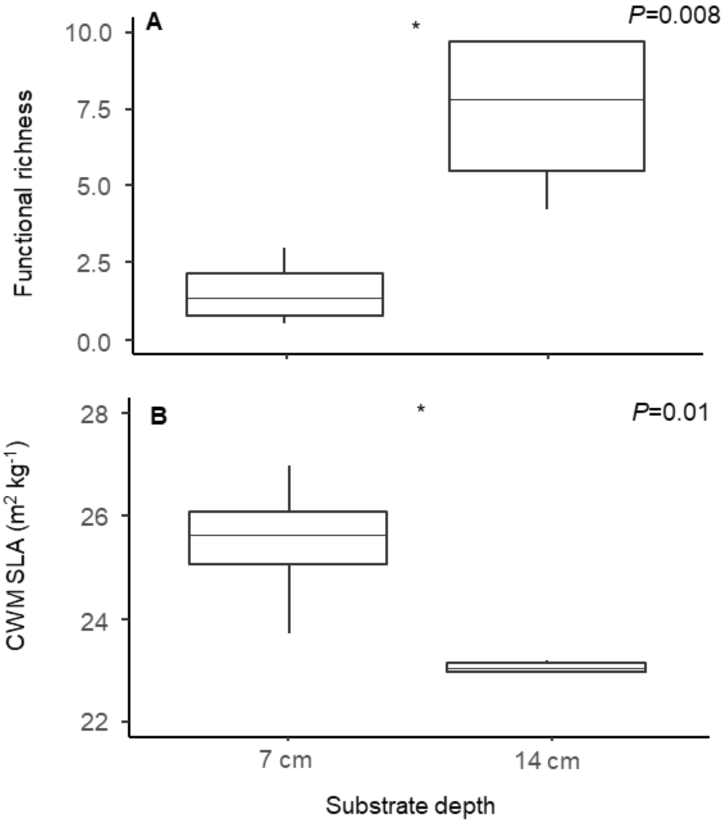

Figure 5.6 Functional richness (A), and community weighted mean (CWM; by biomass) specific leaf area (SLA; B) of the spontaneous communities present in the green roof modules at the end of the experiment. Asterisks indicate significant differences among means (one-way ANOVA, n = 4).

4. **Discussion**

Regardless of vegetation presence/absence or substrate depth, green roof modules retained 80-85% of applied rainfall across the rainfall simulation experiment, in both ‘dry’ and ‘wet’ phases. These results are consistent with previous studies conducted in Melbourne under similar conditions that found an average of 73% rainfall retention over a ‘typical’ year (Zhang et al., 2018) and 89–95% retention on an event basis (Zhang et al., 2019). However, the observed retention rates are at the upper end of rainfall retention reported globally (Zheng et al., 2021) and are notably higher than those reported in comparable studies undertaken in oceanic (Stovin et al., 2012), continental (Sims et al., 2016), and temperate (Locatelli et al., 2014) climates.

Low rainfall likely contributed to high retention during the dry phase i.e., all applied water was depleted by evapotranspiration and events rarely exceeded substrate retention capacity (Sims et al., 2016). In the wet phase of the experiment, larger rainfall events (>14 mm) should have decreased retention efficiency (Berretta et al., 2014, Poë et al., 2015). However, retention remained notably high, especially in modules with vegetation cover and deeper substrate. Longer periods between rainfall events during the wet phase likely allowed substrate water to be depleted by greater evaporative demand and plant transpiration (Berndtsson, 2010). Melbourne’s temperate oceanic climate (Köppen climate classification Cfb) (Beck et al., 2018) with hot and dry summers, alongside differences in green roof design such as substrate type and depth (Czemiel Berndtsson, 2010) and species composition (Lundholm et al., 2010; Nagase and Dunnett, 2012), may also explain the relatively high rainfall retention.

Nevertheless, these results indicate that in regions with similar climates to Melbourne, green roofs with substrate depth equal to or greater than 7 cm can have high retention performance, regardless of vegetation cover. However, as spontaneous vegetation offers a range of other potential benefits on green roofs, while requiring less input and maintenance than conventional plantings (Schrieke et al., 2021), it may still offer an effective vegetation treatment.

4.1 Evaporation and rainfall retention

During both the dry and wet phases, modules with spontaneous vegetation cover had 6-30% greater retention than bare substrate modules of equivalent depth. Rainfall retention in modules with spontaneous vegetation cover was like that recorded in modules planted with monocultures and mixtures of native Australian rocky outcrop plant species by Zhang et al. (2018) that were specifically selected for traits considered advantageous for stormwater mitigation on green roofs (Farrell et al., 2013). Spontaneous vegetation in the deep substrate had 62-72% cover at the end of the dry phase and 47-63% cover at the end of the wet phase, depending on substrate depth. Therefore, even with moderate cover, spontaneous vegetation could achieve similar stormwater mitigation on green roofs as designed plant communities specifically selected for this functionality. This indicates that evaporation from substrate is a key determinant of rainfall retention.

4.2 Rainfall regime and other factors influencing retention

The importance of vegetation and substrate depth on retention varied across the dry and wet phases of the simulated rainfall experiment. During the dry phase, retention was greatest in green roof modules with spontaneous vegetation, regardless of substrate depth. Whereas, during the wet phase, there was an interaction between substrate depth and vegetation, with the greatest retention in the deep substrate with spontaneous vegetation cover. As transpiration increases cumulative evapotranspiration (ET), reduces soil water content, and increases the retention capacity of substrates between rainfall events (Poë et al., 2015), greater retention in vegetated modules was expected and has been shown in other comparable studies (Stovin et al., 2012; Locatelli et al., 2014; Sims et al., 2016; Zhang et al., 2018). We also expected that modules with deeper substrate would have greater retention than those with shallow substrate due to greater substrate volume and storage capacity, resulting in greater ET.

While green roof modules with deep substrate and vegetation cover had greater ET during both the dry and wet phases of the experiment, retention in the dry phase was not greater in deep substrates with vegetation cover. During the dry phase, most rain events were too small to generate runoff, reducing the effect of greater substrate depth on retention. This observation aligns with the findings of several other studies that report minimal or no significant difference in rainfall retention between substrate-only green roofs and those with vegetation cover, following minor rainfall events (VanWoert et al., 2005; Getter et al., 2007; Sims et al., 2016). In contrast, during the wet phase of the rainfall simulation, runoff was generated from most events as rainfall exceeded the retention capacity of both substrate depths. During the wet phase deep substrates had greater rainfall retention due to greater storage volume and greater ET achieved through increased spontaneous vegetation cover and biomass. We therefore suggest that vegetation cover is more important for rainfall retention on green roofs in wetter seasons or years, and that deep substrates will retain more water by virtue of greater substrate volume and increased vegetation cover and biomass.

4.3 Spontaneous community vegetation cover and biomass allocation

Vegetation cover was greater in deep substrate in both the wet and dry phases of the experiment, and this was reflected in greater shoot biomass in the deep substrate at the end of the experiment. Vegetation cover on green roofs is linked to substrate depth. For example, cover of 25 species from genus *Graptopetalum*, *Phedimus*, *Rhodiola*, and *Sedum*, was greatest (96%) in a 7.5 cm deep substrate, compared with 74% cover in a 5 cm deep substrate and 47% in a 2.5 cm deep substrate (Durhman et al., 2007). Likewise, Dunnett et al. (2008b) found that coverage of 15 herbaceous perennial grass and herb species in experimental green roofs was significantly greater in 20 cm than 10 cm substrate depth after five consecutive growing seasons. However, differences in plant cover between substrate depths can be seasonal, as Heim and Lundholm (2014) showed green roof plots with heterogenous substrate depth (5-10 cm) had greater plant cover than plots with 10 cm substrate depth, but only at specific points in the growing season. Responses to substrate depth can also be species specific, as Gabrych et al. (2016) showed grasses and forbs on green roofs in Finland generally had greater cover in deep substrate, whereas *Sedum* spp. cover responded negatively to increased substrate depth. During the wet phase of the study, spontaneous vegetation in the shallow substrate had the lowest cover (47%). This cover value fails to meet the FLL green roof guideline requirement of 60% (FLL, 2008). It was the only treatment that failed to do so but highlights the seasonal nature of most spontaneous vegetation on green roofs. Reconsidering the rationale for high year-round vegetative cover may be desirable for green roofs outside of temperate climates (Schrieke et al 2021).

Spontaneous plant communities in shallow substrate had greater root:shoot ratios than in deep substrate. In the experiment soil water content was lower in modules with shallow substrate during the wet phase. Allocation of resources between root and shoot growth is a key plant adaptive strategy; as plants dedicate limiting resources to structures that capture limiting resources (Bloom et al., 1985). Likewise, the greater shoot biomass in spontaneous communities in deep substrates reflects greater investment in leaves to capture the limited light in a non-water-limited environments (Poorter et al., 2012). It is likely that this greater investment in leaves drove the greater ET observed in modules with deep substrate and spontaneous vegetation cover than modules with shallow substrate and vegetation cover. Although greater water use is desirable for stormwater mitigation on green roofs (Farrell et al., 2012), in a water limited environment, greater investment in leaves and growth can result in increased drought stress (Schrieke and Farrell, 2021) and ultimately plant senescence (Szota et al., 2017a).

The species richness of the spontaneous community was not affected by substrate depth but was greater during the dry phase of the experiment. As the experiment commenced in winter, several winter annual species (*Euphorbia peplus*, *Sonchus oleraceus* and *Stellaria* *media*) completed their lifecycles prior to the wet phase census of species richness which was undertaken in mid-summer. Commencing the wet phase in early November also meant that spontaneous vegetation cover was well established, and this may have inhibited the germination and establishment of slow growing summer annuals like *Euphorbia maculata* and *Portulaca oleracea*. Nevertheless, at the end of the experiment (i.e., end of the wet phase) the functional richness of spontaneous communities was greater in deep compared to shallow substrate. Spontaneous communities in deep substrate included a range of species with annual, biennial, and perennial life-cycles, whereas communities in shallow substrate were dominated by perennial species. Greater functional diversity has been hypothesised to increase green roof ecosystem services, such as stormwater mitigation (Lundholm et al., 2010) and in the experiment, during the wet phase, deep substrates had greater retention. However, we are not able to disentangle the relative importance of vegetation cover, species richness or functional diversity to rainfall retention.

As slow traits like lower specific leaf area (SLA) are associated with environments that are water-limited (Reich, 2014; Westoby, 1998), we expected lower community weighted mean (CWM; by biomass) SLA in modules with shallow substrate. However, we found that spontaneous communities in shallow substrate had greater CWM SLA than those in deep substrate. Greater CWM SLA in shallow substrate was likely affected by the dominance of *Trifolium repens*, which had 53% greater biomass in modules with shallow substrate than deep substrate. *Trifolium repens* fixes nitrogen from the atmosphere and can develop a shallow root system (Lane et al., 2000), giving it a competitive advantage in the low nutrient substrate used in the study, regardless of depth. The lower CWM SLA of modules with deep substrate was also likely influenced by the greater abundance of *Helichrysum luteoalbum*, which has a relatively low SLA and was absent from modules with shallow substrate. The relatively long tap root of *H. luteoalbum* (personal observation) may have limited its abundance in shallow substrate modules. Therefore, while functional richness was related to greater retention in the study, individual traits at the community level, such as CWM SLA, did not reflect their retention performance.

5. Conclusions

The results show that spontaneous vegetation can increase stormwater retention on green roofs relative to bare substrate and has similar retention performance to commonly utilised species. The degree to which spontaneous vegetation can improve retention is influenced by rainfall regime, with no difference in retention between shallow and deep substrate during ‘dry’ periods of rainfall and greater retention in deep substrate during ‘wet’ periods. Deep substrate resulted in greater plant cover and shoot biomass, and this was related to greater ET. Species richness was not affected by substrate depth and decreased over time. Changes in functional diversity, for example the dominance of species with certain life cycles, could reduce the effectiveness of spontaneous vegetation at retaining stormwater on green roofs, however due to the relatively short experiment in this study, we were not able to test this. This experiment assessed the effect of spontaneous plant community coverage, biomass and species and functional diversity resulting from a single colonisation event (sowing of seed), whereas spontaneous vegetation communities on green roofs are structured by multiple events over time. Future long-term studies are necessary to determine the effectiveness of spontaneous vegetation for stormwater mitigation on green roofs over time. Future research could specifically allow spontaneous colonisation to occur instead of manually sowing spontaneous species. This approach could yield a more accurate understanding of how the contribution of this vegetation community to rainfall retention evolves over time. Moreover, studies could further investigate the influence of different regional climates, substrate compositions, and building designs on spontaneous vegetation and its impact on stormwater mitigation. However, the results of this study demonstrate that spontaneous vegetation can reduce runoff from green roofs and maintain green roof functionality where original designed plantings are no longer present.

