Maximising the environmental benefits of gardens through optimal planting choices and understanding occupants' engagement

Doctor of Philosophy

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Declaration of original authorship

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

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Abstract

Flooding risk in urban areas has increased due to the expansion of impervious surfaces, removal of garden vegetation, and predicted rise in heavier rainfall events due to climate change. Domestic gardens cover up to 30% of UK urban areas, so plants they contain could have a significant environmental impact, with the potential to retain rainfall, reduce runoff and mitigate localised flooding.

The hypothesis was tested that plants with certain traits, including higher evapotranspiration rates and hairy leaves, or mixtures of plants with diverse traits, would provide greater rainfall retention compared to certain monocultures and non-vegetated surfaces. To test this, popular perennial garden plants representing these traits were grown in monocultures or mixed planting and exposed to simulated rainfall and short-term flooding. Species with higher transpiration rates and/or hairy-leaved canopies (such as *Oenothera lindheimeri* 'Whirling Butterflies'), or planting combinations including them, provided greater rainfall retention compared to planting without these traits (for example, *Oenothera* gardens reduced runoff by 6-20%). Plant function, and therefore ecosystem service provision, of higher transpiring 'drought-tolerant' *Oenothera* and *Verbena bonariensis* was unaffected by flooding, and increased the flooding tolerance of companion plants when grown in mixed pairs, reducing substrate moisture by ≥ 79% compared to monocultures of lower transpiring plants.

Gardens are privately designed spaces, therefore people's preferences and willingness to change is also crucial to maximise the environmental benefits of planting. An experimental survey found that a combination of environmental information and trait-based planting recommendations based upon the preceding chapters, made participants more willing to change preference in favour of plants linked to greater environmental benefits. Climate change concern also increased respondents' positivity towards pro-environmental planting by 141%. Simple planting recommendations and concern for the climate were both highlighted as key avenues to explore for influencing plant choices and improving the potential environmental benefits of gardens.

List of symbols and abbreviations

Abbreviations

A	Net CO_2 assimilation rate
ESs	Ecosystem services
ET	Evapotranspiration
GR	Green roof
g_s	Leaf stomata conductance to water vapour (mol m^{-2} s^{-1})
IRGA	Infrared gas analyser
LA	Leaf area
LAI	Leaf area index
CEL	Crops and Environment Laboratory

Statistical terms

ANOVA	Analysis of variance
R^2	Coefficient of determination
SD	Standard deviation
SE	Standard error of the means

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Chapter 1

Introduction and literature review

1.1 Introduction

The phrase ‘right plant, right place’, credited to English plantswoman, garden designer and author Beth Chatto, has been used extensively in garden design to identify plants suitable for a particular location based on their traits and environmental preferences (Garden Museum, no date). This leads to use of plants (in gardens and wider landscapes) with a higher likelihood of survival and less input required by gardeners and landscape managers. Plants can provide a multitude of benefits, from being food sources (Cameron & Hitchmough, 2016) to providing environmental ‘services’ such as improvement of air quality (Blanuša *et al.,* 2015; Jeanjean *et al.,* 2017; Säumel *et al*., 2016; Tiwary *et al.,* 2016), microclimate and water cycle regulations, to biodiversity and habitats’ support (Cameron & Blanuša, 2016; Salisbury *et al.,* 2023; Thompson *et al.,* 2003). The selection of plants using ‘right plant, right place’ approach could also apply to plant choices for the provision of these environmental benefits (‘ecosystem services’ ESs) within domestic gardens.

Climate change is anticipated to alter precipitation patterns and seasonal temperatures in the UK, with a predicted increase in infrequent, heavier rainfall in the summer, and an increase in average temperatures in all seasons and regions (IPCC, 2021; Webster *et al.,* 2017). The UK is also projected to experience, and to an extent has already experienced, increased extreme weather events in the form of summer heat waves, drought, flooding and flash flooding (Beidokhti & Moore, 2021; IPCC, 2021; Kendon *et al.,* 2023; Met Office, no date; Webster *et al.,* 2017). Flooding is the accumulation of water on normally dry areas due to rainfall or the rising water table from an existing waterway, causing inundation that can last for days or weeks. Flash flooding is caused within minutes or hours of heavy rainfall and results in fast flowing water through, for example, rivers or urban streets (USA National Weather Service, no date). Water availability in urban areas is going to fluctuate between water shortages at periods with elevated outdoor temperatures, and excess water during heavy rainfall events (Met Office, no date; Webster *et al.,* 2017).

Urbanisation has led to land use change, specifically the replacement of natural ecosystems with buildings and impervious surfaces, and this has been linked with negative environmental impacts including increased temperatures (urban heat island effects), pollution, flooding, and reduced biodiversity, to name a few (Maragno *et al.,* 2018; Kadavergu *et al.,* 2021; Warhurst *et al.,* 2014), all of which reduce quality of life and are exacerbated by climate change (Webster *et al*., 2017).

Reintroducing vegetation into urban areas in the form of green infrastructure can help alleviate the impacts of climate change and urbanisation (Cameron *et al.,* 2012; Chapman & Hall, 2022; Choi *et al.,* 2021; Dover, 2015; Gush *et al.,* 2023; Säumel *et al*., 2016). Green infrastructure comes in many forms, including vegetation added to buildings as green roofs and living walls, parks and nature reserves, and domestic gardens (Cameron & Hitchmough, 2016), which are the focus of this review. Different vegetation types are able to provide greater environmental benefits than others, with previous research focusing predominantly on larger plants such as trees and shrubs, or infrastructure changes such as green roofs. Domestic gardens account for approximately 30% of total urban area in the UK, which is a relatively large expanse to provide environmental benefits if planting is retained and enhanced for increased ecosystem services' provision (Chalmin-Pui *et al.,* 2021a). Therefore, the importance of domestic gardens and their contribution to the environmental impact of urban areas cannot be underestimated (Cameron *et al.,* 2012; Cameron, 2023). Popular garden plants often come in the form of flowering perennials, which populate borders and planting beds, and this review will focus on their potential to reduce flooding risks in urban areas.

1.2 Domestic gardens in the UK and Global North

Domestic gardens are privately owned open areas connected to or associated with a property and function as a space for recreation and leisure, food production, and extension of the home for outdoor dining or domestic activities (Cameron, 2023; Dixon, 2022). Domestic gardens cover 3-4% of total landmass in the UK (Cameron *et al.,* 2012), and 87% of households have access to a garden (Gush *et al.,* 2023). As privately owned spaces the design and maintenance fall to the homeowner, therefore domestic gardens have a higher level of individuality than parks or public gardens, and their layouts and amount of vegetation vary greatly (Cameron *et al.,* 2012). Gardens can enhance a sense of pride in the home and boost creativity (Chalmin-Pui *et al.,* 2021a), although ironically despite these potentials there are significant levels of homogeneity in gardens, particularly in the UK and USA, with similar designs and planting composition observed on a neighbourhood scale (Francis, 2018).

Due to their proximity to the home, gardens can allow people to have a close link to, and engage with, nature (Chalmin-Pui *et al.,* 2021a). They also have the potential to provide environmental benefits in the form of ecosystem services, particularly if they have a higher proportion of greenery (Cameron, 2023; Royal Horticultural Society, 2021). However, the amount of vegetation contained in gardens has decreased, replaced by impervious surfaces (Perry & Nawaz, 2008; Warhurst *et al.,* 2014). Assessment in 2015 found a three-fold decrease in plant numbers in UK front gardens in a 10-year period (Royal Horticultural Society, 2015). This trend has been observed across the UK, with a nationwide average of one in four front gardens covered by paving (Royal Horticultural Society, 2015). City specific examples include Leeds, where impervious surfaces have increased by 13% in a 33-year period, 75% of which were in the form of paved front gardens (Perry & Nawaz, 2008). In Southampton there was a 22% increase in impervious surfaces covering front gardens between 1991 and 2011, coinciding with a decrease in all vegetation types including a 37% decrease in garden lawns (Warhurst *et al.,* 2014). In London the total area of paved front gardens equates to approximately 32 km^2 (Kelly, 2016; London Assembly, 2005). Increased use of impervious surfaces such as paving or tarmac, has been linked with increased surface water runoff and subsequent flood risk (Kelly, 2016; Perry & Nawaz, 2008; Simpson & Francis, 2021). Removing vegetation and sealing away soil prevents water infiltration into the substrate and reduces the possibility for evapotranspiration from plants to return moisture to the atmosphere (Kelly, 2016; Simpson & Francis, 2021; Stovin *et al.,* 2015). Urban drainage systems are designed to remove water quickly into drains, which can become overwhelmed (Cameron & Hitchmough, 2016; Dover, 2015), and although sustainable urban drainage systems (SUDs) are implemented in the UK to retain water within property boundaries and mitigate runoff, this is limited in its scope as it does not include keeping or replacing garden vegetation as part of flood prevention (Dover, 2015; Susdrain, no date). Yet vegetation can help reduce or slow runoff accumulation and minimise flood vulnerability (Kadavergu *et al.,* 2021; Kelly, 2016).

The reasons for increased impervious surfaces within domestic gardens are multiple. Easy or low maintenance gardening has become preferable for many homeowners due to lack of time or skills to engage in garden maintenance, therefore replacing vegetation with paving for patios is a simpler option for upkeep (Chalmin-Pui *et al.,* 2019). The increase in car ownership and fees for on-road parking in many urban areas has driven a desire for off-road parking spaces, with one in three front gardens in the UK now containing no plants, replaced instead by impermeable surfaces such as tarmac to accommodate cars (Chalmin-Pui *et al.,* 2021a; Royal Horticultural Society, 2015). Car ownership has also been found to influence streetscape green infrastructure, with a recent survey in Brussels that asked participants to select from various green infrastructure installations finding that 81% of car owners preferred street designs that ensured parking spaces were kept at the expense of vegetation (Phillips *et al.,* 2023). Artificial turf has also replaced natural lawns, becoming popular in recent years as an easy maintenance alternative to vegetation (Cameron, 2023; Francis, 2018; Simpson & Francis, 2021). Garden lawns are a key feature of British gardens, covering 60% of UK gardens (Gaston *et al.,* 2005). Although it is recognised that the intensive management of lawns has a negative impact on the environment (Cameron, 2023; Hostetler, 2021) they can still provide ecosystem services (Monteiro, 2017; Simpson & Francis, 2021), and have also been found to reduce rainfall runoff in comparison to artificial turf (Chang *et al.,* 2021; Simpson & Francis, 2021). Replacement with sterile, impervious plastic surfaces promotes 'aesthetics' over nature, creating the illusion of a 'good lawn' that conforms to the societal norm i.e. uniform and green, without the maintenance, but it is unable to support biodiversity and contributes to rainwater runoff and flooding in a similar way to paving (Francis, 2018; Simpson & Francis, 2021).

This situation is exacerbated by planners, with residential gardens decreasing in size (Tahvonen & Airaksinen, 2018), city planners viewing gardens as a luxury (Haaland & Konijnendijk van den Bosch, 2015), and some new housing schemes removing gardens completely from their plans (Tahvonen & Airaksinen, 2018). Many historic zones within UK towns and cities were not designed to support cars, and there is an acknowledgement that urban planning must move away from car-centric designs to reduce pressure on the environment (Cameron, 2023; Phillips *et al.,* 2023). This would force a reduction in car ownership and increase public transport networks, encouraging planting back into front gardens. Domestic gardens have no protected status in the UK so ensuring vegetation retention is difficult without overarching policy change (Chalmin-Pui *et al.,* 2019). A change in UK law in 2008 ensured impermeable areas over 5 m^2 requires planning permission to install (Department for Communities & Local Government, 2008). Other measures have been suggested by academics including development of policies recommending a minimum of 50% vegetation in all gardens, garden vegetation protection within legislation, at least two-thirds of all gardens consisting of permeable surfaces and artificial turf restricted, and grants for pro-environmental management (Cameron, 2023; Goddard *et al.,* 2013).