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Chapter 6 : Global patterns and drivers of spontaneous vegetation on urban green roofs

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Abstract

Green roofs can contribute to healthier urban environments, yet their success hinges on careful plant selection and maintenance to sustain vegetation coverage. The harsh conditions of green roofs, including extreme heat and drought, pose challenges to plant survival. Moreover, green roof plantings are prone to changes over time due to the natural recruitment and establishment of spontaneous plant species, often considered weeds. While the study of spontaneous plant species dispersal and establishment in urban settings has traditionally focused on ground-level habitats, green roofs offer a distinct set of challenges and ecological attributes that are comparatively less explored. Research in this area has often been prescriptive and focussed on functional objectives rather than underlying ecological processes. Better understanding the factors that influence the formation of spontaneous plant communities on green roofs is important, since the cover and composition of vegetation is pivotal to green roof functionality. Therefore, we compiled data from presence/absence surveys of spontaneous vegetation on 192 green roofs worldwide to determine how various factors, including green roof design characteristics (age, surface area, substrate depth, elevation, and pre-existing vegetation), as well as accessibility, maintenance, irrigation, adjacent vegetation cover, and local climate, influence these spontaneous plant communities. Using regression analyses, we assessed the impact of these variables on species richness and applied Hierarchical Modelling of Species Communities (HMSC) to understand their role in the dispersal and establishment of spontaneous species, based on their traits. We found that seasonal differences influence spontaneous community composition within both dispersal and establishment models. The primary factor influencing the dispersal traits of spontaneous vegetation on green roofs was the surrounding landscape vegetation cover. In contrast, the establishment of spontaneous

vegetation was chiefly governed by climatic factors, although green roof design features, such as roof height, accessibility and maintenance intensity also shaped the community structure. Spontaneous species richness was greater in spring and winter, increased with substrate depth and tended to decline as green roofs aged. These insights enable more informed decision-making in the design and maintenance of green roofs in alignment with specific ecological or aesthetic objectives.

1.0 Introduction

The importance of vegetation in counteracting the adverse impacts of urbanisation is well-documented (Ferrini et al., 2020), but expanding vegetation cover in densely populated cities remains a challenge. Green roofs offer a potential solution as they enable plant cover on previously unvegetated rooftops and reduce the area of impervious surfaces without competing for ground-level space. Green roofs have been shown to reduce stormwater runoff and delay peak flow (Stovin et al., 2012; Viola et al., 2017), serve as habitats for biodiversity (Baumann, 2006; Madre et al., 2014), aid in cooling buildings and their immediate surroundings (Santamouris, 2014), and contribute to human health and wellbeing (Lee et al., 2015; Williams et al., 2019). These benefits rely on good plant survival and coverage (Lundholm, 2015; Stovin et al., 2015). However, maintaining the desired coverage and composition is a challenge, particularly in hot and dry climates, due to poor plant survival (Rayner et al., 2016; Williams et al., 2021).

In addition to mortality from heat and drought, green roof plantings can also change over time due to recruitment and establishment of spontaneous plant species, or weeds (Catalano et al., 2016; Köhler, 2006; Madre et al., 2014). In the absence of maintenance these spontaneous species can persist, spread, and outcompete the flora originally planted on the roof (Catalano et al., 2016). Although usually perceived negatively, spontaneous vegetation provides plant cover on green roofs and can enhance stormwater mitigation (Schrieke et al., 2021), support invertebrate biodiversity (Kadas, 2006) and maintain flowering continuity for pollinators (Wang et al., 2017). Embracing spontaneous vegetation on green roofs can yield various socio-ecological advantages, making cost-effective green roofing more accessible in economically disadvantaged areas (Schrieke et al., 2021). Comprehending the factors influencing the formation of spontaneous plant communities on green roofs is essential, since the composition of plant communities is pivotal to green roof functionality (Lundholm, 2015; Xie et al., 2018).

Understanding spontaneous plant species dispersal and establishment in urban ecosystems has largely focused on ground-level habitats (Piana et al., 2019). Yet, green roofs present unique challenges and ecological characteristics that are less understood. The initial recruitment of vegetation in urban areas, encompassing the dispersal and establishment of propagules and seedlings (Clark et al., 2013) is influenced by both invasive species and the decline of native flora (Hahs et al., 2009; Knapp, 2010). Urban landscapes, shaped by habitat change and fragmentation, act as filters that alter species diversity by changing the quantity, quality and spatial configuration of habitats (Williams et al., 2009). Plant traits like seed size, plant height, and woodiness have been associated with urbanisation (Williams et al., 2015), and urban seed dispersal mechanisms differ markedly from rural processes, as influenced by the modified composition of seed rain and dispersal networks in cities (McConkey et al., 2012). The urban seed dispersal network is further complicated by human activity, which can transport seeds over significant distances (Wichmann et al., 2009).

In their meta-analysis of urban plant characteristics, Williams et al. (2015) found that, while wind-dispersed native species might face heightened extinction risks in urban settings, dispersal strategy was not consistently related with plant species presence in urban areas. Within Central European cities, annual spontaneous plants were found to predominantly rely on wind or animal dispersal mechanisms, more so than their regional counterparts (Lososová et al., 2006). Ground-level urban spontaneous vegetation is further influenced by the proximity of seed sources (Clark et al., 2013), with nearby vegetation increasing propagule pressure (Catford et al., 2009). Therefore, colonisation of green roofs by spontaneous vegetation, may be significantly influenced by factors such as the height of the roof, which affects wind and animal dispersal efficiency; and human access, which likely influences anthropogenic dispersal; and the coverage of nearby vegetation, which can be a source of seeds.

Ground-level urban habitats showcase how environmental factors can selectively hinder or facilitate plant establishment, shaping unique ecological communities (Piana et al., 2019).

Urbanisation transforms land use and alters climatic, hydrological, and biological cycles (Grimm et al., 2008), leading to distinctive urban plant communities (Aronson et al., 2016; Hahs et al., 2009; Sukopp, 2004; Williams et al., 2009).Green roofs often have more extreme conditions than their ground-level counterparts, due to thin substrates that drain quickly and exposure to high levels of wind and solar radiation, which can lead to rapid water loss (Durhman et al., 2007; Guo et al., 2021; Williams et al., 2021). Consequently, the vegetation that spontaneously establishes on green roofs might follow a unique trajectory of community establishment, adapting to these environmental constraints in ways distinct from plants in ground-level urban settings.

Due to their relatively uniform construction and shared challenges like limited soil and water resources, green roofs provide an ideal model for comparative urban ecology studies that help to understand the impact of urbanisation on ecological processes (McDonnell et al., 2009). We compiled data from presence/absence surveys of spontaneous vegetation on 192 green roofs worldwide to determine how various factors, including green roof design characteristics (age, surface area, substrate depth, elevation, and pre-existing vegetation), as well as accessibility, maintenance, irrigation, adjacent vegetation cover, and local climate, influence these spontaneous plant communities. This study aims to enhance our understanding of the factors that influence the dispersal and establishment of spontaneous vegetation that occurs on green roofs.

2.0 Methods

2.1 Site selection and data collection

We include 192 green roofs (Figure 6.1) on which presence/absence vegetation surveys were conducted between May 2011 to September 2020 in our global analysis. Green roofs are concentrated in Western Europe, a region with an extensive history of green roof development and research (Oberndorfer et al., 2007). We encountered challenges in procuring data from regions with more tropical climates, which may be due to a scarcity of green roofs or difficulties in establishing communication with researchers in these areas.

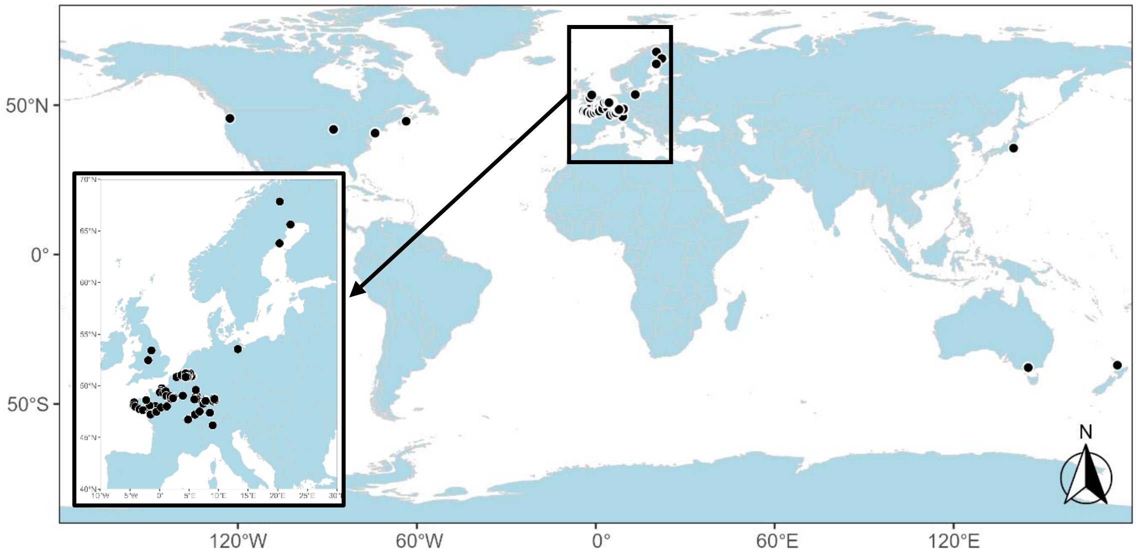


Figure 6.1 Map showing sampled roofs (black icons), with inset showing large number of roofs sampled in Western and Northern Europe.

2.1.1 Spontaneous vegetation surveys

For the 192 green roofs, we compiled data from vegetation surveys which were conducted either a) across the whole green roof surface or b) within quadrats distributed across the roof surface. Data from surveys using quadrats were pooled to obtain a list of all spontaneous species occurring on the green roof. For green roofs where multiple surveys had been conducted over time, we used the most recent survey in our analysis. Most surveys were conducted in spring (46%), followed by summer (41%), autumn (11%) and winter (2%). Where available, original planting plans were used to differentiate between planted and spontaneously colonising species. For sites lacking planting plans, we only included those with a ten or more-year history of low or negligible maintenance. This criterion is based on studies that survey unmanaged green roofs (Catalano et al., 2016; Madre et al., 2014; Vanstockem, Somers, & Hermy, 2019), which suggest that under such conditions, vegetation is predominantly composed of spontaneous vegetation.

2.1.2 Taxonomic nomenclature and phylogeny

We used the Taxonomic Name Resolution Service (TNRS) (Boyle et al., 2013) to ensure consistent nomenclature. We aggregated subspecies and varieties to the species level, considering them as conspecific, and excluded species that were recorded on less than three green roofs. We chose five easy to measure plant traits to represent a plant's ecological strategy (Leishman et al., 2000; Nathan & Muller-Landau, 2000; Reich, 2014; Westoby et al., 2002; Wright et al., 2004): dispersal syndrome, life cycle, height at maturity, seed mass and specific leaf area. Species trait data was obtained from the TRY 3.0 database (Kattge et al., 2011). We filtered numerical traits (i.e., height at maturity, seed mass and specific leaf area) that were more than three standard deviations from the species mean. For categorical traits (i.e., dispersal syndrome and life cycle), we selected the most frequently occurring value for each species. Where traits were missing, we obtained values from published literature (seven species; three traits) and omitted species with missing trait information (three species). For the remaining 117 spontaneous species, we built a phylogenetic tree using the V.PhyloMaker 2 package running an ‘S3’ scenario (Jin and Qian, 2022). This package integrates and refines Smith & Brown's (2018) phylogeny of seed plants and the clade detailed in the pteridophyte phylogeny by Zanne et al. (2014).

2.2 Environmental characteristics

2.2.1 Green roof characteristics

We collected data on green roof age, area, height, and substrate depth (Figure 6.2), accessibility (no access, resident access, public access), maintenance (low; 6 – 12-month interval, medium; monthly, high: fortnightly, or none), irrigation (yes or no) and percent vegetation cover (Table 6.1, overleaf). These variables have been shown to influence plant community development on green roofs (Catalano et al., 2016; Czemiel Berndtsson, 2010; Dunnett et al., 2008; Emilsson, 2008; Köhler, 2006; Lönnqvist, Hanslin, et al., 2021; Madre et al., 2014; Monterusso et al., 2005; Oberndorfer et al., 2007; Vanstockem, Bastiaens, et al., 2019). For green roofs with multiple substrate depths across the roof, we calculated a weighted mean substrate depth where each unique substrate depth was multiplied by its corresponding area.

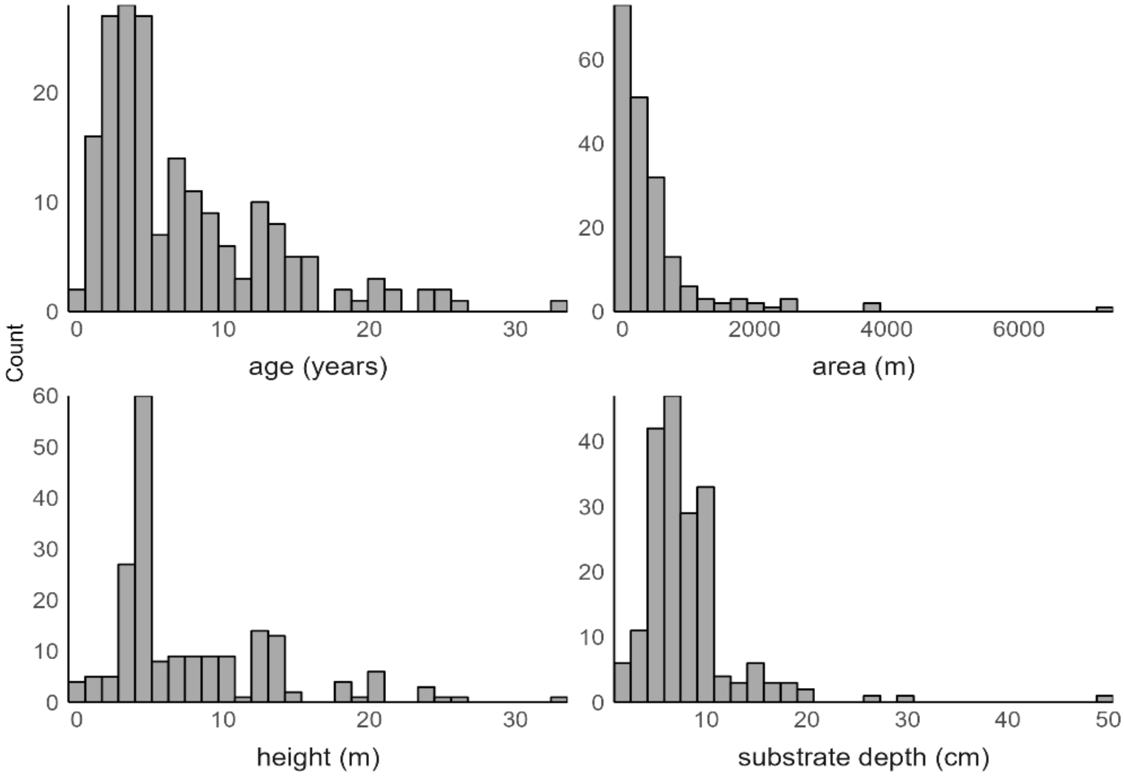


Figure 6.2: Frequency distributions of age, area, height, and substrate depth for the 192 green roofs included in our global analysis of spontaneous vegetation communities on green roofs.