Environmental conditions in gardens can vary depending on their location and site conditions, including the different types of substrates, which all affect how well planting will grow (Royal Horticultural Society, 2021; Webster *et al*., 2017). However, key risks for gardening in the UK - due to climate change - include heavy rainfall, which could result in damage to plants due to waterlogging or flooding, and heat stress and drought/drier soils, with the anticipated need for increased irrigation during the summer (Webster *et al*., 2017). Twenty-seven million adults in the UK identify as gardeners (Chalmin-Pui *et al.,* 2019), and while recent Royal Horticultural Society surveys indicate that 80% of respondents are concerned about water use (Gush *et al.,* 2022), only 2% of participants in another survey feel equipped to garden in a changing climate (Webster *et al*., 2017). Therefore, information about plants that will be able to survive changing climatic conditions (flooding and drought) and provide ecosystem services is required in UK gardens.

1.3 Ecosystem services by plants and the role of green infrastructure for regulating ecosystem service provision

Ecosystem services are the benefits that people derive from ecosystems that 'contribute to making human life both possible and worth living' (UK National Ecosystem Assessment, 2014). Ecosystem services can be divided into four categories - provisioning, supporting, cultural, and regulating (UK National Ecosystem Assessment, 2014), the latter of which being the focus of this review.

Green infrastructure is the collective term for formal and informal green spaces and vegetation within urban areas, and can include gardens, green roofs and walls, parks and woodlands, street trees and hedges, allotments, and rain gardens (Blanuša *et al*., 2019; Cameron & Blanuša, 2016). Vegetation in urban areas has been shown to provide a multitude of regulating ecosystem services in comparison to unvegetated surfaces and buildings (Blanuša *et al*., 2019; Cameron *et al.,* 2012; Choi *et al.,* 2021; Jato-Espino *et al.,* 2023; Säumel *et al*., 2016). For example, green roofs have been shown to provide aerial and surface cooling and rainwater runoff mitigation (Blanuša *et al.,* 2013; Kemp *et al.,* 2019; Lundholm *et al.,* 2010; Heim *et al.,* 2023; Vaz Monteiro *et al.,* 2017), green walls can provide insulation for buildings in winter and cool internal temperatures during the summer (Cameron *et al.,* 2014; Thomsit-Ireland *et al*., 2020), and street trees can reduce flooding risk (Beidokhti & Moore, 2021; Levia & Herwitz, 2005; Ow & Chan, 2021; Xiao & McPherson, 2011) and provide cooling services (Rahman *et al.,* 2020; Säumel *et al*., 2016; Tiwary *et al.,* 2016). Depending on the types of plants used, domestic gardens and perennials within them could also provide these services.

The type of plants and their traits, and site conditions, influence how effective green infrastructure can be at providing ecosystem services (Berretta *et al.,* 2014; Lundholm *et al.,* 2010; Schrieke & Farrell, 2021; Tiwary *et al.,* 2016; Xie *et al*., 2018). Some traits present across different types of green infrastructure have been found to result in increased service delivery. Plants with larger leaf area generally capture and store within the canopy greater volumes of rainwater in comparison to those with smaller leaf area (Beidokhti & Moore, 2021; Blanuša & Hadley, 2019; Lundholm *et al*., 2015). Rough-surfaced or hairy-leaved plants can trap greater quantities of airborne particulate matter (Blanuša *et al.,* 2020; Shao *et al.,* 2019; Weerakkody *et al.,* 2018a) and provide cooling services (Blanuša *et al.,* 2013; Vaz Monteiro *et al.,* 2017). However, site conditions can alter this outcome. For example, in streets parallel to prevailing winds trees can mitigate pollution, but in street canyons with perpendicular winds trees can actually exacerbate pollution build up as they block air flow (Jeanjean *et al.,* 2017; Buccolieri *et al.,* 2018a & 2018b). Individual plant traits, and how they interact with their environment needs to be taken into account when selecting plants for ecosystem service delivery.

1.4 Green infrastructure and stormwater management

Plants have the potential to reduce the impacts of heavy rainfall events and mitigate flooding by intercepting and retaining rainfall in their canopies, and by removing water from the substrate using evapotranspiration (Berretta *et al.,* 2014; Blanuša & Hadley, 2019; Kemp *et al.,* 2019). In comparison to unvegetated or impervious surfaces, plants can significantly reduce rainwater runoff (Berretta *et al.,* 2014; Kemp *et al.,* 2019; MacIvor & Lundholm, 2011; Stovin *et al.,* 2015). For example, Pataki *et al.* (2011) found forest environments lost 13% of precipitation as runoff, whilst urban areas that had majority impervious surfaces lost 40-83% of rainfall as runoff. A modelling study of Hyderabad city, India, also found that vegetated spaces (urban vegetation and open spaces) could reduce runoff by up to 50% compared to buildings and built-up areas, depending on rainfall intensity (Kadaverugu *et al.,* 2021).

Less research has been conducted on runoff reduction within domestic garden settings compared to other forms of green infrastructure, although inferences can be made using certain plants from existing green roof or rain garden studies, particularly with regards to perennials.

1.4.1 Green roofs

Green roofs (GRs) are vegetated roofs that can provide a range of ecosystem services in comparison to standard roofs, including increased rainwater capture (Kemp *et al.,* 2019; Ksiazek-Mikenas *et al.,* 2023; Lundholm *et al.,* 2010; Nagase & Dunnett, 2012), and aerial and surface cooling (Blanuša *et al.,* 2013; Heim *et al.,* 2023; Lundholm *et al.,* 2010; Vaz Monteiro *et al.,* 2016 & 2017). There are typically two categories of green roofs, based on substrate depth and vegetation type - extensive and intensive. Extensive green roofs have a shallow substrate layer, usually under 150 mm, and are dominated by a carpet of *Sedum* plants, which are the industry standard and require minimal water and maintenance whilst surviving well in the exposed conditions experienced on a roof (Nagase & Dunnett, 2010). Growing conditions on a green roof mean plants are exposed to high wind speeds and temperature extremes, as well as drought (Nagase & Dunnett, 2010), which is why succulent plants with their crassulacean acid metabolism (CAM) metabolism and adaptations to reduce plant water loss are a good choice (Butler & Orians, 2011; MacIvor & Lundholm, 2011; Matsuoka *et al.,* 2019). However, *Sedum* does not provide a significant runoff reduction service (Dunnett *et al.,* 2008) so alternative plants including perennials, have been researched to assess their ecosystem service potential (Dunnett *et al.,* 2008; Farrell *et al.,* 2013; Kemp *et al.,* 2019; Ksiazek-Mikenas *et al.,* 2023; Lundholm *et al.,* 2010; Nagase & Dunnett, 2012). Intensive green roofs, which have a substrate deeper than 200 mm, would support perennials and enable them to establish root systems, therefore increasing the scope for what plants could be used (Nagase & Dunnett, 2010).

Plant water use, specifically higher evapotranspiration rate, has been found to improve both stormwater management and air and substrate temperature adjustment (Blanuša *et al.,* 2013; Chu & Farrell, 2022; Schrieke & Farrell, 2021;

Stovin *et al.,* 2015). Perennials including *Salvia officinalis* and *Stachys byzantina* provided the greatest daytime surface and ground cooling compared to *Sedum* (Vaz Monteiro *et al.,* 2016 & 2017), whilst *Stachys* was also found in another study to reduce the substrate temperature beneath its canopy by 12°C compared to *Sedum* during the summer (Blanuša *et al.,* 2013). Grass species on a green roof were able to provide better insulation compared to other plants tested in winter conditions (Lundholm *et al*., 2015), whilst combinations of plants with different traits could provide greater temperature reductions during summer compared to *Sedum* or unvegetated surfaces (Lundholm *et al.,* 2010; Heim *et al.,* 2023).

Drought tolerant plants are regularly tested for their ability to withstand green roof conditions, however their ability to provide greater rainwater retention than *Sedum* could enable improved ecosystem service provision. Kemp *et al.* (2019) found *Salvia* and *Stachys* were also better able to reduce substrate moisture content and surface runoff compared to *Sedum* as they had a greater demand for water and therefore removed moisture from the substrate more quickly. Both *Salvia* and *Stachys* are Mediterranean species anticipated to have lower transpiration rates. This indicates that plant water use, and therefore its capacity for rainwater runoff reduction, cannot be assumed based on climate of origin (Cameron *et al.,* 2006; Schrieke & Farrell, 2021; Tabassum *et al.,* 2021). Other plants that are typically considered to have a lower water demand have also provided greater runoff reduction than *Sedum*, including plants originating from granite outcrops (Farrell *et al.,* 2013) and prairie species (Ksiazek-Mikenas *et al.* 2023; Whittinghill *et al.* 2014). Prairie species including *Achillea millefolium* and *Oenothera rhombipetala* were able in a green roof setting to provide up to 16% greater stormwater retention compared to succulent plants (Ksiazek-Mikenas *et al.* 2023). Graminoids have also been found more effective at runoff reduction than *Sedum*, and this was potentially due to the greater height, shoot and root biomass (Dunnett *et al.,* 2008; Lundholm *et al.,* 2010 & 2015; MacIvor & Lundholm, 2011; Nagase & Dunnett, 2012). Other plants with these traits, including tall forbs and spontaneous coloniser plants, have all been found to remove moisture more quickly from the substrate than slower-transpiring species that conserve water (Lundholm *et al*., 2015; Nagase & Dunnett, 2012;

Schrieke & Farrell, 2021), and this resulted in greater reduction of runoff. Herbaceous and perennial plants *Trifolium repens, Melilotus officinalis* (syn. *Trifolium vulgare*), and *Viola tricolor* had the highest transpiration rates of tested species in well-watered conditions, removing the greatest volumes of water from the substrate (Lönnqvist *et al.,* 2023; Schrieke & Farrell, 2021), and grass *Lolium perenne* was also found to thrive in these conditions, growing 300% faster than the slowest growing species (Shrieke & Farrell, 2021).

Meadow flower mixes have also been tested although runoff reduction was comparable to *Sedum* when examined in a green roof setting (Heim *et al.,* 2017; Poë *et al.,* 2015; Stovin *et al.,* 2015). However, this has been linked with the rate of plant growth, as the meadow plants were not able to establish as quickly as *Sedum* and therefore ground cover was significantly reduced (Heim *et al.,* 2017), and also the substrate type and shallow depth used did not allow for adequate growth of some plants with deeper roots, which can be typical of meadow plants (Stovin *et al.,* 2015).