Table 6.1 Landscape and green roof variables collected in our global analysis of spontaneous vegetation communities.

Green roof characteristics	Age
	Area
	Height above ground-level
	Substrate depth
	Accessibility (No access, resident access, public access)
	Irrigation (yes or no)
	Maintenance (low; 6 – 12-month interval, medium; monthly, high: fortnightly, or none)
	Percent vegetation cover
Landscape context	Landscape vegetation cover within 200 m of the green roof
	Landscape vegetation cover within 1000 m of the green roof
	Climate (Annual mean precipitation and temperature, aridity index)
	Season of vegetation survey

2.2.2 Landscape context

To assess landscape vegetation cover, we imported Copernicus Sentinel-2 Surface Reflectance (S2_SR) data from the Google Earth Engine COPERNICUS/S2_SR dataset (Gorelick et al., 2017). Satellite imagery for each site were selected based on the survey date (i.e., images captured as close as possible to the survey date for each sampled roof), to better depict prevailing conditions. We excluded images with more than 20% cloud cover to ensure clear visibility of the surface, minimise the risk of misinterpreting cloud shadows as surface features, and maintain consistent spectral reflectance values essential for accurate vegetation analysis. The red (B4; 665 nm) and near-infrared (B8; 842 nm) bands were selected for further analysis because these bands are most sensitive to vegetation characteristics. The red band tends to absorb light in healthy vegetation, while the near-infrared band strongly reflects it. The contrast between these two bands is commonly used in vegetation indices like the Normalised Difference Vegetation Index (NDVI). Using this imagery, we implemented a function to calculate the NDVI using the formula: NDVI = (B8 - B4) / (B8 + B4). The NDVI values range from -1 to 1, where higher values indicate higher vegetation density. The NDVI calculation function was applied to the Sentinel-2 images to generate a new image collection containing only NDVI values. By setting a threshold value for the NDVI of > 0.3 (Carlson & Ripley, 1997), we then classified pixels as either vegetation or non-vegetation. We used the latitude and longitude coordinates of each green roof site to extract NDVI values and determine the percentage of vegetation within 200m and 1000m buffers around the green roof sites. We selected buffer sizes based on the distances for potential wind (200m) and bird (1000m) dispersal of plant propagules (Nathan & Muller-Landau, 2000). The percentage of vegetation within each buffer was calculated by dividing the total number of vegetation pixels by the total number of pixels within the buffer.

The local climate data for each green roof was described using aridity index, annual mean temperature, and annual mean precipitation data at a resolution of 0.5 minutes of a degree from the CliMond database (Kriticos et al., 2012) (Figure 6.3). These climate characteristics are shown to influence plant community development on green roofs (Czemiel Berndtsson, 2010; Lönnqvist, Hanslin, et al., 2021; Lundholm, 2006).

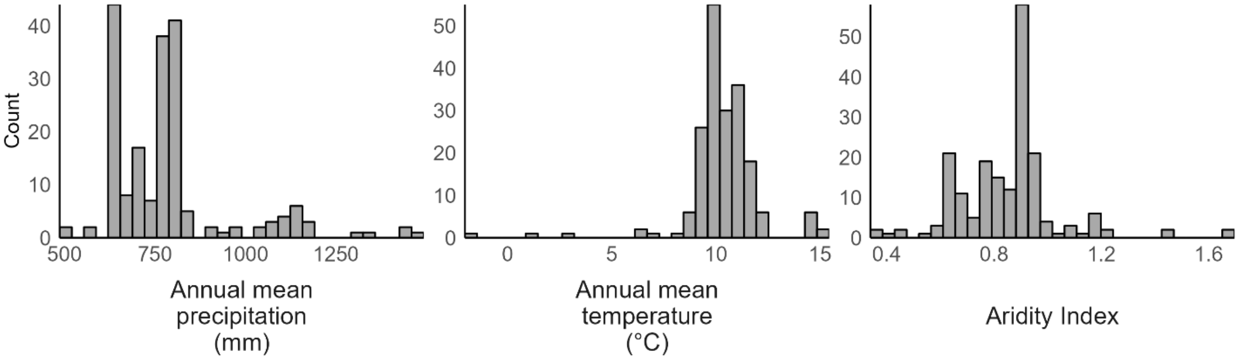


Figure 6.3: Local climate characteristics of 192 green roofs included in our global analysis of spontaneous vegetation communities.

2.4 Examining relationships between spontaneous species richness and green roof characteristics and landscape context

To explore variables influencing the species richness of spontaneous vegetation across the green roofs, we conducted linear regression analysis. Our initial model encompassed the full set of green roof characteristics and landscape context. Preliminary diagnostic plots were assessed to ensure the appropriateness of linear regression. Categorical variables were transformed into a binary matrix for linear modelling, with each category represented by a distinct binary column. After the initial regression analysis, non-significant predictors were systematically removed to refine the model. The significance of each predictor was determined by p-values, and variables with a p-value below 0.05 were considered significant. The final model's goodness-of-fit was evaluated using the adjusted R^2. Additionally, the regression coefficients were visualised using a coefficient plot, wherein the point estimates and their respective 95% confidence intervals were graphically presented.

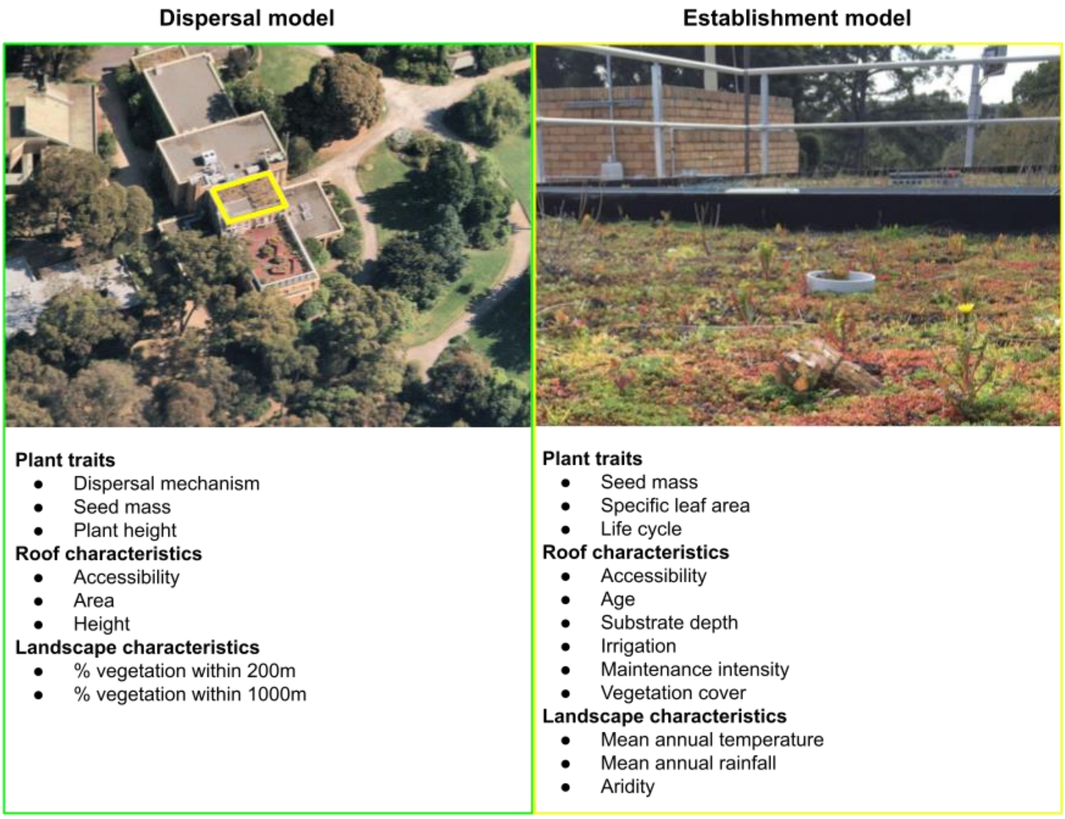
2.5 Examining relationships between spontaneous species traits and green roof characteristics and landscape context

We utilised the hierarchical model of species communities (HMSC) framework to examine connections between spontaneous species and green roofs in terms of traits and environmental factors (Ovaskainen et al., 2017). HMSC is a multilevel generalised linear mixed model that applies Bayesian statistics, utilising Markov Chain Monte Carlo (MCMC) sampling. The HMSC framework functions as a Joint Species Distribution Model (JSDM), as described by Warton et al. (2015), allowing for the exploration of factors that influence species assemblages and the contribution of trait/environment relationships to community structure (Ovaskainen et al., 2017).

We included data on species abundances, represented as a matrix Y of green roofs against species, environmental variables (matrix X of sampled locations against selected predictor variables), species traits (matrix T of species against the included traits), and taxonomic relationships between the species (depicted as a taxonomic tree with levels of species, genus, family, and order; with each taxonomic level assuming equal branch length). As surveys were conducted at different times of year, we included survey seasonality as a fixed effect in both models because of its potential influence on the temporal fluctuation in species presence. To adjust for possible spatial autocorrelation among plant species situated on proximate green roofs, we included site coordinates as a random effect.

2.5.1 Partitioning variables into dispersal and establishment models

Biological communities in cities are shaped by complex, interacting habitat filters (Williams et al., 2009). Consequently, we divided the environmental covariates and species traits relevant to different processes into two distinct models - 'dispersal' and 'establishment' (Figure 6.4). This decision was taken to avoid 'data dredging' and better align our modelling efforts with ecological theory (Ovaskainen et al., 2017). By partitioning the variables into two models, we aimed to assess the distinct contributions of dispersal and establishment in shaping community composition of spontaneous vegetation on green roofs.



Dispersal model

Plant traits
- Dispersal mechanism
- Seed mass
- Plant height

Roof characteristics
- Accessibility
- Area
- Height

Landscape characteristics
- % vegetation within 200m
- % vegetation within 1000m

Establishment model

Plant traits
- Seed mass
- Specific leaf area
- Life cycle

Roof characteristics
- Accessibility
- Age
- Substrate depth
- Irrigation
- Maintenance intensity
- Vegetation cover

Landscape characteristics
- Mean annual temperature
- Mean annual rainfall
- Aridity

Figure 6.4: Diagram illustrating key variables incorporated in the a) dispersal and b) establishment models. The featured images highlight the Burnley Research green roof in Melbourne Australia, a roof included in our analysis. Images © Nearmap (2023) and Schrieke, D. (2021).

2.4.2 Dispersal model

The 'dispersal' model emphasises traits relevant to the movement of plants from one location to another, following metapopulation theory of Hanski (1998). The environmental covariates included in this model are site access, area, height, plant cover, percent vegetation within a 200 m buffer, and percent vegetation within a 1000 m buffer. These factors are known to influence the availability and accessibility of suitable habitats, as well as the physical conditions that determine the probability of successful species dispersal (Zobel, 1997). The dispersal model also incorporates species dispersal mechanism, seed mass, and plant height, reflecting the theory that species' morphological traits play a significant role in their dispersal ability in cities (Piana et al., 2019).

2.4.3 Establishment model

The 'establishment' model focuses on factors that influence the successful growth and establishment of species in a new location, drawing from the theory of environmental filtering (Keddy, 1992). This model considers site age, substrate depth, irrigation regime, maintenance intensity, green roof plant cover, mean annual temperature, mean annual rainfall, aridity, and site accessibility as environmental covariates, all of which are linked to the suitability of a site for species establishment. Species’ traits seed mass, specific leaf area, and life cycle were included. Seed mass can impact germination success and seedling survival (Leishman et al., 2000), while specific leaf area and life cycle can influence a species' ability to establish and persist under varying environmental conditions (Wright & Westoby, 2002).

2.4.4 Additional model variations

We also ran the models without site coordinates as a random effect to assess the explanatory power of site location.

2.4.5 Data analysis

All data analyses were conducted in R, version 4.1.2 (R Core Team 2022). To account for the non-independence of traits among taxa, we integrated phylogenies into the model. Due to the extensive spatial nature of the data, we could not employ Bayesian JSDM. Instead, we used the nearest neighbour Gaussian process (NNGP). The models were specified with species occurrence (matrix Y) as the response variable and a combination of plant traits (matrix T), climate characteristics and environmental factors (matrix X) as predictor variables. We used the default HMSC priors for all parameters and estimated them using a Markov Chain Monte Carlo (MCMC) algorithm with 1000 iterations. We examined the estimated parameter values and their credible intervals to infer the relationships between plant traits, environmental factors, and species occurrence. We considered relationships to be statistically significant if the 95% credible interval of the parameter estimate did not include zero.