1.4.2 Rain gardens

Garden perennials have been studied in rain garden scenarios for their ability to withstand waterlogging, and this could also link with the potential for providing rainwater runoff reduction. Rain gardens are shallow depressions in the ground that contain vegetation and are designed to minimise rainwater runoff (Royal Horticultural Society, no date, a; Yuan & Dunnett, 2018). Runoff is channelled into these gardens from impervious surfaces or urban infrastructure and over several hours to days will drain away, reducing surface water accumulation on roads or around buildings (Royal Horticultural Society, no date, a). Rain gardens are created with different depths for plants to populate, known as 'moisture zones', each experiencing varying water tables and levels of waterlogging. The deepest bottom layer is almost permanently waterlogged or moist, the sides have moderate moisture levels, and the margin around the edge is relatively dry except during stormwater events (Yuan & Dunnett, 2018). Rain gardens undergo cycles of waterlogging and drying and because of this vegetation growing in the slope or margin zones will need to withstand periods of inundation and water deficit as the rain garden collects water and subsequently drains (Royal Horticultural Society, no date, a; Yuan & Dunnett, 2018). Many of these plants are classified as drought tolerant and yet can withstand waterlogging, and in some cases thrive in both conditions of reduced and excess water (Bortolini & Zanin, 2019; Nasrollahpour *et al.,* 2022; Yuan & Dunnett, 2018). These planting conditions could be comparable to domestic gardens after rainfall events and therefore provide examples of plants that can withstand waterlogging and deliver runoff reduction.

Popular garden perennials *Echinacea* and *Hemerocallis* have both been grown successfully in rain gardens (Bortolini & Zanin, 2019; Champagne-Caron *et al.,* 2024; Laukli *et al.,* 2022b; Nasrollahpour *et al.,* 2022; Yuan *et al*., 2017), the latter of which had 0% mortality in cold climate rain gardens (Laukli *et al.,* 2022b) and in another study showed greatest adaptability to all the positions in a rain garden (Bortolini & Zanin, 2019). This is surprising considering *Hemerocallis* is listed in the gardening literature as not growing well in waterlogged substrate (Royal Horticultural Society, no date, b). Similarly to this, the gardening literature states that popular cut flower *Chrysanthemum* does not tolerate waterlogging (Royal Horticultural Society, no date, c) yet tolerant varieties were found to adapt to waterlogging and produce adventitious roots (Yin *et al.,* 2009).

Ornamental perennial plants originating from prairies are popular in UK gardens (Horton, 2023; Taylor, 2012). Prairie biomes encompass large swathes of North America and can form zones that are classified as dry, mesic, or wet depending on location and environmental factors (National Geographic, no date). Plants in these communities respond to soil moisture gradients and nutrient availability. For example, *Veronicastrum virginicum* displayed adaptive responses to cyclical flooding (Yuan & Dunnett, 2018) but this plant's natural distribution is wet-mesic prairies therefore waterlogged substrates are its preference (Gleason & Cronquist, 1991). Yet many prairie species that prefer lower substrate moisture have also been found to survive in rain gardens (Laukli *et al.,* 2022b; Nasrollahpour *et al.,* 2022; Nocco *et al*., 2016; Yuan & Dunnett, 2018). *Liatris* species have been shown to grow well in rain garden settings despite being drought tolerant (Laukli *et al.,* 2022b; Nasrollahpour *et al.,* 2022), whilst *Oenothera lindheimeri*, which is typically grown on drier soils (Royal Horticultural Society, no date, d), was able to withstand cyclic waterlogging treatments but was not suitable for long-term flooding, although it survived with reduced biomass (Yuan & Dunnett, 2018). Several species of *Rudbeckia*, including *R. hirta* and *R. fulgida var. deamii* have also grown well in rain gardens and endured cyclical flooding (Dudrick *et al.,* 2024; Nasrollahpour *et al.,* 2022; Yuan & Dunnett, 2018; Yuan *et al*., 2017), although *R. hirta* also had a high mortality rate in cold climate bioretention cells (Champagne-Caron *et al.,* 2024), indicating it might tolerate waterlogging but be susceptible to cold or freezing water.

Salvia and *Stachys*, previously mentioned with regards to their green roof rainwater retention potential, have also been assessed for flood tolerance. King *et al.* (2012) tested garrigue plants to determine their tolerance in UK flooding conditions, and found that *Stachys byzantina* was resilient to summer floods even after seventeen days of total submergence, and *Salvia officinalis* adapted to waterlogging when pre-treated with hypoxic conditions. Popular garden shrub *Lavandula* also tolerated both summer and winter waterlogging, despite its preference for drier substrate (King *et al.,* 2012).

Plant survival rates, and biomass and root mass increase or decrease, are commonly used to gauge a plant's tolerance to flooding (Bortolini & Zanin, 2019; Laukli *et al.,* 2022a; Laukli *et al.,* 2022b; Nocco *et al*., 2016; Yuan & Dunnett, 2018; Yuan *et al*., 2017). As with rainwater runoff reduction on green roofs, plants with higher transpiration rates have also been associated in some studies with greater survival in waterlogged conditions as well as providing stormwater retention, although whether this trait is always positively correlated with waterlogging tolerance is to be determined (King *et al.,* 2012; Lundholm *et al.,* 2010; Nasrollahpour *et al.,* 2022; Yuan *et al*., 2017).

1.5 Plant traits for improved rainfall capture

Plant traits are defined as ‘any morphological, physiological or phenological feature measurable at the individual level’ (Violle *et al.,* 2007). Vegetation can provide a reduction in rainwater runoff using two main mechanisms, and specific plant traits can aid with this. Plants can intercept and store rainwater in their canopies, and remove water from the substrate by evapotranspiration, which is the combination of evaporation from the substrate and plant surface, and transpiration by plants. The transpiration rate of a plant has been shown to be one of the key mechanisms that lead to restoration of the substrate’s water retention capacity following rainfall (Berretta *et al.,* 2014; Lundholm *et al.,* 2010; Stovin *et al.,* 2012; Thompson *et al.,* 2022). Plants with higher transpiration rates remove water more quickly from the substrate, which restores its capacity to store additional water (Berretta *et al.,* 2014; Kemp *et al.,* 2019; Stovin *et al.,* 2012). Previous research has found that higher transpiring perennial *Stachys byzantina* can provide greater substrate and aerial cooling, and rainwater retention services compared to unvegetated surfaces and *Sedum* species, and the higher water use was also key to temperature regulation and associated with greatest reduction in substrate temperature during the summer (Blanuša *et al.,* 2013; Cameron *et al.,* 2014; Vaz Monteiro *et al.,* 2016 & 2017). For rainwater reduction, *Stachys byzantina* and *Salvia officinalis* retained 72% of the applied rainfall (either through canopy or substrate retention) compared to *Sedum* at 46% (Kemp *et al.,* 2019).

1.5.1 Basic principles and the importance of evapotranspiration for rainfall capture

Evaporation is the conversion of a liquid, in this context water, into its gaseous state of water vapour, which then diffuses into the atmosphere. This process is powered by solar radiation, and is not specific to plants, but can occur on any surface. Transpiration is the process of water loss from plants through stomata and subsequent evaporation from the surface of leaves and stems (Kramer & Boyer, 1995). The combination of the two is known as evapotranspiration and is the collective water loss from plants and their associated substrate (O’Carroll *et al.,* 2023; Tan *et al.,* 2015).

Water loss through the stomata is regulated, and resistance to diffusion of water vapour can be due to stomatal resistance. This pathway allows water loss as well as carbon dioxide into the leaf simultaneously, which can be a conflict, as a plant cannot restrict water loss by closing the stomata without restricting carbon dioxide intake and therefore growth and reproduction potential. In well-watered, full sun conditions stomata will open during the day as the conditions enable high photosynthetic activity as well as high transpiration rate (Buckley, 2019; Taiz & Zeiger, 2002). In dry conditions when water availability is restricted a plant may close their stomata to conserve moisture and reduce water loss, but reduce photosynthesis as well. There are exceptions to this, for example plants that have adapted to low soil moisture by using a different photosynthetic pathway such as C_4 carbon fixation or crassulacean acid metabolism (CAM). The majority of plants in temperate climates however, use a C_3 photosynthetic pathway (Basu *et al.,* 2016; Nagase & Dunnett, 2012; Raines, 2011). Within this very broad group there are examples of various strategies that plants employ to aid water conservation during periods of low soil water availability. Some however, continue to transpire, keeping their stomata open and stomatal conductance rates high despite lowering leaf water potential, to make use of available light for photosynthesis whilst risking damage from water deficit (Cameron *et al.,* 2006).

The air surrounding the leaf also impacts diffusional resistance, resulting in leaf boundary layer resistance to water vapour flow. Still air can be a deterrent to diffusion, whilst high wind speeds reduce resistance, leading to higher transpiration rates (Jones, 1998; Tan *et al.,* 2015). Waxy coatings to leaves can additionally limit water loss, operating as a preventative barrier (Nagase & Dunnett, 2012). Also, the size and shape of the leaf changes the wind velocity and the amount of water loss, and this is also linked with potential to capture particulate matter and rainwater as well (Beidokhti & Moore, 2021; Ginebra-Solanella *et al.,* 2020).

1.5.2 Factors affecting evapotranspiration

The rate of transpiration can differ from plant to plant (Blanuša *et al.,* 2013; Chapman & Augé, 1994; Chu & Farrell, 2022; Kemp *et al.,* 2019; Nazemi Rafi *et al.,* 2019; Toro *et al.,* 2019), and this can be due to a number of anatomical and physiological factors including the number and overall size of stomata, with some plants only having stomatal aperture on the underside of the leaf (abaxial surface) or on both the lower and upper sides (abaxial and adaxial respectively) (Caird *et al.,* 2007; Driesen *et al.,* 2023; Kozlowski & Pallardy, 2002; Medrano *et al.,* 2009; Wall *et al.,* 2022). A larger leaf area corresponds with a greater evapotranspiration rate (Lundholm *et al.,* 2010; Yuan *et al.*, 2017), and the type of plant and their subsequent adaptations to drought or heat impacts transpiration rate as well (Gourdji *et al.,* 2013; Hatfield & Prueger, 2015; Poë *et al.,* 2015).

Water availability within soil is one of the main drivers of transpiration. Soil hydrostatic pressure contributes to water uptake by the roots; as the roots absorb more water the soil moisture decreases and the soil pores fill with air. The remaining water has fewer channels to flow through and soil hydraulic conductivity declines (Buckley, 2019; Davies *et al.,* 2002; Hsiao, 1973). In dry or droughted substrate the soil water potential will continue to fall until the permanent wilting point is reached, after which plants cannot regain turgor pressure even when guard cells react by closing the stomatal pores and transpiration ceases (Buckley, 2019; Nagase & Dunnett, 2010; Poë *et al.,* 2015; Szota *et al.,* 2017).

Environmental factors in addition to water availability impact transpiration rates; including time of year which influences when plants are actively growing and thus transpiring more, and temperature (Gourdji *et al.,* 2013; Hatfield & Prueger, 2015; King *et al.,* 2012; Poë *et al.,* 2015). The humidity gradient between the air and leaf that drives water vapour evaporation from the leaf is also impacted by air temperature and humidity (Allen *et al.,* 1998; Poë *et al.,* 2015; Tan *et al.,* 2015). In humid environments plants can have lower evapotranspiration rates because the air is saturated with moisture and does not have the capacity to hold more, leading to a low vapour pressure deficit. Conversely, in arid environments that are hot and dry the evapotranspiration rates can be much higher because the vapour pressure deficit between the leaf and the atmosphere is also high (Kramer & Boyer, 1995; Poë *et al.,* 2015; Tan *et al.,* 2015).

1.5.3 Retention of rainfall within the canopy

Canopy capture includes rainfall interception on plant leaves, stems and branches; captured rainfall can then evaporate into the atmosphere rather than falling to the ground and adding to potential surface water accumulation (Beidokhti & Moore, 2021; Blanuša & Hadley, 2019; Liu & Zhao, 2020). The size and shape of the canopy can directly influence the volume of water intercepted and stored, and plants with a larger canopy or denser canopy structure, and greater leaf area, are all shown to store larger volumes of water (Beidokhti & Moore, 2021; Blanuša & Hadley, 2019; Liu & Zhao, 2020; Lundholm *et al*., 2015; Nagase & Dunnett, 2012). Rain throughfall and runoff has been found to decrease with an increase in leaf area index or specific leaf area (Beidokhti & Moore, 2021; Dunnett *et al*., 2008; Heim *et al.,* 2023; Nagase & Dunnett, 2012), and larger leaf areas have been associated not just with canopy retention but also with greater evapotranspiration rates (Chu & Farrell, 2022; Xie *et al*., 2018). Forb perennial planting with a large collective leaf area was found to provide 54% and 32% greater stormwater detention than bare substrate and lawn respectively (Yuan *et al*., 2017). Blanuša and Hadley (2019) found that hedge plant *Cotoneaster*, which had the largest area coverage in comparison to other hedge species investigated, also had one of the lowest runoff volumes.

Previous research with trees has also shown that the greater leaf area index of evergreen needleleaf species has the highest rainfall retention in comparison to broadleaf deciduous trees (Beidokhti & Moore, 2021; Xiao & McPherson, 2002). Larger leaves, however, are not always better at supporting rainfall retention within the canopy: smooth-textured leaves have been found to contribute more to runoff than other leaf types (Kemp *et al.,* 2019). Conversely, presence of leaf trichomes (hairs) has also been found to increase retention of water droplets and assist with canopy storage (Kemp *et al.,* 2019; Vaz Monteiro *et al.,* 2017). Branch architecture and density has an impact on canopy retention, with denser canopies providing greater interception (Liu & Zhao, 2020; Xiao & McPherson, 2002). Rough-barked species have also been found to produce lower stemflow volumes compared to those with smooth bark (Beidokhti & Moore, 2021; Ginebra-Solanellas *et al.,* 2020; Levia & Herwitz, 2005). Hedge species *Thuja plicata* was observed to have significantly higher volumes of runoff compared to other hedges due to the branch architecture funnelling water directly to the ground rather than retaining rainfall in its canopy (Blanuša & Hadley, 2019). Leaf angle and resistance of the individual leaf to movement can alter retention on a small scale, and plants with stiffer leaves that are less likely to move when impacted by water droplets also shed less water from the canopy, something observed in tree species *Quercus gambelii* (Ginebra-Solanella *et al.,* 2020).

1.5.4 Retention of rainfall within the substrate

However, canopy interception has a minimal influence on runoff reduction, and only contributes an extra 4% of rainwater retention in addition to the substrate storage capacity, which previous research has found to be the most significant rainwater storage (MacIvor & Lundholm, 2011; Stovin *et al.,* 2015). Substrate has a maximum water holding capacity, after which runoff is generated (Stovin *et al.,* 2015), therefore a plant with a high transpiration rate can aid runoff reduction by removing water from the substrate and restoring storage capacity (Kemp *et al.,* 2019; Stovin *et al.,* 2015). The type of substrate also effects retention, with soil characteristics having an impact on evapotranspiration rate (Poë *et al.,* 2015; Nasrollahpour *et al.,* 2022) and on water holding capacity (Berretta *et al.,* 2014; Dusza *et al.,* 2016; Kelly, 2016; Monteiro, 2017; Stovin *et al.,* 2015). The substrate's field capacity is impacted by particle size, and the void size and distribution between soil particles, which fill with water when saturated (Poë *et al.,* 2015; Stovin *et al.,* 2015). Substrates with a higher proportion of smaller voids have a greater water holding capacity (Berretta *et al.,* 2014; Stovin *et al.,* 2015; VanWoert *et al.,* 2005). Gardens in the UK have different soil classifications and this impacts their propensity for waterlogging and runoff generation, with higher infiltration occurring in sandy substrates, whilst clay soils have lower infiltration and linked with increased surface water accumulation (Kelly, 2016; Monteiro, 2017). Increased substrate depth also increases water retention capacity as it provides a larger water storage volume (Stovin *et al*., 2012 & 2015; VanWoert *et al.,* 2005), and compared to field trials, pot experiments with their reduced substrate volume, or green roofs with their shallow substrate, can limit water storage capacity and impact plant growth and behaviour (Chapman & Augé, 1994; Chu & Farrell, 2022; Ksiazek-Mikenas *et al.,* 2021). Plant roots can impact retention, with larger root biomass found to have greater water uptake (Dunnett *et al.,* 2008; Lundholm *et al*., 2015; Nagase & Dunnett, 2012; Stovin *et al.,* 2015; Yuan *et al*., 2017). Roots also alter the structure of the substrate (Nasrollahpour *et al.,* 2022; Stovin *et al.,* 2015); previous research found plants with dense, fibrous roots reduced the porosity of the substrate by reducing the void space and led to greater runoff volumes generated on a green roof (MacIvor & Lundholm, 2011).

1.5.5 Additional factors impacting rainfall capture

Increased rainfall intensity also results in greater runoff volumes due to the finite capacity of the canopy to retain larger water volumes, or due to the force of water droplet impact on the leaves of a plant that results in rainfall droplet shedding (Beidokhti & Moore, 2021; Boyd *et al.,* 1993; Chang *et al.,* 2021; Kelly, 2016; Liu *et al.,* 2020).

The time of year and growing season impacts when plants are actively transpiring and also retaining water in their canopies, with evapotranspiration rates higher in the summer than winter (Lundholm *et al.,* 2010), particularly for deciduous plants (Peters *et al*., 2011; Tiwary *et al.,* 2016). Evergreen plants continue to transpire throughout the year, and evergreen needleleaf trees have higher transpiration rates in April and November compared to deciduous trees, but deciduous broadleaf trees were found to produce the highest total evapotranspiration rate in late summer (Peters *et al*., 2011), which would impact potential runoff reduction. Another study found canopy retention throughout the year was higher for broadleaf evergreen trees compared to deciduous trees, intercepting 27% of annual total rainfall compared to 15% respectively (Xiao &

McPherson, 2002) therefore evergreen plants could have the ability to provide greater annual canopy retention and deciduous plants could provide greater annual transpirational water loss.

Plant traits and how they link to growth and also water use has been categorised by some researchers into a spectrum of 'fast' and 'slow' traits (Chu & Farrell, 2022; Reich, 2014; Schrieke & Farrell, 2021). Fast traits, including greater leaf area and shoot mass, and faster growth rates, are advantageous in resource-rich environments and enable the plant to quickly acquire resources, whereas slow traits such as smaller biomass and specific root length, and slower growth rate, enable plants to conserve resources (Chu & Farrell, 2022; Schrieke & Farrell, 2021). The former are associated with greater water use than the latter, with slower traits linked to drought tolerance (Chu & Farrell, 2022; Reich, 2014; Xie *et al*., 2018). Schrieke & Farrell (2021) found that plants with fast traits had higher transpiration rates and greater water use in well-watered conditions on a green roof. These traits have been found to also correlate with runoff reduction in many scenarios, and could be useful indicators of stormwater management service delivery. Many plant traits in combination have been found to produce the greatest runoff reduction, including larger leaf or stem biomass, leaf hairs, and high transpiration rates, rather than a singular over-contributing trait (Blanuša & Hadley, 2019; Heim *et al.,* 2023; Kemp *et al.,* 2019; Lundholm *et al.,* 2010; MacIvor *et al.,* 2018; Schrieke & Farrell, 2021).

1.6 Plants' responses to environmental stress

Stress is defined as any factor that has a 'disadvantageous influence on a plant' (Taiz & Zeiger, 2002) and reduces growth (Laukli *et al.,* 2022b). Changes in environmental factors including air temperature and water availability have the potential to become stressful conditions for plants, resulting in decreased survival rates (Farooq *et al.,* 2012; Hatfield & Prueger, 2015; Luo, 2011; Seleiman *et al.,* 2021; Vartapetian & Jackson, 1997). Stress tolerance is a plant's ability to cope with these environmental conditions and the focus of this thesis will stay within abiotic stresses (such as water deficit and waterlogging). Stress adaptation manifests itself as morphological, chemical and molecular changes

(Ahluwalia *et al.,* 2021; Basu *et al.,* 2016; Davies & Zhang, 1991) and enables plants' survival. Some plants can also develop tolerance to climatic stress conditions after initial exposure, leading to acclimation (Bester *et al.,* 2024; Blanuša *et al.,* 2009; Cameron *et al.,* 2006; Drew *et al.,* 1979; Li *et al.,* 2023; King *et al.,* 2012), however many plants are vulnerable to stress and suffer leaf wilting or scorching, reduction in growth, root death, and loss of yield (Bechtold *et al.,* 2016; Dickin & Wright, 2008; García-Navarro *et al.,* 2003). Yield loss is a substantial problem for crop plants and the agricultural industry (Byrne *et al.,* 2022; Davies *et al.,* 2000; Dickin & Wright, 2008; Cannell *et al.,* 1980; Gupta *et al.,* 2020; Hatfield & Prueger, 2015; Ide *et al.,* 2022), but in a domestic garden the aesthetics of the plant, rather than the yield is important for homeowners (Frantzeskaki, 2019; Stobbelaar *et al*., 2021). Understanding stress tolerance in popular garden plants is important because if a plant dies under stress, or if it looks aesthetically unappealing as it exhibits stress responses, then people will be less likely to use these plants in their gardens (Francis, 2018; Hostetler, 2021; Stobbelaar *et al*., 2021), and their potential ecosystem service provision would be lost.

Plants' responses to abiotic stresses have been studied extensively (Byrne *et al.,* 2022; Dickin & Wright, 2008; Else *et al.,* 2009; Geng *et al.,* 2023; Ide *et al.,* 2022; King *et al.,* 2012; Li *et al.,* 2023; Rivière *et al.,* 2024; Yin *et al.,* 2009). However, the majority of these studies are on individual plants, and an additional important aspect for domestic garden research is how plants interact together during periods of stress. Rolhauser *et al.* (2023) recently discussed the concept of a stress gradient framework for green roof planting design, which takes into account the stress tolerance of individual plants and their relationships with other plants that could lead to facilitation or competition. The stress gradient hypothesis theorises that as the environmental stress increases, some plant interactions may change from negative (competition) to positive (facilitation) (Bertness & Callaway, 1994; Heim *et al.,* 2023; Rolhauser *et al.,* 2023). Key to this change is the type of stress experienced, with non-resource stress such as temperature leading to facilitation and resource stress such as water availability leading to competition (Grime, 1974; Rivière *et al*., 2024; Rolhauser *et al.,* 2023).

Species with stress-tolerant traits (including lower biomass or leaf area, which were found to aid plant survival during drought, Chu & Farrell, 2022; Fagundes *et al.,* 2022; Nagase & Dunnett 2010; Rolhauser & Pucheta, 2016; Schrieke & Farrell, 2021), are also more likely to support those plants with stress-intolerant traits as they can ensure, due to their lower water use, increased soil moisture for example (Fagundes *et al.,* 2022; Rivière *et al*., 2024; Rolhauser & Pucheta, 2016; Rolhauser *et al.,* 2023). However, this focus on drought-facilitative interactions does not account for the traits that would provide companion planting in the opposite conditions, i.e. waterlogging or excess water. Which traits will result in companion planting facilitation is therefore not straightforward. Plant traits and adaptions to aid water stress tolerance are well documented (Lundholm *et al.,* 2010; Nagase & Dunnett, 2010; Nazemi Rafi *et al.,* 2019; Rivière *et al.,* 2024; Wiström *et al.,* 2023; Yin *et al.,* 2009) and is an interesting factor to consider for garden plant selection both as individuals, and as a community within a planting bed to aid survival and possible ecosystem service delivery. Further information on planting design, companion planting and ecosystem service delivery can be found in section 1.7.