Prior to applying the HMSC models, we assessed potential collinearity among all environmental variables under investigation. Correlations between continuous and categorical variables were identified using Biserial correlation tests, while Pearson's product-moment correlation tests were employed for pairs of continuous variables. To compare models, we utilised area under the receiver operator curve (AUC) and the Widely Applicable Information Criterion (WAIC) as performance metrics for explanatory and predictive capacities respectively (Ovaskainen et al., 2017). AUC serves as an indicator of model fit by averaging the AUC for all species included in the model. An AUC value of 0.5 signifies predictions as good as random, whilst a value of one denotes perfect discrimination between presences and absences (Ovaskainen and Abrego 2020). The WAIC, on the other hand, balances the reward for goodness-of-fit and the penalty for model complexity (Watanabe and Opper 2010), with lower values indicating a more parsimonious model. Given its similarity to Bayesian cross-validation and generalisation, WAIC is advisable for model comparisons in HMSC analyses (Ovaskainen and Abrego 2020).

We evaluated the impacts of environmental variables by obtaining posterior parameter estimates with 95% credible intervals (CIs) for plant species (Beta estimates) and traits (Gamma estimates). Parameters whose 95% CIs didn't overlap zero suggested an effect of the environmental variable on a species or trait. To visually represent this, we plotted Beta and Gamma parameters using ggplot2 (Wickham 2016), indicating species/traits responses to environmental variables as neutral (CI includes zero), negative, or positive (CI does not include zero). In the application of MCMC sampling, convergence of the MCMC chain is crucial for an accurate approximation of the posterior distribution and thereby the parameter estimates (Ovaskainen and Abrego 2020). To ensure sufficient model convergence for all parameters across all HMSC models, we implemented four chains with 1000 samples each and a thinning interval (the period between recorded samples) of 10.

3.0 Results

3.1 Relationships between species richness and green roof characteristics, landscape context, and climate

Species richness had significant associations with several environmental and management variables (Figure 6.5). Linear regression analysis showed that for each year increase in roof age, there was a decrease of 0.17 in species richness. Whereas, for every cm increase in substrate depth, species richness increased by 0.22. The maintenance of the sites also influenced species richness. Sites with low maintenance had 7.6 more species, whereas sites with no maintenance had 9.93 additional species. Seasonality, particularly spring and winter, positively influenced species richness, with increases of 6.55 and 9.48 species, respectively. Other variables, such as area, mean annual temperature, and seasonality, also had associations with species richness, but these were not as pronounced. The adjusted R^2-of the model was 0.24, indicating that the included variables accounted for approximately 24.31% of the variability in species richness.

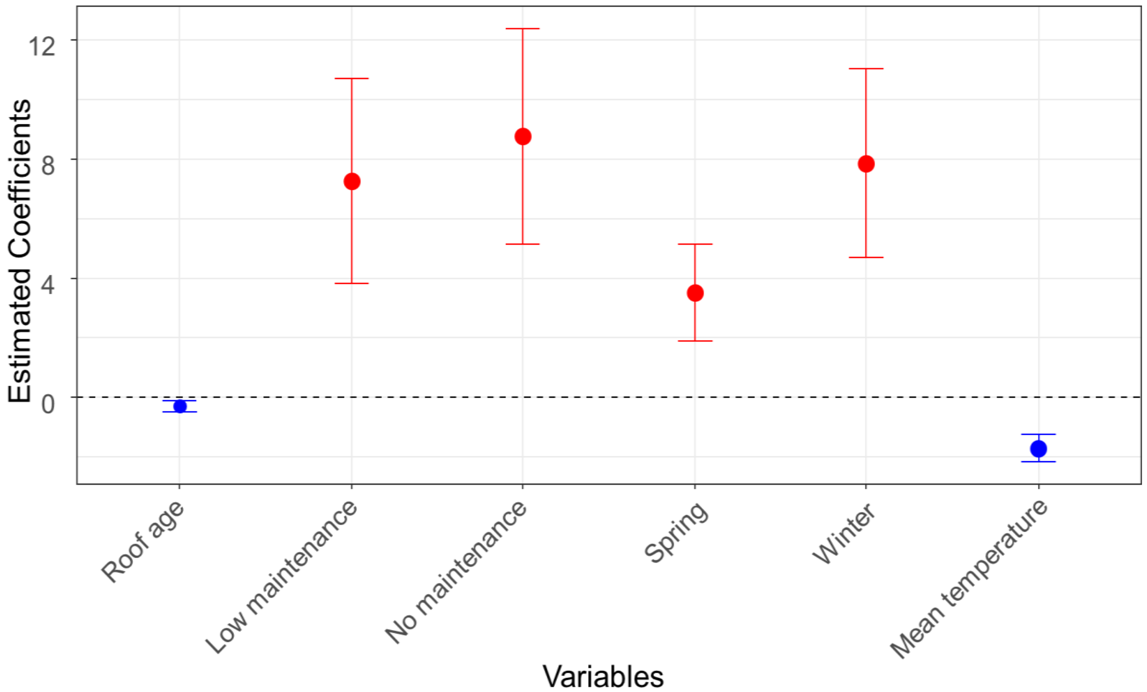


Figure 6.5: Relationship between species richness and key environmental variables. Coefficients represent the change in species richness for a one-unit increase in the predictor variable, derived from a linear model. Bars indicate the 95% confidence intervals. Colours indicate the direction of the relationship, with red indicating a positive association and blue indicating a negative association.

3.2 Hierarchical Modelling of Species Communities

3.2.1 Model diagnostics

Model diagnostics of dispersal and establishment models (Table 6.2, overleaf) show distinct patterns based on the inclusion or exclusion of site location as a random factor. The consistent AUC values of ‘complete’ models where site location is included as a random factor (dispersal; 0.88, establishment; 0.90) indicates high discriminative ability. The drop in AUC values when excluding site-specific factors (i.e., ‘incomplete’) in both models emphasises the significance of accounting for site variability. The Watanabe-Akaike Information Criterion (WAIC) values further support this; lower WAIC values for complete models signify a better trade-off between model fit and complexity, whereas a rise in WAIC values when excluding sites suggests reduced model efficacy. Tjur's R^2 , which indicates the proportion of variance explained, further confirms these patterns. Higher values for complete models' underscore their enhanced ability to explain variability in the data. Together, these metrics signal that while the incomplete models still exhibit a satisfactory fit, considering site location is crucial for robust model diagnostics. We will henceforth only report the results from the complete models.

3.2.2 Proportion of explained variance

Dispersal model

Among the landscape variables, landscape vegetation cover within a 200 m radius of the roof accounted for 8.2% of the variation in species occurrences, while landscape vegetation cover within a 1000 m radius exhibited a larger influence, accounting for 15.8% of the variation (Table 6.3, overleaf). Seasonality of the survey accounted for 24.3% of the variation. Moving to the roof characteristics, roof accessibility accounted for 5% of the variation in spontaneous species occurrences, roof area accounted for 7.2%, and roof height accounted for 6.7%.

Table 6.2: Comparison of two competing models: Dispersal and Establishment. Each model is further categorised into 'No Traits' (i.e., plant traits omitted) and 'Complete' (i.e., plant traits included). Entries marked with an 'X' indicate that the corresponding variable was included in the model.

		Dispersal		**Establishment**	
		Incomplete	**Complete**	**Incomplete**	**Complete**
Landscape context	200m veg	X	X		
	1000m veg	X	X		
	Climate			X	X
	Season	X	X	X	X
Roof characteristics	Accessibility	X	X	X	X
	Age			X	X
	Area	X	X		
	Height	X	X		
	Irrigation			X	X
	Maintenance			X	X
	Substrate depth			X	X
	Veg cover	X	X	X	X
Plant traits	Dispersal	X	X		
	Life cycle			X	X
	Plant height	X	X	X	X
	Seed mass	X	X	X	X
	SLA			X	X
Random effects	Site location		X		X
	AUC	0.81	0.88	0.85	0.90
	WAIC	26.16	24.89	24.73	23.77
	$TJUR^2$	0.09	0.14	0.15	0.19

Additionally, vegetation cover on the roof accounted for 11.6% of the variation. Finally, the site-specific random effect, capturing unaccounted-for variations at each study site, accounted for a significant portion (21.2%) of the variation in species occurrences. Overall, variables within ‘Landscape context’ explained 48.3% of the variation in species occurrences, ‘Roof characteristics’ explained 30.5% and the site-specific random effect, capturing unaccounted-for variations at each study site, accounted for a 21.2% of the variation.

Establishment model

Aridity accounted for 16.3% of the variation in species occurrences. Precipitation closely followed, accounting for 16.1% of the variance (Table 6.3). Temperature accounted for 8.6% of the explained variance and seasonal variations accounted for 14.9%. Among roof characteristics, area contributed 6.8% to the variation in species occurrences while irrigation explained 1.4%. Maintenance frequency accounted for 11% of the explained variance. Substrate depth accounted for 3.6% of the variance, and vegetation cover on the site contributed 6.1%. Lastly, site location, capturing unexplained variations unique to each site, explained 11.1% of the variance in species occurrences the establishment model.

Table 6.3: Comparison of the proportion of variance (%) explained by different roof characteristics and landscape variables of the two competing models: Dispersal and Establishment.

		Proportion of explained variance (%)	
		Dispersal	**Establishment**
Landscape context	200m veg	8.2	
	1000m veg	15.8	
	Aridity		16.3
	Precipitation		16.1
	Temperature		8.6
	Season	24.3	14.9
Roof characteristics	Accessibility	5.0	4.1
	Age		6.8
	Area	7.2	
	Height	6.7	
	Irrigation		1.4
	Maintenance		11
	Substrate depth		3.6
	Veg cover	11.6	6.1
Random effects	Site location	21.2	11.1

3.3 Parameter estimates

Dispersal model

In the gamma-plot that examines trait-environment responses (Figure 6.6) seed mass displayed a weakly negative correlation with surveys conducted during the summer season and a weakly positive correlation with landscape vegetation cover within a 200 m buffer. Wind dispersal showed a moderately positive association landscape vegetation cover within a 1000 m buffer and a weaker positive correlation with surveys conducted in spring. Unassisted dispersal had a weak positive relationship with spring and summer, and a moderate negative relationship with public access. Animal dispersal (ingested) had a moderately positive relationship with surveys conducted in spring. There was a strong negative correlation between plant traits and the combined intercepts of green roof characteristics, surrounding vegetation, and climate variables. When considering seed mass, a weakly negative relationship with these intercepts was observed. In relation to roof height, a weakly positive correlation with spontaneous plant traits was found. Landscape vegetation

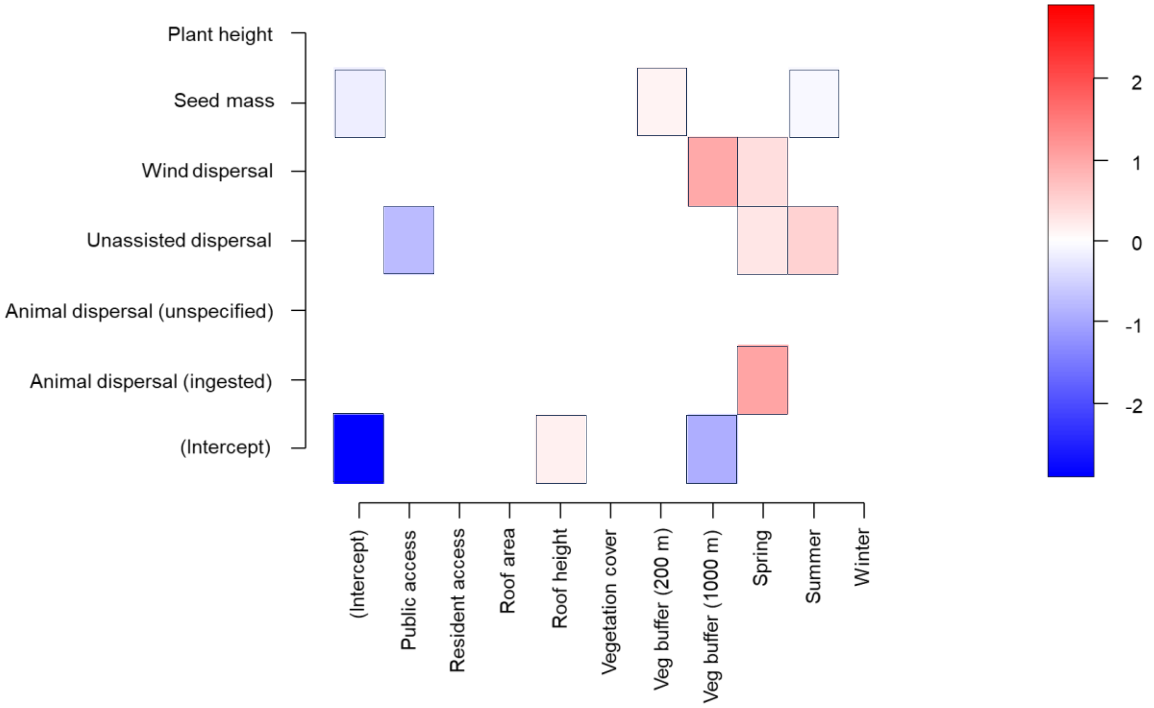


Figure 6.6: Gamma plot illustrating trait-environment correlations in the dispersal model. Coloured rectangles indicate significant positive (red) or negative (blue) correlations (gamma = 0.95 i.e., <0.05). The colour intensity reflects the strength of the correlation.

cover within a 1000 m radius of the green roof exhibited a moderately negative correlation with spontaneous plant traits.

Establishment model

In the trait-environment responses of the establishment model (Figure 6.7), perennial lifecycles showed a moderate negative correlation with public access and a weak positive correlation with summer surveys. Biennial lifecycles exhibited a moderate positive association with spring surveys. Specific leaf area displayed weak positive associations with irrigation and resident access, and a moderately weak negative association with low maintenance and winter. Seed mass demonstrated a weak negative association with aridity. The results indicated a strong negative association between irrigation, resident access, and the intercept of spontaneous species traits. In contrast, both low maintenance and winter seasonality displayed a strong positive correlation with this intercept.

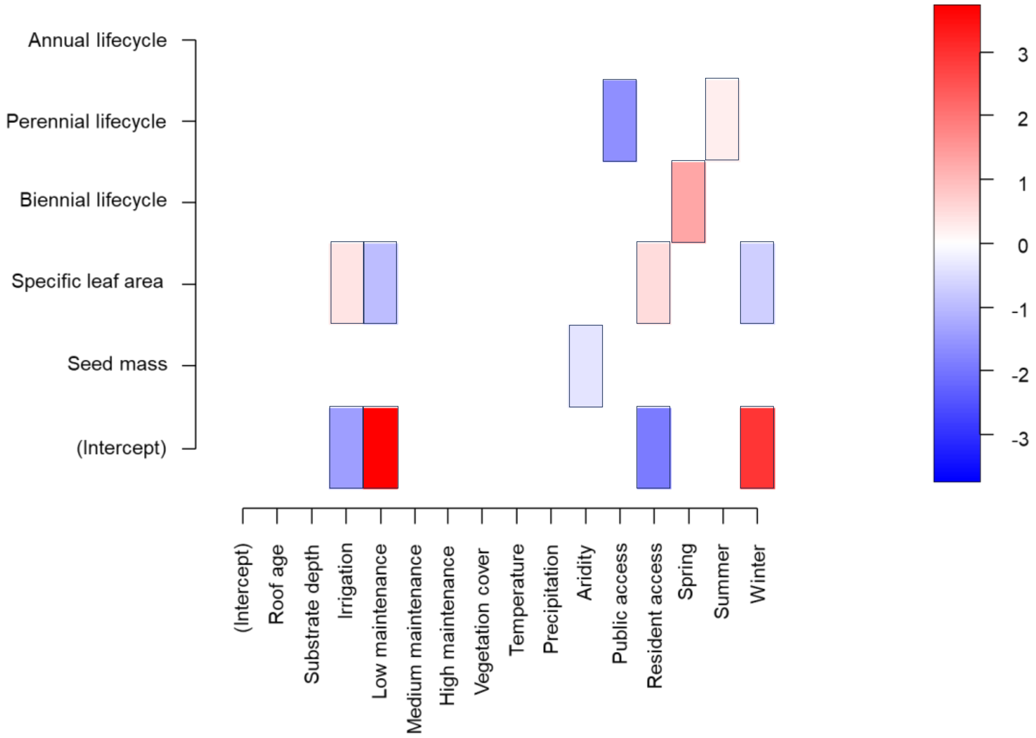


Figure 6.7: Gamma plot illustrating trait-environment correlations in the establishment model. Coloured rectangles indicate significant positive (red) or negative (blue) correlations (gamma = 0.95 i.e., <0.05). The colour intensity reflects the strength of the correlation.

4.0 Discussion

In our global analysis of 192 green roofs, we investigated how roof characteristics (age, size, substrate depth, and height), management practices (maintenance and irrigation), and landscape vegetation cover within 200 and 1000 m radii, as well as season and climatic conditions, shape spontaneous vegetation communities. Using regression analyses, we assessed the impact of these variables on species richness and applied Hierarchical Modelling of Species Communities (HMSC) to understand their roles in the dispersal and establishment of spontaneous species. Seasonal dynamics exerted a marked influence on spontaneous community composition within both dispersal and establishment models. Surrounding landscape vegetation cover was the primary driver of spontaneous vegetation dispersal traits on green roofs. Conversely, the establishment of spontaneous vegetation was chiefly governed by climatic factors, although green roof design features, such as roof height, accessibility and maintenance intensity also shaped the community structure. Spontaneous species richness was greater in spring and winter, increased with substrate depth and tended to decline as green roofs aged.

Seasonal differences of spontaneous species communities

Survey timing, aligned with seasonal changes, impacted the traits of spontaneous vegetation on green roofs, in both dispersal and establishment models. Animal-mediated dispersal showed a moderate positive correlation with the spring season, likely mirroring increased animal activity during this period, driven by enhanced food supply and fruit production that promote seed dispersal via ingestion (Howe & Smallwood, 1982). Wind dispersal demonstrated a slight positive relationship with spring, while unassisted dispersal was moderately associated with both spring and summer seasons, aligning with peak periods of seed dispersal (Howe & Smallwood, 1982). In the establishment model, a weak positive correlation was observed between perennial plants and summer survey periods, which may reflect life-cycle completion of annual species or mortality due to drought stress (Du et al., 2019). Similarly, the weak positive link between biennial lifecycles and spring surveys could be attributed to the favourable germination and growth conditions in spring.

The establishment model also identified a weak negative correlation between winter surveys and specific leaf area (SLA). This is consistent with the notion that species with lower SLA are slower-growing and more conservative in resource use (Reich, 2014; Westoby, 1998), and better equipped to endure colder winter temperatures and desiccation due to frost (Gong & Gao, 2019). This reflects European climates where most surveyed roofs were located. Furthermore, the strong positive correlation between winter surveys and the baseline traits of spontaneous species suggests seasonal shifts in trait expression, aligning with the die-off of summer annuals during winter and compositional change in spontaneous plant communities. This seasonal trait turnover is further supported by Bates et al. (2013), who noted the emergence of annual spontaneous species following alleviation of drought conditions on green roofs. All these results highlight the seasonal nature of spontaneous green roof plant communities.

Determinants of green roof species richness

Species richness was greater in spring and winter, suggesting that the milder temperatures and seasonal precipitation typically associated with these times of the year may be favourable to a more diverse vegetation community (Adler & Levine, 2007). Additionally, our findings suggest a decline in species richness with increasing mean annual temperature, a trend that may be attributed to several interrelated factors. Heat stress can negatively impact germination and survival rates while favouring heat-tolerant species on green roofs (Savi et al., 2016) and elevated temperatures typically lead to increased evaporation rates, reducing water availability and disadvantaging species that are not drought resistant on green roofs (Chu & Farrell, 2022; Monterusso et al., 2005; Rayner et al., 2016), limiting species richness. Roof age presented a weak relationship with species richness, which tended to decline as green roofs aged. This pattern may result from ecological succession, where initial colonisation by a diverse array of pioneer species is gradually replaced by competitive exclusion and the dominance of a few species well-adapted to the stressful green roof environment (Catalano et al., 2016; Vanstockem, Bastiaens, et al., 2019).

The positive relationship between substrate depth and spontaneous species richness shown in our establishment model echoes Madre et al. (2014) and Vanstockem, Bastiaens, et al. (2019), who found that green roofs with deeper substrate had greater species richness. Deeper substrates have a higher water retention capacity and provide more thermally stable environments, which can support a broader spectrum of plant functional types (Brown & Lundholm, 2015; Getter & Rowe, 2008). Nonetheless, this is in contrast to the findings of Lönnqvist, Blecken and Viklander (2021) in a study of 42 extensive green roofs (3 – 8.5 cm substrate depth) across nine locations in Norway and Sweden (temperate to subarctic climates), who found no relationship between substrate depth and spontaneous species richness. It should be noted, however, that the green roofs in our analysis exhibited a wider range of substrate depths (2 – 50 cm) compared to those in their research, suggesting there may be a threshold substrate depth before the influence of temperature and drought are mitigated and species richness increases.

The effect of landscape vegetation cover on spontaneous vegetation dispersal

Landscape vegetation cover within a 1000 m radius influenced the composition of spontaneous plant communities on green roofs, accounting for 15.8% of the variability in species occurrences. This was more influential than landscape vegetation cover within a 200 m radius which only accounted for 8.2% of the variability. This suggests that colonisation of spontaneous vegetation is largely dependent on the range and abundance of propagules in the surrounding environment. In our study, the larger buffer area (1000 m vs 200 m) likely captured a greater extent of animal-mediated dispersal (Vittoz & Engler, 2007), which is especially relevant in urban environments where animal dispersal vectors are more prevalent (Knapp et al., 2008) and have been shown to be crucial for seed inflow (Lundberg et al., 2008) and dispersal continuity (Hougner et al., 2006). Moreover, the weak positive correlation between wind dispersal and landscape vegetation cover at a 1000 m radius, rather than at 200 m, supports the hypothesis that a wider radius is necessary to adequately represent the influence of wind dispersal. This finding aligns with Vanstockem, Bastiaens, et al. (2019) who noted a lack of relationship between wind dispersal and potential source habitat within a 200 m buffer, and perhaps highlights the need for larger-scale analyses of landscape cover in urban dispersal studies. The moderate negative correlation between the intercept of plant traits and landscape vegetation cover extent within a 1000 m radius suggests that as landscape vegetation cover increases, there is a shift in the spontaneous plant community traits, likely due to a greater diversity of available propagules (Aronson et al., 2014). There was a moderate positive correlation between seed mass and landscape vegetation cover within a 200 m radius, suggesting that green roofs closer to landscape vegetation cover tend to have spontaneous plant species with larger seeds, possibly because these heavier seeds typically disperse over shorter distances (Vittoz & Engler, 2007).

The effect of green roof design on spontaneous species dispersal

Roof height contributed 6.7% to the variance in our dispersal model and was weakly and positively correlated with the intercept of spontaneous plant community traits. This may suggest a high elevation threshold is necessary to significantly affect plant communities, which could be due to the complex effects of higher elevations on wind patterns and microclimates (Mikhailuta et al., 2017), or the challenges animal dispersers may encounter getting to taller structures. Although Madre et al. (2014) identified a significant relationship between green roof height (5.7 m ± 4.7) and the functional composition of spontaneous vegetation on green roofs in northern France, Vanstockem, Bastiaens, et al. (2019) did not find a relationship between roof height (median: 4.56 m; range: 1.36–25.93 m) and the species richness or functional composition of spontaneous species on green roofs in Belgium. Spontaneous plant communities in Vanstockem, Bastiaens, et al. (2019)’s study were predominantly composed of species with wind-dispersed seeds, which might obscure the influence of roof height, and could partially explain the relatively weak effect observed in our study.

The effect of climate on spontaneous vegetation establishment

Aridity index and mean annual precipitation emerged as almost equally influential, each accounting for approximately 16% of the variation in plant traits in our establishment model. Temperature also made a noticeable contribution, albeit smaller, explaining 8.6% of the variation in plant establishment. These findings emphasise the dual impact of water availability on spontaneous vegetation: on the one hand, the scarcity of water and elevated temperatures inherent in arid conditions, and on the other, the abundance of water from precipitation. These factors are consistent with the observed challenges in establishing planted vegetation on green roofs under hot and dry conditions (Durhman et al., 2007; Eksi & Rowe, 2019; Rayner et al., 2016; Williams et al., 2021) and align with the reported prevalence of spontaneous plant cover in wetter Scandinavian climates (Lönnqvist, Hanslin, et al., 2021). These dynamics also mirror global ground-level trends, where climatic variables such as aridity (Berdugo et al., 2020) along with temperature and precipitation (Morison & Morecroft, 2006) are known to be key drivers of plant community structure.

Green roof design characteristics and establishment of spontaneous species

The establishment model suggests that green roof characteristics (accessibility, age, area, height, irrigation, maintenance, substrate depth and green roof vegetation cover) are responsible for 30.5% of the variation in spontaneously occurring species traits. Maintenance regimes of green roofs explained 11% of the variation, with lower SLA associated with low maintenance and strongly positively associated with the intercept of species traits. This finding reflects the fact that lower SLA is associated with slower-growing, stress-tolerant species, which are more susceptible to disturbance (Grime, 1977; Reich, 2014; Westoby, 1998). Our data suggests that low maintenance, characterised by infrequent disturbance, tend to support species with lower SLA. Furthermore, the strong positive relationship between low frequency maintenance practices and the intercept of plant traits indicates that the intensity of maintenance may drive trait divergence among spontaneously colonising vegetation. A maintenance regime with minimal human intervention enables a wider array of species to establish and persist on green roofs, increasing trait diversity within the spontaneous vegetation community. Green roof maintenance, such as weeding, watering, and fertilising, have been shown to influence the moisture and nutrient affinity characteristics of spontaneous vegetation on green roofs in northern France (Madre et al., 2014). This relationship likely mirrors the tendency for species that are adept at resource acquisition to flourish on roofs that are more frequently managed, which are characterised by higher moisture and nutrient availability (Reich, 2014).

The influence of roof accessibility on spontaneous species traits was weak, explaining 4.1% of the variation within the establishment model. Despite the impact on trait variation, roof accessibility did not manifest a significant correlation with species richness. This finding suggests that the frequency and pattern of human access may not be pivotal in determining the diversity of spontaneous species on green roofs. Nonetheless, the moderate negative correlation observed between the presence of perennial species and public access implies a tendency for areas with more human traffic to be populated by non-perennial species. This pattern may be attributed to the increased disturbances associated with higher foot traffic, which may favour disturbance-tolerant annual species (Grime, 1977). Moreover, the association between SLA and resident access was weakly positive, while a strong negative correlation was found between resident access and the intercepts of spontaneous species traits. This dynamic suggests that frequent resident presence may inhibit the establishment of spontaneous species, potentially through informal maintenance activities or other disturbances, and instead promote fast-growing species that can quickly recover from such disturbance.

Substrate depth only explained 3.6% of the variation in plant characteristics in the establishment model. This might be due to all the green roofs in our study being designed with engineered substrates optimised for effective drainage, which might lessen the significance of substrate depth in regions that experience hot and dry weather conditions (Guo et al., 2021). The weakly positive relationship between irrigation and SLA indicates a slight competitive edge for plants with higher SLA in conditions of consistent water availability, which corroborates with the established theory that fast-growing, resource-acquisitive species with greater SLA are more competitive when resources are not limiting (Reich, 2014; Westoby, 1998). Green roofs in higher rainfall regions of Scandinavia (maritime to subarctic climates), tend to have greater spontaneous plant coverage compared to those in drier regions (Lönnqvist, Hanslin, et al., 2021) and it has been observed in greenhouse studies that faster-growing spontaneous species consume more water than their slower-growing counterparts (Schrieke & Farrell, 2021). The pronounced negative correlation between irrigation and the intercept of species traits indicates a prevalence of characteristics favourable to water conservation on roofs without irrigation, thereby suggesting that irrigation practices may induce trait divergence within spontaneous vegetation communities, as evidenced by the recent findings of Schrieke et al. (2023). Yet the overall effect of irrigation on the spontaneous vegetation only explained 1.4% of the variability in our establishment model. This is likely because most roofs in our study were unirrigated.