1.6.1 Water deficit

Low soil moisture results in lower water potential in the leaves and stems of plants, and when the rate of water loss through transpiration becomes greater than the water uptake through the roots this leads to water deficit (Buckley, 2019; Seleiman *et al.,* 2021). Water deficit causes plant leaves to yellow, roll, scorch, or permanently wilt, and overall results in growth reductions and yield losses, and severe water deficit or drought cause plant death (Bechtold *et al.,* 2016; Dickin & Wright, 2008; García-Navarro *et al.,* 2003). Several environmental factors influence the impact of water deficit, including drought duration, intensity and frequency, and the soil characteristics (Ahluwalia *et al.,* 2021; Gupta *et al.,* 2020; Seleiman *et al.,* 2021). The plant species or growth stage of the plant also impacts how the plant tolerates drought, with plants more sensitive during reproduction than vegetative growth stages (Farooq *et al.,* 2012; Gupta *et al.,* 2020). Even after alleviation of water stress plants that experienced water deficit may have a lower growth rate than unstressed plants despite similar turgor pressure (Matthews *et al*., 1984; Taiz & Zeiger, 2002).

At the early stages of water deficit, the plant's water content decreases and cells shrink, resulting in lower turgor pressure that can be observed as wilted leaves or stems (Farooq *et al.,* 2012; Kiani *et al.,* 2007; Matthews *et al.,* 1984). This causes reduced leaf expansion, and the resultant lower leaf area transpires less water, so that a smaller leaf area acts as a water conservation strategy as well as stress response to water deficit (Dodd *et al.,* 1996). Although when plants reach the permanent wilting point they can no longer regain turgor pressure even after stomatal closure or rehydration (Poë *et al.,* 2015; Szota *et al.,* 2017). An additional way to reduce leaf area is leaf abscission, in which ethylene production leads to leaf senescence in response to severe water deficit (Basu *et al.,* 2016; Farooq *et al.,* 2012).

Root apices also lose turgor pressure due to reduced water availability. In response roots grow towards moisture in the substrate, growing deeper into the soil layers as the uppermost layer dries out first (Farooq *et al.,* 2012; Gupta *et al.,* 2020; Wasson *et al.,* 2012). Root growth then becomes greater than shoot growth, which subsequently reduces as cells shrink due to loss of turgor pressure, and root length increase is a sign of adaptation against drought (Fort *et al.,* 2015; Nazemi Rafi *et al.,* 2019). A greater proportion of plant assimilates are sent to the roots which can aid with root growth, however when plants are fruiting there is competition between the root system and fruits. Due to this, root growth is worse when plants are investing energy in the reproductive growth stage compared to vegetative growth, and plants in the reproductive growth stage are more sensitive to water deficit (Farooq *et al.,* 2012; Sharp *et al.,* 2009).

To reduce transpirational water loss plants will close their stomata in water deficit, and this response is a key defence against drought (Bechtold *et al.,* 2016; Chu & Farrell, 2022; Davies *et al.,* 2002; Hsiao, 1973; Kozlowski & Pallardy, 2002; Sobeih *et al.,* 2004; Stoll *et al*., 2000). Decrease in water content and loss of turgor also closes the stomata (Hsiao, 1973; Osakabe *et al.,* 2014). Higher abscisic acid (ABA) synthesis and concentrations in water deficit also prolongs the guard cell response, therefore continuing to conserve water (Davies *et al.,* 2002; Jokhan *et al.,* 1996; Osakabe *et al.,* 2014; Stoll *et al.,* 2000). In a previous experiment with *Zea mays* this response was shown even when only part of the root system experienced water deficit, causing stomata to partially close to maintain leaf water potential even though other root sections were well-watered (Taiz & Zeiger, 2002). The responsiveness of stomata is dependent on plant species, with some crops such as cowpea or maize very responsive to water deficit, closing their stomata and reducing transpiration quickly enough to maintain high leaf water potential during drought (Jones, 1998). Plants with high transpiration rates, whilst able to deplete substrate moisture more quickly, also experience drought stress more frequently due to reduced moisture availability (Szota *et al.,* 2017).

Although photosynthesis is less sensitive to water deficit than stomatal conductance, it can still be reduced by water stress as stomatal closure to reduce water loss also inhibits gas exchange (Ahluwalia *et al.,* 2021; Basu *et al.,* 2016; Farooq *et al.,* 2012; Gupta *et al.,* 2020; Osakabe *et al.,* 2014; Yamance *et al.,* 2003). The dehydration and shrinking of plant cells also inhibit metabolism, especially of the mesophyll cells, and the decreased leaf area mentioned earlier reduces the amount of leaf apparatus able to photosynthesise (Bechtold *et al.,* 2016; Boyer, 1970; Farooq *et al.,* 2012; Yamance *et al.,* 2003).

1.6.2 Plant adaptations to water deficit

Plant adaptation to drought is collectively termed drought tolerance or drought resistance, and is divided into two main types - desiccation postponement/avoiders or desiccation tolerance (Chapman & Augé, 1994; Chu & Farrell, 2022; Kozlowski & Pallardy, 2002; Szota *et al.,* 2017; Wiström *et al.,* 2023).

Desiccation postponement allows plants to maintain tissue hydration and therefore delay the negative effects of drought. To do this the plant decreases its water use by adjusting osmotic potential, or by using a deep rooting system to seek out additional water stores in the soil (Chapman & Augé, 1994; Chu & Farrell, 2022; Szota *et al.,* 2017; Tabassum *et al.,* 2021). This has been observed in perennials *Rudbeckia* and *Althea* (Hollyhock), which used drought-postponement/avoidance mechanisms including osmotic adjustment to tolerate 75% reduction in irrigation (Nazemi Rafi *et al.,* 2019). Within desiccation postponement there are water savers and water spenders - water savers reduce their use to conserve water, and water spenders rapidly consume all available water and are usually deep rooted (Chapman & Augé, 1994; Nazemi Rafi *et al.,* 2019), such as garden plants of prairie origins (e.g. *Helianthus* and *Echinacea* species) that have long roots or taproots to access water deeper in the substrate and remain hydrated (Bortolini & Zanin, 2019; Chapman & Augé, 1994; Kindscher, 1989). Desiccation tolerance on the other hand enables plants to tolerate dehydration and continue to function, aided by traits including stomatal control and small leaves with thicker cuticles, reducing water loss by transpiration (Farrell *et al.,* 2013; Nagase & Dunnett, 2010; Nazemi Rafi *et al.,* 2019; Tabassum *et al.,* 2021). For example, garden shrub *Arbutus* can survive severe drought using progressive stomatal closure to limit water loss, and *Sedum* have fleshly leaves and a low transpiration rate to tolerate drought (Raimondo *et al.,* 2015; Vaz Monteiro *et al.,* 2017). Although, many plants fall into both groups and use a mixture of strategies, rather than exhibiting postponement or tolerance only (Chapman & Augé, 1994; Tabassum *et al.,* 2021; Wiström *et al.,* 2023).

Adaptation to the leaves is one of the ways plants can cope with water deficit. As mentioned previously, wilting and loss of turgor enables plants to reduce their leaf area and conserve limited water. Plants that have adapted to low moisture levels can have smaller leaves or leaf area and this is one of the first defences against drought (Kozlowski & Pallardy, 2002; Nagase & Dunnett, 2010). In addition to this some plants have fleshier leaves to store water, or thicker cuticles, which reduces water loss from the epidermis by transpiration, albeit by a small amount (e.g. 5-10%) (Lönnqvist *et al.,* 2023; Riederer & Schreiber, 2001; Tabassum *et al.,* 2021). Other traits that help conserve water or assist with drought tolerance include leaf trichomes (which cool the leaf), a change of leaf orientation, or greater rooting depth (Chu & Farrell, 2022; Farrell *et al.,* 2013; Kozlowski & Pallardy, 2002; Nazemi Rafi *et al.,* 2019; Tabassum *et al.,* 2021; Toro *et al*., 2019; Wasson *et al.,* 2012).

Plants can also enable osmotic adjustment to accumulate solutes in the plant cells as a way of decreasing water potential without loss of turgor or decreased cell volume (Ahluwalia *et al.,* 2021; Cameron *et al.,* 2006; Farooq *et al.,* 2012; Kiani *et al.* 2007; Nazemi Rafi *et al.,* 2019). Popular garden shrub *Forsythia* was found to maintain relatively high stomatal conductance during water stress, likely helped by osmotic adjustment, to enable continued photosynthesis using available light even during water deficit (Cameron *et al.,* 2006). Herbaceous perennial plants *Rudbeckia hirta* and *Althea rosea* tolerate high water deficit using osmotic adjustment in conjunction with leaf traits including leaf hairs and greater root density (Nazemi Rafi *et al.,* 2019), and *Salvia officinalis* was also found in another study to maintain high stomatal conductance until substrate water was depleted (Raimondo *et al.,* 2015).

Another adaptation is crassulacean acid metabolism (CAM), typical of species of genus Crassulaceae as well as Cactaceae, Epiphytes (e.g. orchids), Asparagales (Aloe, Agave, Yucca etc.), and some fern species (e.g. *Polypodium*) to name a few, which maintain stomata open at night when the leaf to air vapour pressure difference is lower, and close them during the day as an adaptation to water deficit (Basu *et al.,* 2016; Gowik & Westhoff, 2011; Nagase & Dunnett, 2012).

Previous research has found that plants can adapt to lower water quantities and water deficit by preconditioning with lower water availability, which is something that nursery stock plants and shrubs can undertake once they reach a certain size (Cameron & Hitchmough, 2016). Previous studies have also found that ornamental plants can adapt to a reduced watering regime by implementing stomatal control, although, in response, the plants grew smaller and more compact (Blanuša *et al.,* 2009; Cameron & Hitchmough, 2016; Cameron *et al.,* 2006 & 2008). For example, after several weeks of being watered with only 25% of water lost by evapotranspiration, *Petunia* plants were visually healthy but compact, with plant height reduced by 33% (Blanuša *et al.,* 2009). *Lonicera* shrubs also adapted to drought when under a 50% reduced deficit irrigation (RDI) water regime, resulting in reduced shoot growth (Cameron *et al.,* 2006). This has also been found with herbaceous plant *Oenothera* 'Siskiyou Pink', with water restriction resulting in the plant adapting with a smaller number of branches (Burnett & van Iersel, 2008). Reduced watering can result in loss of visual quality of flowering plants, with closed or drooping flowers a response to drought, however there was a significant increase in flowering of some herbaceous plants after water was reinstated (Demotes-Mainard *et al.,* 2013; García-Navarro *et al.,* 2003). Other irrigation techniques, which employ reduction of watering volumes (such as partial root drying, PRD), provide water savings through changes in plant physiology. This may have a positive impact on flowering (e.g. strawberries) with plants using less water but still maintaining quality and may show promise in ornamental horticulture (Davies *et al.,* 2002; Dodd *et al.,* 2006; Dodds *et al.,* 2007; Norton *et al.,* 2017; Stoll *et al.,* 2000).

1.6.3 Waterlogging

Waterlogging is the raising of the water table that results in the submergence of a plant's roots, causing oxygen deprivation and physiological drought (Byrne *et al.,* 2022; Vartapetian & Jackson, 1997). Under normal, well-watered conditions, gaseous oxygen fills spaces between soil pores and diffuses into root cells, which is then used for aerobic mitochondrial respiration (Pan *et al.,* 2021). However, when flooding occurs water replaces air within the soil pores and dissolves the gaseous oxygen. Oxygen diffusion in water is significantly lower, only 1/10,000 the rate compared to its gaseous form, leaving plant roots with an oxygen depletion condition known as hypoxia, or anoxia if severe oxygen depletion occurs, both of which limit aerobic respiration (Armstrong, 1979; King *et al.,* 2012; Lukac *et al.,* 2011; Pan *et al.,* 2021; Vartapetian & Jackson, 1997; Vidoz *et al.,* 2010).