Study limitations

In our study, acknowledging the influence of green roof location as a random variable substantially increased the predictive strength of our dispersal and establishment models. The dispersal model's random effects explained 21.2% of the variation, and 11.1% in the establishment model, suggesting that roofs in closer proximity may share species compositions due to similar environmental factors or seed dispersal mechanisms—a concept supported by the foundational theories of Macarthur and Wilson (1967), resulting in similar regional urban species pools (Aronson et al., 2016). Nekola and White (1999) further corroborate this, noting a decline in community similarity as distance increases, indicating the significance of spatial relationships in ecological research. However, our models did not fully capture the diverse array of environmental and design variables that can influence urban plant communities, which are profoundly affected by regional factors (Aronson et al., 2014; Williams et al., 2015). Future studies should aim to integrate a broader spectrum of location-specific variables, addressing both environmental and human-related elements, to refine the predictive accuracy of these models. Increasing the sample size to include a more diverse age of roofs and a broader range of plant traits, along with the inclusion of abundance data, would enhance our understanding of the evolving patterns of species richness and trait diversity on green roofs over time. As seasonal variation influenced the trait profiles of spontaneous green roof vegetation communities, standardising survey timing may simplify the observed relationships and enhance the clarity of the results.

5.0 Conclusion

Our study highlights the complex interplay between seasonal and climatic factors, green roof design, and landscape vegetation in shaping the composition of spontaneous vegetation communities on green roofs. We found that survey season strongly influenced spontaneous community composition within both dispersal and establishment models. The primary factor influencing the dispersal traits of spontaneous vegetation on green roofs was the surrounding landscape vegetation cover. In contrast, the establishment of spontaneous vegetation was chiefly governed by climatic factors, although green roof design features, such as roof height, accessibility and maintenance intensity also shaped the community structure. Spontaneous species richness was greater in spring and winter, increased with substrate depth and tended to decline as green roofs aged. By considering the distinct advantages of different plant life-history strategies in different seasons, acknowledging the contribution of substrate depth to species richness, fine-tuning maintenance to support trait diversity, and recognising the spatial influences on species dispersal and establishment, green roof designers and managers can optimise green roofs for spontaneous species biodiversity.

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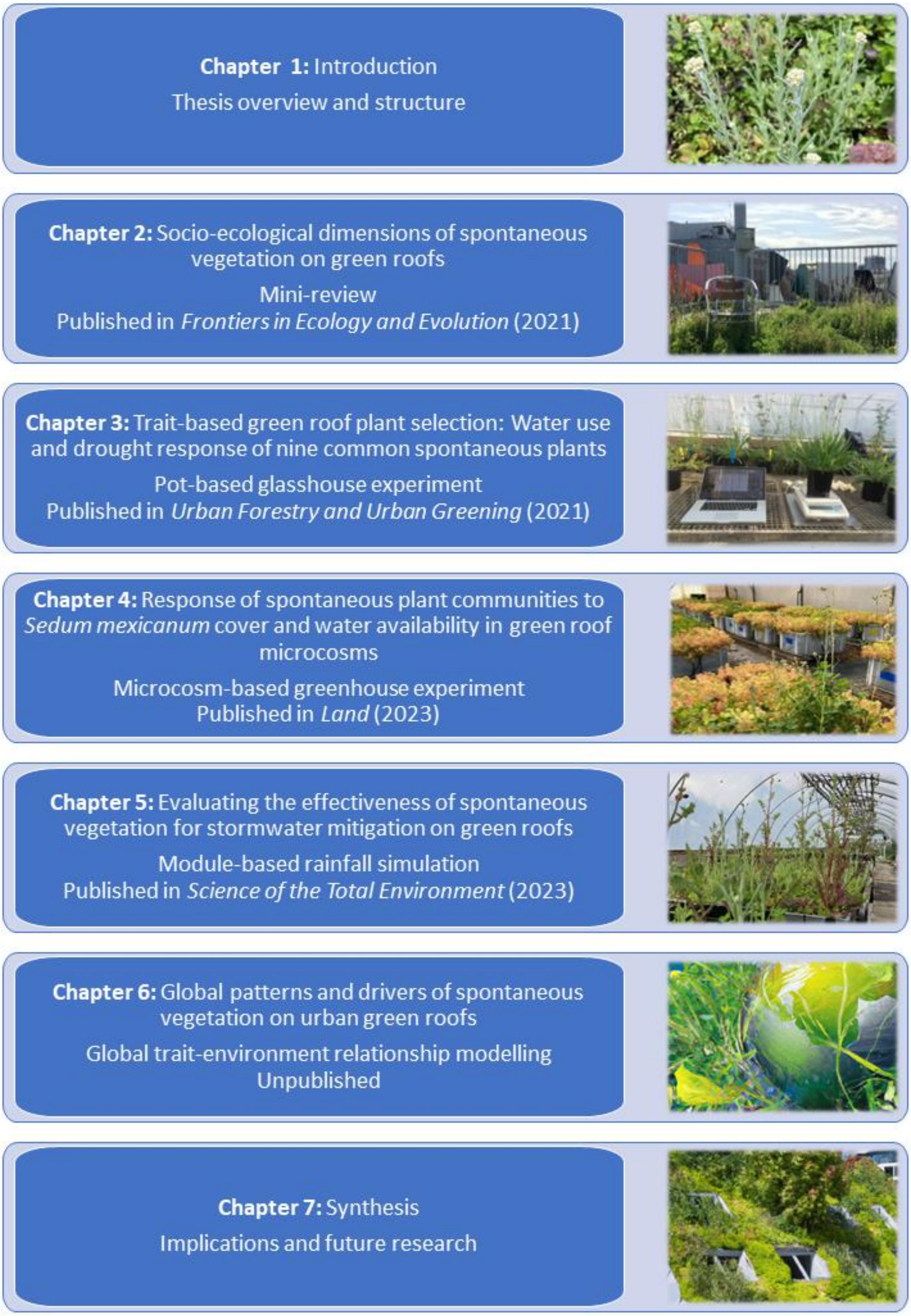
Chapter 7 : Synthesis of key results, implications for green roof design and implementation, and future research

Summary of research approach

This PhD thesis explores the ecological characteristics of spontaneous green roof vegetation and its impact on green roof functionality. It encompasses a general introduction (Chapter 1), a literature review (Chapter 2), and four experimental data chapters (Chapters 3-6) (Figure 7.1, overleaf). A central aspect of this research was to determine if spontaneous vegetation can serve as a cost-effective substitute for traditional green roof plantings, particularly in urban areas where green roofs are increasingly used to mitigate the adverse effects of urbanisation. This chapter (Chapter 7) synthesises key findings from previous chapters, discusses their implications for green roof design and outlines prospective avenues for further research.



Chapter 1: Introduction

Thesis overview and structure

Chapter 2: Socio-ecological dimensions of spontaneous vegetation on green roofs

Mini-review

Published in *Frontiers in Ecology and Evolution* (2021)

Chapter 3: Trait-based green roof plant selection: Water use and drought response of nine common spontaneous plants

Pot-based glasshouse experiment

Published in *Urban Forestry and Urban Greening* (2021)

Chapter 4: Response of spontaneous plant communities to *Sedum mexicanum* cover and water availability in green roof microcosms

Microcosm-based greenhouse experiment

Published in *Land* (2023)

Chapter 5: Evaluating the effectiveness of spontaneous vegetation for stormwater mitigation on green roofs

Module-based rainfall simulation

Published in *Science of the Total Environment* (2023)

Chapter 6: Global patterns and drivers of spontaneous vegetation on urban green roofs

Global trait-environment relationship modelling

Unpublished

Chapter 7: Synthesis

Implications and future research

Figure 7.1 Thesis structure, chapter titles and publication details.

Summary of key results

Can spontaneous vegetation support green roof expansion in urban areas with limited funding or space? (Chapter 2)

Chapter 2 reviewed published literature to examine social and ecological aspects of spontaneous vegetation on green roofs. It first highlighted the benefits of green roofs, particularly in dense urban areas that lack green space, noting that adoption is limited by high construction and maintenance costs. As a result, green roof projects can disproportionately benefit wealthier communities (Sharma et al., 2018) and further marginalise disadvantaged communities by increasing housing costs and property prices (Wolch et al., 2014). If spontaneous vegetation cover on green roofs can provide functionality comparable to that of planted vegetation, it might be considered ‘just green enough’ (Curran & Hamilton, 2012). This approach may reduce the costs associated with green roof installation and maintenance, facilitating wider adoption in urban areas constrained by funding or space.

Spontaneous vegetation contributes to green roof functionality by offering resources for pollinators (Wang et al., 2017), creating habitats for arthropods (Deng & Jim, 2017) and enhancing plant biodiversity in urban areas (Madre et al., 2014). However, spontaneous vegetation with low cover can be perceived as untidy or indicative of neglect (Vanstockem, Somers, & Hermy, 2019) and there could be challenges in establishing spontaneous vegetation cover on green roofs, particularly on tall buildings where colonisation may be limited by lack of seed dispersal (Grant, 2006). If spontaneous green roof vegetation had poor cover, this could exacerbate perceived neglect and diminish the potential mental health benefits. This may limit the applicability of spontaneous vegetation to roofs that are less visible and accessible.

Spontaneous plants, when labelled as 'weeds,' are viewed negatively on green roofs (Vanstockem et al., 2018). This perception is likely influenced by complex human landscape and plant preferences, which are in turn shaped by cultural norms at both the neighbourhood and individual levels. People generally prefer plants that have conspicuous and colourful flowers and are organised within a neat, orderly framework that indicates a human ‘cue to care’ (Joan Iverson, 1995). The flowering continuity provided by spontaneous green roof vegetation (Wang et al., 2017) combined with clearly defined edges of vegetated areas of green roofs could be perceived as cues to care and enhance public acceptance of such vegetation. Outreach efforts aimed at communicating the functional and ecological benefits of spontaneous vegetation on green roofs could also further promote public acceptance. Educating the community about the environmental advantages of spontaneous vegetation, including biodiversity enhancement and ecosystem services, can positively influence acceptance (Kratschmer et al., 2018; Southon et al., 2017).

Chapter 2 highlights the potential trade-offs of accepting and managing spontaneous vegetation on green roofs, particularly in lower socio-economic areas. The success of spontaneous green roofs could hinge on balancing aesthetic preferences with ecological functionality and providing public education about the benefits. By focusing on achieving good plant coverage, better communicating landscape ‘cues to care,’ and choosing less visible or accessible locations, spontaneous vegetation could emerge as an affordable and ecologically valuable choice for green roofs.

How do spontaneous green roof plants use water and respond to drought? (Chapter 3)

Chapter 3 assessed the water use and drought response of nine spontaneous green roof plant species in a glasshouse experiment and related these physiological parameters to their functional traits. In the experiment, well-watered (WW) plants were watered to pot capacity every other day, while water-deficit (WD) plants received 30% of this amount until soil water content dropped to 15%, then they were re-watered to pot capacity, with this cycle repeating until day 51, after which WD plants received no further water. During this final dry-down, when WD pots reached 10% soil water content (SWC), leaf relative water content (leaf RWC) was measured to determine plant water status and plants were harvested for biomass measurements.

I hypothesised that greater transpiration under WW conditions would be associated with ‘fast’ (Reich, 2014) traits, such as greater relative growth rate (RGR). This was reflected in the results, which found that the higher transpiration of spontaneous species under WW conditions was related to ‘fast’ traits, including greater biomass, leaf area and RGR. I also found that in WD conditions, there was a trade-off between transpiration rate under WW conditions and leaf RWC; species with ‘fast’ traits were not able to maintain leaf RWC under WD (i.e., they exhibited greater stress under drought conditions). The spontaneous species that managed to maintain leaf RWC under WD conditions had lower RGR and biomass (i.e., ‘slow’ traits). While ‘fast’ spontaneous species reduced their transpiration to a greater extent than ‘slow’ species under WD (57-72%), this was insufficient to maintain leaf water status (leaf RWC <90%) and avoid drought stress. These findings indicate that ‘fast’ spontaneous species which transpire more water generally have greater flexibility in their water usage. However, the drought conditions in our experiment might not have been severe enough to observe this adaptability in ‘slow’ species that use less water.

The highest transpiring spontaneous species in this study, *L. perenne*, had greater water use than many plants in other similar green roof experiments, surpassing the daily water use of 14 out of 20 native Australian shrub species in Du et al. (2018)’s study and exceeding the top transpiring species, *Isotoma axillaris*, from Farrell et al. (2013)’s study by 19%. Conversely, the species with the lowest transpiration in our study, *E. maculata*, had a daily water use comparable to the *Sedum* species (*Sedum pachyphyllum*) in Farrell et al. (2013)’s study. These results suggest that spontaneous species are transpiring at rates similar or greater than those of commonly planted species, indicating a potential for enhanced rainfall retention on green roofs.

Another key finding was that, contrary to other research that linked specific leaf area (SLA) with RGR and water use (Ackerly, 2004; Du et al., 2018; Farrell et al., 2013; Van Mechelen et al., 2014), this association was not observed in this study. This could suggest that SLA's effectiveness as a predictor of water use might be specific to certain species or life forms, rendering it an unreliable sole criterion for selecting plants for green roofs.

In Chapter 3, the evaluation of nine spontaneous green roof plant species revealed a diverse range of water-use and drought-response strategies, linked to their specific traits. These findings suggest that green roofs naturally select for varied water use and drought response strategies, pointing to the likely benefits of diverse species mixtures in these environments. This diversity may confer a significant advantage, potentially enhancing stormwater management during wet periods and improving plant survival during dry spells. Such versatility is crucial for adapting to the dynamic environmental conditions typical of green roofs. Further, Chapter 3 presents evidence indicating that spontaneous vegetation on green roofs may be equally effective as planted species in mitigating stormwater runoff.

What is the effect of green roof vegetation cover (Sedum mexicanum) on the growth, abundance, traits, and diversity of spontaneous species in extensive green roofs, and how does water availability influence these aspects? (Chapter 4)

Chapter four describes a 10-month study conducted in green roof microcosms planted with *Sedum mexicanum* in varying coverages, ranging from 0 to 100%, and sown with 14 species that are typically found as spontaneous vegetation on green roofs. The microcosms were subjected to either a well-watered or water-deficit irrigation regime. The purpose of this experiment was to investigate how the cover of *S. mexicanum*, in conjunction with water availability, affects the abundance, biomass, traits, species richness and functional diversity of spontaneous plant communities.

I hypothesised that increasing *S. mexicanum* cover and reducing water availability would decrease the abundance of spontaneous vegetation. Yet while Increasing *S. mexicanum* cover was correlated with a decline in the abundance of spontaneous species, this relationship was not affected by watering. This could be attributed to *S. mexicanum* cover potentially improving substrate moisture retention by acting as a 'mulch', thus reducing evaporation under water deficit conditions. This has been observed in other green roof studies (Durhman et al., 2006; Wolf & Lundholm, 2008).

In the microcosms with no *S. mexicanum* cover, which had the highest abundance of spontaneous species, *Euphorbia peplus* emerged as the most prevalent species. However, it was absent in microcosms with 50, 75, and 100% *S. mexicanum* cover, regardless of the watering treatment. A similar pattern was observed for *Euphorbia maculata*, which was abundant in microcosms with no *S. mexicanum* cover but absent in those with higher *S. mexicanum* coverage. Both *Euphorbia* species, having growth, water use (Farrell et al., 2013; Schrieke & Farrell, 2021) and photosynthesis pathways (Batanouny et al., 1991) like *Sedum* spp., might have experienced niche contraction in the microcosms (Chesson, 2000; MacDougall et al., 2009). This contraction, potentially due to resource limitation, increased competition, and changes in the microenvironment, could have hindered the germination and establishment of *E. maculata* and *E. peplus*.

The biomass of spontaneous vegetation communities was not significantly influenced by *S. mexicanum* coverage. The spontaneous species *Trifolium repens* maintained high biomass and abundance with water limitation and increasing *S. mexicanum* cover, likely due to its nitrogen-fixing capability, allowing it to thrive in the low-organic-matter substrate (Farrell et al., 2012; Lane et al., 2000), and its ability to maintain photosynthesis through long petioles, minimising the shading effect of *S. mexicanum* (Caradus et al., 1990).

In terms of diversity, the species richness of spontaneous vegetation communities was primarily affected by the interaction between *S. mexicanum* cover and water availability, with the highest spontaneous species richness observed in well-watered microcosms with no *S. mexicanum* cover. This interaction suggests that *S. mexicanum* may shift from having a competitive to facilitative effect on spontaneous vegetation, depending on water availability, echoing findings from other green roof research (Butler & Orians, 2009). *S. mexicanum* cover had a negative impact on the functional richness of spontaneous plant communities, perhaps because species with similar functional traits to *S. mexicanum* (e.g., conservative water use and facultative CAM/C3 photosynthesis) were outcompeted due to niche overlap (Batanouny et al., 1991; MacArthur & Levins, 1967). This competitive exclusion effect was particularly evident in microcosms with more than 25% coverage of *S. mexicanum*, where functionally similar species (e.g., *Euphorbia peplus and E. maculata*) failed to establish (Chesson, 2000; MacDougall et al., 2009).

The community weighted mean specific leaf area (CWM SLA) of spontaneous plant communities varied across treatments. Lower CWM SLA values in water-deficit microcosms, regardless of *S. mexicanum* cover, highlighted a physiological adjustment towards drought tolerance (Ackerly, 2004). Interestingly, the presence of *S. mexicanum* did not linearly impact CWM SLA. At <75% coverage in water deficit modules, *S. mexicanum* may have enhanced soil moisture sufficiently to support spontaneous species with higher SLA, a trait typically associated with more productive habitats (Wright & Westoby, 1999). Nevertheless, at full *S. mexicanum* coverage, the dominance of *T. repens*, a species with comparatively high SLA, masked the potential effects of *Sedum* presence and water treatment on CWM SLA (Archibold & Wagner, 2007; Van Mechelen et al., 2015).

Chapter 4 highlighted that green roof vegetation cover and water availability interact to affect growth, abundance, traits, and diversity of spontaneous green roof species. Further, the results shows that *S. mexicanum* cover can be both competitive and facilitative depending on water availability. From a maintenance perspective, to preserve a high cover of *Sedum* spp. and limit the establishment of spontaneous species, it is recommended to limit irrigation on green roofs, and occasionally remove any dominant spontaneous species (e.g., *T. repens*). However, combining *Sedum* spp. with high-water-use spontaneous species like *T. repens* may be more beneficial for stormwater management and biodiversity, maximising transpiration of water stored in substrates during wet periods and plant cover during periods of water deficit.

Does spontaneous vegetation enhance stormwater management on green roofs, and how do substrate depth and rainfall patterns impact its effectiveness and the structure of the resulting plant community? (Chapter 5)

Chapter 5 focused on spontaneous vegetation's impact on a green roof’s stormwater management functionality, using a 100-day rainfall simulation in green roof modules. Modules were filled with substrate of either 7 cm (shallow) or 14 cm (deep) depth, either left bare or sown with a seed mixture of 14 species of spontaneous vegetation common to Mediterranean-climate green roofs, which established full cover before the rainfall simulation began. The experiment had 'dry' and 'wet' phases, based on historical Melbourne climate data. Measurements included rainfall retention, evapotranspiration, runoff initiation, and soil water content for 17 events. Additionally, spontaneous vegetation cover, species richness, functional diversity, and end-of-wet-phase biomass were assessed.

In the dry phase, rainfall retention was significantly influenced by the presence of spontaneous vegetation cover, but not by substrate depth or the combined effect of vegetation and substrate depth. Modules with spontaneous vegetation retained 88% of rainfall, showing 6% higher retention than those with bare substrate, irrespective of substrate depth. During the wet phase, retention was affected by vegetation, substrate depth, and their interaction. The highest retention (94%) occurred in modules with vegetation and deep substrate, surpassing other treatments by 30%. In modules with a shallow substrate, those with vegetation had a 7% higher retention rate (78%) compared to bare modules.

The retention findings align with previous Melbourne studies under similar conditions, which reported an average yearly rainfall retention of 73% (Zhang et al., 2018) and 89–95% per event (Zhang et al., 2019). However, these retention rates are at the higher end of global reports (Zheng et al., 2021) and exceed those reported in comparable studies undertaken in oceanic (Stovin et al., 2012), continental (Sims et al., 2016), and temperate (Locatelli et al., 2014) climates. During the dry phase, low rainfall likely led to high retention, as all applied water was depleted through evapotranspiration and events seldom surpassed substrate capacity (Sims et al., 2016). The extended intervals between rainfall events in the wet phase probably allowed the substrate's water to be fully utilised by increased evaporation and plant transpiration (Czemiel Berndtsson, 2010).

Substrate depth proved crucial for rainfall retention, with deeper substrates enhancing evapotranspiration (ET) of spontaneous plant communities, especially in the 'wet' phase. These deeper substrates supported more vegetation cover and biomass, directly linked to increased ET and hence better water retention (Dunnett et al., 2008; Durhman et al., 2007). Although deeper substrates with spontaneous vegetation had higher ET, the retention differences between vegetated and bare substrates were less marked during smaller (2 to 15 mm) rainfall events in the 'dry' phase. However, in the 'wet' phase, the benefits of deeper substrates became apparent due to their superior storage capacity and enhanced ET.

During the dry phase, the onset of runoff was significantly influenced by the presence of spontaneous vegetation cover, substrate depth, and their interaction. With deep substrates, there was no notable difference in runoff initiation time between vegetated and bare modules, and runoff began later in deep substrates compared to shallow ones. In shallow substrates, modules with spontaneous vegetation cover had a 28% greater delay in runoff initiation. In the wet phase, the time to runoff onset was significantly affected by spontaneous vegetation cover and substrate depth, but without a notable interaction between the two. Modules with spontaneous vegetation cover took 20% longer to initiate runoff than bare ones, and those with deep substrate started runoff 28% later compared to modules with shallow substrate.

Substrate depth influenced the structure and species richness of spontaneous plant communities. Communities in deeper substrates exhibited higher species richness. While greater species richness has been linked to enhanced stormwater retention (Lundholm et al., 2010), species richness is not solely dependent on substrate depth and may decrease over time due to natural succession and competitive dynamics (Heim & Lundholm, 2014; Schrieke & Farrell, 2021). In both the wet and dry phases of the experiment, vegetation cover was more substantial in deeper substrates, correlating with higher shoot biomass in these substrates by the experiment's end.

Substrate depth did not affect the species richness of the spontaneous plant community, which was higher during the dry phase of the experiment. The experiment began in winter, enabling the completion of the life cycles of several winter annuals (*Euphorbia peplus*, *Sonchus oleraceus*, and *Stellaria media*) before the mid-summer census in the wet phase. Starting the wet phase in early November meant that established spontaneous vegetation possibly hindered the germination and growth of slower-growing summer annuals like *Euphorbia maculata* and *Portulaca oleracea*. Functional richness was greater in the deep substrate. The community weighted mean (by biomass) specific leaf area was 8% higher in modules with shallow substrate compared to those with deep substrate.

Chapter 5 shows that spontaneous vegetation can significantly enhance stormwater retention in green roofs. This enhancement is influenced by factors such as rainfall patterns, substrate depth, and vegetation cover. Its effectiveness is more pronounced in wet conditions and with deeper substrates, rivalling conventional plantings. In climates like Melbourne's, green roofs with substrates of 7 cm depth (i.e., ‘shallow’ substrate in this experiment) can achieve high retention, irrespective of vegetation cover. However, considering the additional benefits and lower maintenance of spontaneous vegetation compared to conventional plantings, it presents an efficient option for green roof vegetation.

How do variables like roof design, accessibility, maintenance, irrigation, adjacent landscape vegetation, season, and local climate influence the species richness and functional traits of spontaneous vegetation on green roofs globally? (Chapter 6)

In my global analysis of 192 green roofs, I utilised regression analyses and Hierarchical Modelling of Species Communities (HMSC) to investigate how green roof characteristics, management practices, landscape vegetation, season, and climate influence spontaneous vegetation species richness and functional traits. Seasonal changes significantly influenced the dispersal and traits of spontaneous vegetation on green roofs. Spring was associated with increased animal-mediated and wind dispersal, aligning with the peak periods of seed dispersal (Howe & Smallwood, 1982). In contrast, winter conditions favoured species with lower specific leaf areas (SLAs), which are better adapted to cold temperatures and frost (Gong & Gao, 2019). These seasonal variations reflect the adaptive responses of different plant species to climatic conditions.

Seasonal and climatic factors also influenced species richness Higher species richness in spring and winter may be due to milder temperatures and greater precipitation (Adler & Levine, 2007). Rising mean annual temperatures, however, reduced species richness, likely by filtering out species that were not heat-tolerant and drought-resistant (Rayner et al., 2016; Savi et al., 2016). Roof age also impacted species diversity, with older roofs exhibiting reduced richness, likely due to shift towards drier and warmer conditions that favour stress-tolerant species (Catalano et al., 2016; Vanstockem, Bastiaens, et al., 2019). The composition of plant communities on green roofs was also influenced by landscape vegetation and roof design. Landscape vegetation cover within a 1000 m radius explained more of the variation in species presence than within a 200 m radius, highlighting the importance of animal-mediated and wind dispersal (Knapp et al., 2008; Vittoz & Engler, 2007).

Maintenance regimes on green roofs significantly affected spontaneous species traits. Low maintenance frequency was associated with slower-growing, stress-tolerant species (Grime, 1977; Reich, 2014). Furthermore, irrigation had a modest but notable effect, favouring plants with higher SLA, which supports the theory that resource-acquisitive species thrive under consistent water availability (Reich, 2014; Schrieke & Farrell, 2021). Substrate depth and human accessibility were other important factors influencing the traits of spontaneous species on green roofs. Deeper substrates supported greater spontaneous species richness but did not influence their traits. High human traffic areas favoured non-perennial, disturbance-tolerant species, indicating that human disturbance significantly influenced spontaneous plant community composition.

Chapter 6 demonstrated that a combination of environmental factors, roof design, and human interaction shapes the biodiversity and trait distribution of vegetation on green roofs. The dispersal of spontaneous vegetation on green roofs primarily depends on the vegetation cover of the surrounding landscape. Meanwhile, the establishment of such vegetation is mainly driven by climate, with factors like roof height, accessibility, and maintenance intensity also playing roles in shaping community structure. The richness of spontaneous species is higher in spring and winter, increases with substrate depth, and generally decreases as green roofs age.