Waterlogging leads to leaf stomatal closure, and a subsequent decline in photosynthesis (Cameron & Hitchmough, 2016; Else *et al.,* 2009; King *et al.,* 2012; Kozlowski & Pallardy, 2002; Olorunwa *et al*., 2023; Pan *et al.,* 2021; Yin *et* *al.,* 2012). One of the earliest symptoms of waterlogging stress is also a reduction in root hydraulic conductance, which can begin within 2-6 hours of waterlogging (Else *et al.,* 2009) and eventually root death (Chauhan *et al.,* 1997; Davies *et al.,* 2000; King *et al.,* 2012; Lukac *et al.,* 2011).

In these conditions aerobic root respiration is reduced or ceases entirely, inhibiting production of adenosine triphosphate (ATP) and resulting in a plant energy shortage, which is why crop production reports loss of growth/biomass and yield as a costly outcome of waterlogging (Byrne *et al.,* 2022; Cannell *et al.,* 1980; Dickin & Wright, 2008; Dylewski *et al.,* 2011; Pan *et al.,* 2021; Shao *et al.,* 2023). A key response to waterlogging on a whole-plant and physiological level is implementation of anaerobic respiration, but this leads to accumulation of toxic metabolites that poison the plant, leading to cell death and then plant death if prolonged (Cameron & Hitchmough, 2016; Li *et al.,* 2021; Pan *et al.,* 2021; Yin *et al.,* 2009).

Factors affecting the impact of waterlogging on plant function, survival and growth include the time of year, temperature, and growth stage of the plant (Cameron & Hitchmough, 2016; Cannell *et al.,* 1980; Kozlowski & Pallardy, 2002; Ren *et al.,* 2023). Flooding during summer, when temperatures are higher and plants are actively growing and transpiring, is more damaging than winter waterlogging, when deciduous plants are dormant, and even evergreen plants have reduced transpiration in lower temperatures (Cameron & Hitchmough, 2016; King *et al.,* 2012; Kozlowski & Pallardy, 2002; Laukli *et al.,* 2022b; Ren *et al.,* 2023). Increased aerobic respiration of the plant roots in summer means that oxygen deprivation by floodwaters leads to a rapid depletion of available soil oxygen by the plants and soil microbes, resulting in the switch to anaerobic respiration and subsequent cell death occurring more quickly (Cameron & Hitchmough, 2016; Vartapetian, 1973; Vartapetian & Jackson, 1997). This was observed in flooded *Stachys byzantina* and *Lavandula angustifolia*, which had significantly greater biomass loss in summer flooding compared to winter (King *et al.,* 2012). The volume of water causing flooding also has an impact, with subtotal or partial flooding causing less damage than total submergence as it enables plants to still access gaseous oxygen (Byrne *et al.,* 2022; King *et al.,* 2012; Kozlowski & Pallardy, 2002). Duration of flooding can also play a part, with increased inundation time correlating with greater biomass loss and visual damage in shrub plants (Dylewski *et al.,* 2011) and wheat (Dickin & Wright, 2008). Perennials in a rain garden were subjected to either 24 hour or four-day flood cycles, and after 32 days of experimentation (7 flood cycles and 4 flood cycles respectively) were harvested for plant biomass, and 'drought-tolerant' *Oenothera* showed no negative outcomes after the 24 hour of flood cycles, whilst four-day cycles caused biomass loss (Yuan & Dunnett, 2018). Free draining substrate such as sandy soils results in floodwaters reducing at a faster rate than clay rich substrate, the structure of the latter consisting of smaller particles and air pore sizes which prevent water draining away and can remain waterlogged for prolonged periods of time (Cannell *et al.,* 1980; Stovin *et al.,* 2015).

1.6.4 Plant adaptations to waterlogging

Chemical and metabolic changes in waterlogged plants can lead to morphological adaptation, strategies that have been commonly observed in riparian species that are frequently subjected to inundation (Jackson & Attwood, 1996; Justin & Armstrong, 1987; Lukac *et al*., 2011; Vartapetian & Jackson, 1997). Oxygen deficiency from waterlogging results in the production of aminocyclopropane-1-carboxylic acid (ACC) in the submerged roots, which then travels up the plant through the xylem and is converted to ACC oxidase and ethylene (Pan *et al.,* 2021). Ethylene has been linked with several anatomical adaptations that plants can employ to help alleviate waterlogging stress, with the aim that these changes enable access to gaseous oxygen for aerobic respiration (Jackson, 2004; Li *et al.,* 2021; Pan *et al.,* 2021; Yin *et al.,* 2009).

Root regeneration in the form of adventitious roots that grow from non-root tissue, such as the base of the stem, is one rapid response to flooding triggered by ethylene production (Ide *at al.,* 2022; Lukac *et al*., 2011; Pan *et al.*, 2021; Zhao *et al.,* 2022). These roots can tolerate higher levels of carbon dioxide and maintain respiration by growing above the water table and therefore enabling oxygen diffusion into the plant tissue (Kozlowski & Pallardy, 2002; Lukac *et al*., 2011; Steffens & Rasmussen, 2016). Riverside tree species *Alnus glutinosa* and various *Salix* and *Populus* species all grow adventitious roots in response to flooding stress (Lukac *et al.*, 2011), but this has also been observed in crop plants (Pan *et al.,* 2021), including tomatoes (Else *et al.,* 2009; Ide *et al.,* 2022; Vidoz *et al.,* 2010), wheat (Li *et al.,* 2023), cucumber (Qi *et al.,* 2019), herbaceous Cannas (Zhao *et al.,* 2022), and *Chrysanthemum* (Yin *et al.,* 2009 & 2012). *Chrysanthemum* are generally sensitive to waterlogging, however Yin *et al*. (2009) found a tolerant cultivar exhibited a three-fold increase in ethylene production from the submerged stems several days earlier than sensitive cultivars, which led to the formation of adventitious roots, whereas the sensitive cultivar wilted and eventually rotted. However, there is variation within ornamental perennials and crop species to waterlogging tolerance, and speculation that breeding for aesthetics or increased yield may come at the expense of stress tolerance in some plants (Lewis *et al.,* 2019). Differing waterlogging responses have been observed with *Hosta* cultivars and varieties of prairie species *Liatris* (Laukli *et al.,* 2022b), popular perennials *Echinacea* (Bortolini & Zanin, 2019) and *Primula* (Lewis *et al.,* 2019), and crop plants including wheat and maize (Cannell *et al.,* 1980; Dickin & Wright, 2008; Geng *et al.,* 2023; Li *et al.,* 2023; Ren *et al.,* 2023; Shao *et al.,* 2023), tomatoes (Else *et al.,* 2009; Ide *et al.,* 2022), lupins (Bramley *et al.,* 2011; Davies *et al.,* 2000), soybean (Bester *et al.,* 2024), cowpea (Olorunwa *et al.,* 2023) and pigeonpea (Chauhan *et al.,* 1997) to name a few.

Changes to cell structure within roots and stems has also been observed as an adaptation to waterlogging, with interconnected intercellular spaces known as aerenchyma tissues enabling pathways for oxygen diffusion between stems and roots (Armstrong, 1979; Drew *et al.,* 1979; Evans, 2004; Justin & Armstrong, 1987; Lukac *et al.,* 2011; Pan *et al.,* 2021; Vartapetian, 1973; Vartapetian & Jackson, 1997). These gas filled chambers are the result of ethylene-stimulated targeted cell death, creating cavities for gas exchange (Armstrong, 1979; Justin & Armstrong, 1987; Pan *et al.,* 2021; Vartapetian, 1973; Vartapetian & Jackson, 1997) and have been observed in crop plants such as rice, which grow in flooded fields (Jackson, 2004; Yamauchi *et al.,* 2014), but also in wheat (Jackson, 2004; Li *et al.,* 2023) and maize (Yamauchi *et al.,* 2016), the latter of which can also be stimulated by pre-treatment with ethylene (Geng *et al.,* 2023) or hypoxia before full submergence (Drew *et al.,* 1979). Flood-tolerant *Chrysanthemum* cultivars also developed aerenchyma within their adventitious roots (Yin *et al*., 2012).

Rapid stem elongation is also supported by aerenchyma formation, and has been observed in rice and water lilies (Jackson, 2004; Kuroha *et al.,* 2018; Pan *et al.,* 2021). Ethylene stimulates cell elongation, enabling leaves and roots to rapidly grow and extend above the waterline and increase their access to aerial oxygen. In rice this enables leaf extension, and in water lilies cell extension is observed in the petiole (Jackson, 2004; Kuroha *et al.,* 2018).

Additional aboveground changes include leaf epinasty, which is the downward curvature of leaves, induced by hypoxic roots producing increased ACC and subsequently faster shoot ethylene production (Jackson, 2004). Ethylene sensitive receptors in the topside of the leaf promote rapid growth, which reduces the energy spent on overall foliage growth and decreases stomatal water loss (Jackson *et al.,* 1978; Jackson, 2004; Vartapetian & Jackson, 1997). This strategy makes the leaves appear wilted although there is no loss of turgor pressure, and is deployed by pea (Zhang & Zhang, 1994), sunflowers (Jackson, 2004), and *Chrysanthemums* (Yin *et al.,* 2009) in flooded conditions.

As mentioned previously, pre-treatment of hypoxia can result in increased flood-tolerance in maize (Drew *et al.,* 1979). Additionally, this has been observed in soybean, leading to maintained leaf potential and stomatal opening (Bester *et al.,* 2024), and wheat, which after two days of pre-treatment developed adventitious roots and aerenchyma and had improved gas exchange compared to control plants (Li *et al.,* 2023). In perennials, drought-tolerant *Salvia officinalis* was susceptible to flooding but when pre-treated with subtotal flooding exposing the plants to hypoxia and then gradually increasing the water table, plants grew roots near the surface of the water that remained viable for longer than the roots of control plants and indicated acclimatisation to anoxia (King *et al.,* 2012). Priming plants with ethylene has also had similar positive effects, resulting in soybean producing aerenchyma and adventitious roots (Geng *et al.,* 2023; Kim *et al.,* 2018), and adventitious roots in cucumber (Qi *et al.,* 2019) and tomato (Vidoz *et al.,* 2010). Pre-treating or priming plants could enable plants that were not otherwise considered flood tolerant to survive waterlogging.

1.6.5 The impact of water deficit and waterlogging in the UK

Both too little and too much water can be stressful for plants. Water deficit and flooding are expected to occur in the UK with increased frequency due to climate change, and heavy rainfall events in the summer occurring after periods of limited or no precipitation (Beidokhti & Moore, 2021; IPCC, 2021; Kendon *et al.,* 2023; Maragno *et al.,* 2018; Webster *et al.,* 2017). Flash flooding events in recent years (e.g. in Birmingham in May 2018 and London in July 2021) had a substantial impact on urban infrastructure (Kendon *et al.,* 2023). It is estimated that in England 3 million properties are at risk of flooding due to changing climate (Kendon *et al.,* 2023). Garden plants will therefore need to be able to survive drought and inundation.

When investigating stormwater management ecosystem services and perennial garden plants, three questions from existing research present themselves. The first is whether plants will tolerate excess water, the second is whether they will remove this excess water and provide an ecosystem service, and the third is whether they will survive periods of drought in addition to inundation during the UK summers. Following the heat wave experienced in the UK in the summer of 2022 the media cited several lists of plants that could ‘stand up to climate change’ because they were ‘drought resistant’ or ‘heat-proof’ (Beth Chatto’s Plants & Gardens, 2022a & 2022b; Brown, 2022; Horton, 2023; Wallington, 2022). It is necessary to understand if these plants are able to survive and thrive in a seasonal UK climate, which includes winter rainfall and summer waterlogging in addition to water deficit.

1.7 Ecological concepts applied to planting design

Plants in domestic gardens cannot be viewed in isolation when the majority of plants are situated in planting ‘beds’, resulting in interactions between species.

How these plants behave and interact when growing together is key to understanding how they can survive during stressful weather events such as flooding or drought, and also whether their interactions hinder or facilitate the delivery of ecosystem services.

Contemporary planting design in the UK uses a palette of species that are visually appealing and manageable, with aesthetic outcome intended to be beautiful but also neat and organised, without weeds or unruly, spreading vegetation (Droz *et al.,* 2011; Oudolf & Kingsbury, 2016). The phrase 'right plant, right place', used by Beth Chatto, enabled plant selection based on its suitability to a particular niche, with plant growth supported by the environmental conditions such as moisture or light availability (Garden Museum, no date). This theory encouraged people to work with the plant's requirements, rather than fight against them, and provided a way for gardeners to connect plants with their environments (Garden Museum, no date; Taylor, 2012). Chatto developed her planting style by taking inspiration from naturally occurring plant communities, which is something that internationally renowned landscape and garden designers including Piet Oudolf, Sarah Price, Dan Pearson, James Hitchmough and Nigel Dunnett also do today to great effect, with the design style labelled the 'New Perennial' movement (Rainer & West, 2015; Taylor, 2012).

Species in vegetation communities have interactions with both abiotic and biotic factors. Abiotic factors including soil moisture and temperature are believed to significantly influence establishment and survival, but biotic factors such as competition with other plants is significant for developing planting community composition (Aguiar *et al.,* 2019). These factors occur on a gradient depending on the community, and co-occurring species can reduce or avoid competition for abiotic factors by using niche complementarity, becoming more efficient at exploiting available resources (Cardinale *et al.,* 2011; Droz *et al.,* 2021). Several planting theories have developed over the years that try to explain the interactions between naturally occurring plant communities and apply this to designed planting schemes. This review will focus on key theories relevant to contemporary planting design.

Hansen and Stahl (1993) in the 1970s focused on perennial plants and their habitats as a way of understanding how planting design in domestic gardens could be improved. They suggested that if species were planted in similar conditions to their wild habitats this would lead to more resilient and easier to manage planting designs, and extend the lifespan of the individual plants (Hansen & Stahl, 1993; Taylor, 2012). An example could be combining Mediterranean and Californian plants (with similar climatic requirements) forming a new planting community (Alizadeh & Hitchmough, 2020), and although this theory works in principle, many designers also combine plants from different habitats within the same planting scheme with successful outcomes (Rainer & West, 2015).

Grime (1974) developed a different theory, based on plant competition and survival strategies. He created the CSR strategy model, which proposes that plants in a community are competitors (C), stress tolerators (S), or ruderals (R). Competitors were able to exploit low stress environments (such as roadsides), stress tolerators could - as the name suggests - tolerate high stress and low disturbance (such as derelict land or droughted rocky outcrops), and ruderals preferred low stress and high disturbance (such as trampled paths) (Grime, 1974; Rainer & West, 2015; Rivière *et al*., 2024). Habitat disturbance ranges between herbivory to fire, and ruderals associated with this were usually annuals and what gardeners would consider weeds (Rainer & West, 2015). This model has been applied to many plant community studies (Lönnqvist *et al.,* 2023; Rivière *et al*., 2024) but at the same time has been identified as problematic because it is rare that plants fall solely into one of the three categories and many have traits of several groups (Lönnqvist *et al.,* 2023; Rainer & West, 2015; Wilson & Lee, 2000). Grime indicated that plants could also use intermediate strategies from these three groups (Grime, 1974; Rivière *et al*., 2024), but plants have also been found to switch between behaving like competitors and facilitators depending on the environmental conditions (Rolhauser *et al.,* 2023). A study using *Sedum* showed the succulent facilitated growth of neighbouring herbaceous plants during water deficit, but competed and reduced their overall growth when resources were plentiful (Butler & Orians, 2011). Plant trait and survival strategy plasticity needs to be taken into account when selecting plants for survival and aesthetics within a planting bed. Kühn (2011) developed their planting design model based on the principles of both Hansen and Stahl, and Grime, and included integral additions such as plant responses to site conditions and how plants develop within a temporal niche. This model was the first time that plant adaptive behaviour was included in a tool used to create designed planting communities (Rainer & West, 2015). To simplify what could become a very complicated model, Kühn created eight categories that plants could fall into, and these took into account stress avoidance or adaption strategies.

Most recently, Rainer and West (2015) developed the earlier models (Hansen & Stahl, 1993, Grime 1974 and Kühn, 2011) to include layers of planting, each with a different function (structure/framework, erosion control, weed suppressors, stress tolerators etc.). This simplified the community theory and enabled garden designers to apply it practically. The layers are split into the 'design' layers of structural and seasonal plants, and the 'functional' layers, named as such because they provide ground cover and erosion control, act as nectar sources, and incorporate filler plants including short-lived perennials or annuals that would fall into Grime's ruderal category. Rainer and West (2015) also note that the ground cover layer could provide ecosystem services, including stormwater management. Ground cover plants have been found to provide service delivery including runoff reduction and air and substrate cooling (Blanuša *et al.,* 2013; Dunnett *et al*., 2008; Kemp *et al.,* 2019; Vaz Monteiro *et al.,* 2017), and can collect particulate matter that washes from trees, making a ground cover understory valuable for pollution mitigation as well (Säumel *et al*., 2016; Weerakkody *et al.,* 2018b). However, previous research on ecosystem service delivery links many different types of plants with service provision, and this is not specifically related to ground cover plants. For example, using erect forbs or graminoids has been found to significantly reduce runoff (Lundholm *et al.,* 2010; MacIvor & Lundholm, 2011; Nagase & Dunnett, 2012; Yuan *et al.,* 2010), therefore Rainer and West's theory should expand and adapt as research continues in the field of ecosystem service delivery, ensuring it includes a wider variety of plants for service provision.

Incorporating large swathes of perennial planting has become more popular over the years, particularly in urban areas, with notable examples including the High Line in New York and Hauser and Worth in Somerset (both designed by Piet Oudolf), and Olympic Park and the Barbican Centre in London (designed by Nigel Dunnett, James Hitchmough and Sarah Price), the latter two gardens using the concept of designed plant communities. Using individual plant traits as an indicator of how they will perform in a planting bed (in terms of their survival, growth and aesthetics) has also been applied to perennial plants with increased effectiveness, for both aesthetics and for ecosystem service delivery (Dunnett *et al.,* 2008; Oudolf & Gerritsen, 2000; Oudolf & Kingsbury, 2013; Lönnqvist *et al.,* 2023; Lundholm *et al.,* 2010; MacIvor *et al.,* 2018).

As previously discussed in section 1.5.5, fast or slow plant traits associated with water use have been applied to understand how plants will use or save water in varying water availabilities, which can then inform planting design (e.g. on a green roof, Chu & Farrell, 2021; Lönnqvist *et al.,* 2023; Shrieke & Farrell, 2021). Combining plants with different traits, or increasing the phylogenetic diversity on a green roof has also been found to provide greater runoff reduction or reduced roof surface temperatures (Lundholm *et al.,* 2010; MacIvor *et al.,* 2018). Heim *et al.* (2023) found that combining plants with similar traits had no positive facilitation effect on overall plant growth, which indicates that how plants are combined in a planting bed can hinder or aid the growth and, potentially, ecosystem service provision of that bed.

Competition between plants can also have detrimental impacts on plant growth (Aguiar *et al.,* 2019; Alizadeh & Hitchmough 2020; Droz *et al.,* 2021; Grime, 1974; Rainer & West, 2015). Three-year-old ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings in combination showed ash had a greater competitive nature, with belowground competition between species resulting in increased fine root mortality of beech compared to beech as a monoculture (Beyer *et al.,* 2013).

Blanuša *et al.* (2009) also found that in water deficit conditions pairings of bedding plants *Petunia* and *Impatiens* resulted in a 75% reduction in flower numbers in *Impatiens*. The reduced growth of *Impatiens* was attributed to the more competitive nature of the vigorous *Petunia*, which grew greater shoot biomass and leaf area, enabling it to transpire more than *Impatiens*. Plants using ruderal or competitive strategies have been found to have greater shoot biomass, enabling them to outgrow plants that had a conservative water use strategy (Lönnqvist *et al.,* 2023), although in contrast the stress tolerance strategy of *Sedum* plants was found in a four-year green roof study to enable its dominance in the planting bed compared to other plant species using competitive or ruderal strategies (Rivière *et al*., 2024). This could be due to resource availability at the time of study. Lönnqvist *et al.* (2023) only noted competitive growth increase when water availability was high. Additionally, Rivière *et al*. (2024) found that only after several years of study when resource availability decreased did the stress tolerant plants became the dominant species and outcompete the others. Therefore, when resources are lower a stress tolerance strategy might be a better long-term solution to such conditions. Lack of facilitation between plants does not, however, automatically mean that competition is occurring instead. Heim and Lundholm (2014) found no facilitative effects when combining moss, lichen and bunchgrass with *Solidago bicolor*, but there was no negative impact on *Solidago's* growth either.

1.7.1 The concept of companion planting and its benefits

Companion planting is the combination of different plants that aid each other's growth; additionally, so-called nurse plants that enhance the growth of the neighbouring vegetation (Filazzola & Lortie, 2014; Griffiths-Lee *et al.,* 2020; Rolhauser & Pucheta, 2016). This facilitation has been found to improve growth and survival rates of other plants in a number of circumstances by improving the environmental conditions. For example, a study of dryland areas around metal mines in Spain showed that perennial nurse plants (in the form of grasses, trees and shrubs) increased soil fertility (and reduced metal toxicity), leading to improved soil microbial activity and re-colonisation by other plant species (Navarro-Cano *et al.,* 2017). In another study, planting perennial herbs and shrubs that acted as nurse plants provided shade and cooling effects for undergrowth planting (including reducing soil temperatures by 15°C on hot days) resulting in more preferable growing conditions and increased biomass of target plants (Aguiar *et al.,* 2019). Facilitation is typically enabled when paired plants have different traits or growth forms that result in different resource uptake, with nurse plants using resources conservatively which provides greater resource availability for other plants (Fagundes *et al.,* 2022; Muratet *et al.,* 2024; Rolhauser & Pucheta, 2016; Rolhauser *et al.,* 2023).