Implications for green roof design and maintenance, and future research

Spontaneous green roofs are "just green enough"

The concept of accepting spontaneous vegetation cover on green roofs as 'just green enough' was introduced in Chapter 2. Defined by Curran and Hamilton (2012), this approach focusses on plantings meeting socio-ecological needs rather than adhering to traditional design norms or species conservation goals. Despite some views of spontaneous vegetation as undesirable (Vanstockem, Somers, & Hermy, 2019), Chapter 2 suggested that extensive (shallow substrate) green roofs with spontaneous vegetation cover could be functional and economical, offering broad benefits (Table 7.1, overleaf). However, Chapter 2 also suggested that a shift in people's perception of green roofs would be necessary, as well as maintaining good plant cover in areas where the roofs are visible or accessible.

The spontaneous green roof species evaluated in Chapter 3 exhibited 'fast' and 'slow' characteristics (Reich, 2014), which were related to transpiration and drought response. The water usage per pot of *L. perenne*, the highest transpiring spontaneous species, exceeded that of 14 out of 20 shrub species studied by Du et al. (2018) and was 19% higher than *Isotoma axillaris*, the top transpiring species in Farrell et al. (2013)'s study. *E. maculata*, the species with the lowest transpiration, had a daily water use equal to the *Sedum* species (*Sedum pachyphyllum*) in Farrell et al. (2013)'s study. As water use was related to growth rate, this indicates that even if spontaneous species on a green roof consisted of slow growing species, they are still transpiring as much as commonly planted *Sedum* spp.

The potential functionality of spontaneous vegetation for stormwater mitigation was further reinforced in Chapter 5, which showed that spontaneous vegetation cover performs similarly to planted green roof vegetation (Zhang et al., 2018). Furthermore, Chapter 5 showed that spontaneous vegetation can achieve almost complete coverage on shallow (8 cm) substrates and maintain greater water retention than bare substrates even when coverage is

Table 7.1 Potential trade-offs between spontaneous green roof vegetation traits and their social and ecological function. Colours represent perceived beneficial (green) and unfavourable (red) outcomes.

Spontaneous green roof vegetation traits	**Social function**	**Ecological function**	**Trade-off**
Prolonged flowering continuity[1]	Cue to care[5], ecological beauty[6], high preference[7]	Support butterfly biodiversity[1], floral resource for pollinators[8]	No clear trade-off
High biodiversity[2]	Biodiverse vegetation preferred[4], acceptance increases when residents informed of ecological function[9]	Habitat for rare insects and spiders[10], increased GR functionality[11,12,13]	Perceived messiness of naturalistic plantings[9]
Fast growth/ annual lifecycle[3]	Accumulation of organic matter when plants senesce perceived as 'messy'[9]	High transpiration[3] may increase stormwater mitigation and cooling	Accumulation of organic matter when annual plants senesce provides arthropod habitat[18]
Gaps in vegetation[4]	Significant negative impact on green roof aesthetic[4]	Gaps provide safe sites for plant colonisation[15]	Loss of transpiration and canopy cooling when vegetation senesces[16]
Low maintenance	Reduction to green roof costs, overcoming a significant deterrent to adoption[4]	No fertiliser, herbicide, or pesticide application	No clear trade-off

[1](Wang et al., 2017), [2](Madre et al., 2014), [3](Schrieke and Farrell, 2021), [4](Vanstockem et al., 2019), [5](Nassauer et al., 2009), [6](Sutton, 2014), [7](Lee et al., 2014), [8](Bretagnolle and Gaba, 2015), [9](Southon et al., 2017), [10](Kadas, 2006), [11](Dunnett et al., 2008), [12](Farrell et al., 2012), [13](Kemp et al., 2019), [14](Kyrö et al., 2020), [15](Harper et al., 1961), [16](Speak et al., 2013)

reduced (~50%). This coverage on shallow substrates is significant, as it is typically recommended that green roofs have ~15 cm substrate depth to maximise planted vegetation cover, particularly in hot and dry climates (Williams et al., 2021). These results imply that spontaneous vegetation cover, with reduced dependence on substrate depth, could lower the costs of installing and maintaining green roofs. This increases the feasibility of implementing green roofs, particularly in less affluent areas that might not be able to afford traditional designs and high frequency maintenance. This approach is in line with the 'just green enough' strategy (Chapter 2).

The variation in spontaneous species water use and drought responses observed in Chapter 3 likely reflects fluctuating conditions on green roofs that favour different plant strategies over time. Likewise, Chapter 6 highlights how spontaneous vegetation communities can shift between seasons and with differing climatic conditions, pointing out challenges in achieving optimal spontaneous plant diversity, especially on taller buildings due to limitations on spontaneous species dispersal. As a result, green roofs with spontaneous plants will change, particularly when there is minimal maintenance and a lack of irrigation (Figure 7.2). This may result in dead plants on green roofs. On ‘brown roofs’, these changes are embraced as part of successional processes (Grant, 2006). Likewise, should spontaneous vegetation cover on green roofs be embraced for their ‘biodiversity’ characteristics, and these shifts be understood as a natural dynamism, the acceptance of these roofs could be increased (Jungels et al., 2013; Sutton, 2014).

Figure 7.2 Green roof vegetation exhibits dynamic changes regardless of initial design, especially under varying water availability. Clockwise from top left: Burnley biodiversity green roof in Spring 2016; the same in Summer 2020; green roof modules in the 'dry ' regime from Chapter 5's stormwater experiment; and the same modules in the 'wet' regime.

What if "just green enough" just isn't green enough?

On some green roofs the presence of spontaneous vegetation will never be desirable. On these roofs, the results of this thesis can also inform maintenance regimes that aim to minimise the success of spontaneous vegetation. The findings of Chapter 4 indicate that cover of planted green roof vegetation, in this case *Sedum mexicanum*, can significantly influence the variety and number of spontaneous plant species. Specifically, while the spread of *S. mexicanum* reduces the diversity of similar plants, its impact varies with water availability. In water-scarce conditions, its role can shift from hindering to supporting other species. If the aim is to limit spontaneous species, the results of Chapter 5 suggest that planting drought tolerant species and minimising irrigation will limit the types of spontaneous species that can colonise.

The traits that make spontaneous plants successful on green roofs can also be used to inform plant selection for typical green roofs. Chapter 3 revealed that spontaneous species exhibit varied water-use and drought-response strategies, highlighting plant traits like growth rate, leaf size, and biomass for selecting species that efficiently use water and withstand drought, crucial for adapting to different rainfall regimes. On irrigated green roofs, or those in climates with higher rainfall, selecting fast growing species with greater leaf size, biomass and relative growth rate may enhance stormwater mitigation. Whereas the opposite may apply on unirrigated green roofs or those in hot and dry climates.

Chapter 6 demonstrated the adaptation of spontaneous species to various green roof designs and the influence of surrounding vegetation and local climate. Research shows that functional diversity enhances various aspects of green roof functionality (Lundholm, 2015; MacIvor et al., 2018). Findings from Chapters 3, 5, and 6 suggest that roofs with mixed-species communities may be more resilient to environmental changes. However, Chapter 6 indicates that spontaneous communities are sensitive even to low maintenance. This suggests that minimal, targeted maintenance actions, like the selective removal of dominant species, can prevent overgrowth and maintain functional diversity on green roofs.

Integrating spontaneous vegetation into intentional plantings

Integrating both intentionally planted and spontaneous species may enhance the overall functionality of green roofs. As detailed in Chapter 5, *Sedum mexicanum*, even with 100% cover, was interspersed with *Trifolium repens* (Figure 7.2). Based on the findings in Chapter 3, this combination unites the 'fast', high water-using *T. repens* (Reich, 2014) with a slower-growing, drought-resistant *Sedum* species. The *Sedum* cover may offer continuous vegetation cover during dry spells and facilitate the survival of *T. repens* by conserving soil moisture (Chapter 5), whereas in times of increased water availability, the presence of *T. repens* could improve the roof's capacity for stormwater mitigation.

Figure 7.3 Trifolium repens and Sedum mexicanum coexisting in experimental green roof microcosms, suggesting a potentially functional pairing.

Future research

Green roofs are multifunctional, and this thesis mainly focuses on one facet of green roof functionality: stormwater mitigation. However, to understand the effect of spontaneous vegetation more fully on green roof functionality, the following research topics need to be addressed:

1. **Biotic interactions in spontaneous green roof vegetation**: It is important to examine how different spontaneous plant species, pollinators, and other organisms interact on green roofs. Understanding these relationships is key to knowing how spontaneous vegetation influences pollination and the provision of habitats for biodiversity.
2. **Long-term impact of spontaneous vegetation on green roof functionality**: Research should focus on how spontaneous plant communities on green roofs evolve over time and their ongoing effect on ecosystem services. Monitoring changes in the types of spontaneous species present can offer insights into how these communities function and contribute to green roof functionality.

Addressing these research areas will deepen our understanding of green roof ecosystems. This knowledge is key to developing more effective design and management strategies, thereby maximising the ecological and social benefits of green roofs.

Conclusion

This thesis suggests that shallow extensive green roofs, which allow for the growth of spontaneous plants on shallow substrates, could provide similar advantages to traditional plantings at a reduced cost. The ability of spontaneous vegetation to flourish in shallow substrates reduces the need for costly engineering to support heavier and deeper substrates. This approach underscores the importance of accepting plant dispersal, establishment, and succession as integral and advantageous elements of green roof ecosystems. Adopting this perspective on green roofs could lead to their wider implementation, thereby extending socio-ecological benefits to urban areas that have, until now, been largely neglected.

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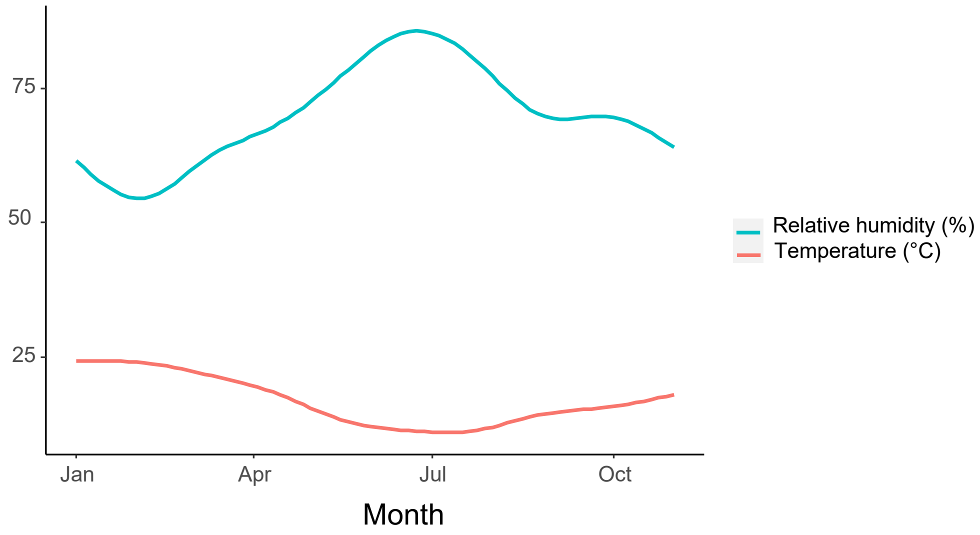
Appendix 1.1

Appendix 1.1: Mean seed weight (mg), germination (%), viability (%) and relative growth rate (RGR mg g^{-1} day^{-1}) of spontaneous species used in this experiment.

Species	**Seed weight (mg)**	**Seed germ (%)**	**Seed viability (%)**	**Relative growth rate (mg g-1 day-1)**
Epilobium parviflorum	0.4	92	96	120.63
Euphorbia maculata	1.3	0	95	106.02
Euphorbia peplus	4.8	80	92	89.51
Helichrysum luteoalbum	0.4	45	90	153.4
Malva neglecta	10	36	65	123.6
Nepeta cataria	5.4	52	85	199.8
Polycarpon tetraphyllum	0.3	83	95	118.1
Portulaca oleracea	4.4	90	100	217.3
Rumex crispus	10.5	96	100	179.7
Solanum nigrum	8.5	57	88	193.9
Sonchus oleraceus	1.6	100	100	217.7
Stellaria media	2.9	21	95	189.5
Taraxacum officinale	3.8	87	95	163.7
Trifolium repens	5.4	94	100	197.5

Appendix 1.2



Appendix 1.2: Daily mean relative humidity (%) and temperature (°C) in Tunnel 13 from January to November 2021

Appendix 1.3

Appendix 1.3: Mean (n=5) biomass (g) of spontaneous vegetation in well-watered (WW) or water deficit (WD) microcosms with different Sedum cover classes (%). Bold values indicate significant differences between WW and WD treatments within each Sedum cover class (one-way ANOVA; P≤0.05).

Species	0%		25%		50%		75%		100%	
	WW	WD	WW	WD	WW	WD	WW	WD	WW	WD
E. parviflorum	<0.01	-	-	-	-	-	-	-	-	-
E. maculata	**0.27**	**<0.01**	-	0.03	-	-	-	-	-	-
E. peplus	**0.09**	**<0.01**	-	0.05	-	-	-	-	-	-
H. luteoalbum	**0.02**	**0.41**	**0.03**	**0.78**	**0.15**	**1.52**	0.19	-	-	-
M. neglecta	<0.01	-	-	-	-	-	-	-	-	-
N. cataria	<0.01	0.03	-	-	-	-	-	-	-	-
P. tetraphyllum	1.18	-	2.15	2.50	1.24	1.30	1.06	1.50	-	6.60
R. crispus	0.13	0.06	**0.16**	**0.07**	0.13	-	0.23	-	0.12	-
S. nigrum	0.69	-	0.67	-	-	-	-	-	-	-
S. oleraceus	0.16	0.10	**0.20**	**0.15**	**0.20**	**0.14**	**0.20**	**0.21**	-	1.20
T. repens	70.44	48.49	128.78	68.08	**127.81**	**59.84**	**143.40**	**30.85**	**130.87**	**46.25**