Succulent *Sedum* plants, which have a lower water use than many herbaceous perennials (Kemp *et al.,* 2019; Vaz Monteiro *et al.,* 2017), have been found to facilitate the growth of other plant species in various conditions. *Sedum album* has reduced substrate temperature by 5-7°C during the summer, which enabled herbaceous plants *Agastache rupestris* and *Asclepias verticillata* to increase their growth in water deficit conditions (Butler & Orians, 2011), and also increased soil moisture availability when paired with plants of different growth forms including erect plants and shrubs Lavender and Rosemary (Matsuoka *et al.,* 2019 & 2020). The facilitative effects were not found when *Sedum* was paired with similar prostrate growth forms, as potentially the carpet spread of both plants induced competition (Matsuoka *et al.,* 2019). Combinations of different growth forms, including succulents, grasses and forbs resulted in forbs aiding the establishment of grasses (Chell *et al.,* 2022). In another study looking at plant establishment and growth on 34 green roofs in Paris over 3 years, cultivated plant species facilitated the growth of less tolerant spontaneous colonisers during environmental stresses encountered on a green roof such as high winds, reduced water availability, and sun and heat exposure (Muratet *et al.,* 2024). Companion planting can also result in increased pollinator attraction, rather than specifically changing growing conditions, for example growing strawberries with *Borago officinais* attracted a greater range of pollinators for the strawberries, which led to increased yield and quality of the fruit produced (Griffith-Lee *et al*., 2020).

1.7.2 Planting combinations for ecosystem service delivery

Planting combinations of perennial plants have also been used to great effect at optimising ecosystem service delivery, particularly in the context of green roofs (Leotta *et al.,* 2023). MacIvor *et al.* (2018) found that increasing the phylogenetic diversity of a planting scheme (using *Sedum* and perennials) on eight green roofs in Toronto led to a more diverse vegetative canopy structure and greater surface temperature reductions in the summer. Several green roof studies have found that mixed planting, usually combinations of forbs, succulents, and grasses, rather than certain monocultures provided greater ecosystem service delivery for rainwater capture and surface cooling. For example, grasses, *Sedum* and forbs in combination increased evapotranspiration rates and rainfall retention in three locations in Canada (O'Carroll *et al.,* 2023), and increased coverage and visual appeal (particularly during drought) in the UK (Nagase & Dunnett, 2010) and Australia (Chell *et al.,* 2022). A combination of grasses and forbs provided greater runoff reduction compared to *Sedum* on a green roof trial in Illinois (Ksiazek-Mikenas *et al.,* 2023), and combinations including succulents, forbs, graminoids and a creeping shrub provided greater substrate cooling in Canada (Heim *et al.*, 2023). Lundholm *et al*. (2010) found that mixing 3-5 life forms including forbs, grasses, and succulents, optimised several ecosystem services at once (rainfall capture, evapotranspiration rate, and surface temperature reductions). Mixed planting with a high diversity in leaf thickness and root length density led to the greatest substrate cooling, with the different leaf thickness filling gaps and increasing substrate coverage compared to other planting combinations (Heim *et al.,* 2023). Xie *et al.* (2018) found that species richness was not the main determinant of increased ecosystem service potential, but more specifically the traits of the combined plants made the greatest difference, with four key canopy traits - leaf area, specific leaf area, leaf dry matter content, and plant height, providing ecosystem service multifunctionality, and increased soil carbon content and niche complementarity. The introduction of 'less efficient' species within planting combinations was also found to reduce the overall runoff retention on green roof planting beds (Dunnett *et al.,* 2008; Nagase & Dunnett, 2012).

Within a garden planting bed, mixes of herbaceous plants (*Althea rosea* and *Rudbeckia hirta*) with deciduous shrubs (*Elaeagnus angustifolia* and *Colutea persica*) could decrease substrate temperature the most in summer and also increase substrate moisture content compared to herbaceous or shrub species alone (Nazemi Rafi & Kazemi, 2021). Within a green façade, allowing two ivy taxa to climb the wall together provided better thermoregulation and higher invertebrate abundance compared to using single species (Salisbury *et al.,* 2023; Thomsit-Ireland *et al.,* 2020). Planting design on a green wall also found that increasing the heterogeneous topography using *Buxus* plants increased particulate matter capture, with the mix of tall and short plants increasing airflow turbulence and therefore particulate matter accumulation on the plant leaves (Weerakkody *et al.,* 2019). Although this example is not using mixed planting types or species, the change in layout heights, which would also occur using mixed planting species, improved pollution mitigation and has the potential to be applied to other service provision as well.

1.8 People's preferences for garden plants

The aesthetic experience gained from a plant or garden falls under the category of cultural ecosystem services, which are nonmaterial benefits from ecosystems including 'spiritual enrichment, cognitive development, reflection, recreation, aesthetic experience and creative inspiration' (UK National Ecosystem Assessment, 2014). Aesthetically pleasing planting benefits mental and physical health, resulting in prevention or reduction of stress (Cervinka *et al.,* 2016; van den Berg *et al*., 2014; Young *et al.,* 2020), better mood and reduction in incidences of depression (Grahn & Stigsdotter, 2010), relaxation and mental restoration (Chalmin-Pui *et al.,* 2019; Hidalgo, 2021; Hoyle *et al.,* 2017a), and improved self-esteem and confidence (Cammack *et al.,* 2002; Eum & Kim, 2016). Planting can provoke positive or negative emotions depending on planting preferences of the individual (Berger *et al.,* 2022), with some planting designs eliciting feelings of happiness or excitement (Hoyle *et al.,* 2017a).

Plant traits such as leaf hairs can aid with delivery of specific ecosystem services including rainfall runoff reduction, air and substrate cooling, and pollution mitigation (Blanuša *et al.,* 2013; Kemp *et al.,* 2019; Weerakkody *et al.,* 2018a). However, a number of other traits influence people's aesthetic preference for the planting. Foliage type and colour, plant shape, the colour of flowers, and fragrance has all been shown to have an influence on people's preferences (Kendal *et al.,* 2012). Flower colours are a strong influencing factor for plant preference (Hansen & Alvarez, 2010) and have been found to positively aid psychological wellbeing (Haviland-Jones *et al.,* 2005). Blue flowers induce feelings of relaxation or reduce stress in people, and warm colours such as orange make people feel positive, whilst white can cause both relaxation and positivity (Zhang *et al.,* 2023). In another study with 1411 visitors to UK public gardens, most participants preferred colourful flowers (Hoyle *et al.,* 2017a). Preference for colourful planting in turn was correlated with their perceived restorative effect on people and perceived benefit of those colourful species for insect biodiversity (Hoyle *et al.,* 2017b). Focusing on foliage colour as another example of how plant aesthetics can sway preference, several studies have found that people perceive green leaves as healthy, that both green and red-leaved plants elicit positive responses, and that purple, yellow and orange-brown foliage is disliked overall (Kaufman & Lohr, 2004 & 2008). Green plants can also lead people to perceive the environment as more comfortable and restorative (Hoyle *et al.,* 2017a), especially compared to variegated foliage that includes red or white (Elsadek & Fujii 2014). Grey coloured foliage was shown to elicit a mixed response (Kendal *et al.,* 2012). With lightly coloured leaves also linked with cooling ecosystem services (Van Monteiro *et al.,* 2016 & 2017) selecting plants based on their foliage colour would in this instance have an impact on more than just the design of a garden space.

Aesthetics have been found to be one of the most important aspects influencing garden design (Hanson *et al.,* 2021; Hoyle *et al.,* 2017b). Restorative effects for people have been correlated with the increased number of plant species in a garden (Young *et al.,* 2020), however this does not automatically mean that the garden designs with the greatest number of plants, or designs found to produce health benefits for people, are preferred by everyone. A recent survey found exotic gardens were popular in the UK but cottage gardens were less popular despite being found to be most restorative (Hoyle, 2021). Significant associations have also been found between biodiversity or nature and self-estimated mental health (Southon *et al.,* 2018), and informal or naturalistic garden designs have a stronger potential to provide restoration than formal gardens (Twedt *et al*., 2016). However, manicured or formal roof gardens containing neatly clipped turf were more popular among 135 study participants than meadow roofs in Japan despite the latter benefitting biodiversity more; there was a preference for designs that gave the impression of human intervention (Nagase & Koyama, 2020). Planting style can also be influenced by the perceived 'nativeness' of the planting used in a garden. In the UK, the majority of people surveyed by Hoyle *et al.* (2017b) were accepting of non-native and exotic planting but this increased when the planting was also known to be better adapted to climate change conditions than UK native planting. In Australia, however, their native planting garnered both strong positive and negative responses when participants were surveyed, with the plant traits (such as leaf width, foliage colour, flower size, drought tolerance) influencing individual preferences (Kendal *et al.,* 2012).

Despite garden design aesthetic preferences, there are many other factors influencing overall domestic gardens' style, including household income, cultural backgrounds, physical site conditions such as rainfall or soil type, and how people would like to use their garden (Cameron *et al.,* 2012; Cameron, 2023; Kendal *et al.,* 2012; Peterson *et al.,* 2012). Psychological factors including what a person considers beautiful is important for overall design outcome, and research suggests an appealing garden is an important goal for many people (Stobbelaar *et al*., 2021). A desire for formality within garden design has also been linked with an individual's need for structure (also referred to as a Personal Need for Structure), which results in more manicured garden styles as people feel the need for control within the landscape (van den Berg & van Winsum-Westra, 2010). Expanding beyond individual gardens, cultural expectations are influential, and how your garden is 'expected' to look in a given area can result in garden design styles being very similar at a neighbourhood scale (Doll *et al.,* 2023; Francis, 2018; Minor *et al.,* 2016; Peterson *et al.,* 2012; Stobbelaar *et al*., 2021). Cues to care are also important, with neater gardens associated with well cared-for spaces that meet a common expectation of maintenance standards, which is not achieved with wild or naturalistic gardens (Hostetler, 2021). Expectations from others, plus a lack of time or skill to undertake garden maintenance has led to garden plants replaced by impervious surfaces, and the use of artificial turf (Brooks & Francis, 2019; Francis, 2018; Simpson & Francis, 2021). This meets the cultural expectation for a 'good' lawn in the UK (and Europe and the USA) and contributes to a neat and tidy garden, but as it imitates vegetation is does not provide any of the benefits living plants can provide (Brooks & Francis, 2019; Francis, 2018; Robbins & Sharp, 2003; Zhang *et al.,* 2015). The concern with the increased installation of artificial turf and paving, is that pressure from expectations, and a reluctance to accept weeds or naturalistic garden styles over formal ones, may continue to result in gardens with reduced vegetation and artificial replacements masquerading to meet neighbourhood standards.

However, education on environmental choices and the impact of climate change can lead to increased willingness by people to change their gardening and planting preferences (Egerer *et al.,* 2021; Hoyle, 2021; Liu *et al*., 2020a; Spence *et al*., 2011; Webster *et al*., 2017; Wong-Parodi & Berlin Rubin, 2022). When questioned on implementing more environmental gardening practices it was found that both aesthetics and education played an important role (Royal Horticultural Society, 2021), although the visual appeal of a plant has also been found to be one of the main facilitating factors enabling people to value a plant's ecosystem service provision (Frantzeskaki, 2019) so aesthetics could be an enabling factor to help environmentally improve gardens. Environmental gardening has also been found more acceptable if the results are aesthetically appealing (Hanson *et al.,* 2021; van den Berg & van Winsum-Westra, 2010). Egerer *et al.* (2019) found only 30% of Australian gardeners surveyed were willing to change their plant selection in response to climate change, due to aesthetic preferences, but were willing to change watering practices. However, environmental practices were more likely to be adopted when education was provided with xeriscape design significantly more likely to be adopted by homeowners in southern Spain that had prior knowledge, with those unwilling to change citing lack of knowledge as the reason why (Fernández-Cañero, *et al.,* 2011). When provided with environmental education manicured garden design and 'cues to care' mentioned earlier became less important (Hostetler, 2021).

1.8.1 The psychology of decision-making

To influence pro-environmental (planting) choices, the way people undertake decisions and adopt particular behaviours needs to be understood. Two theories have been used in several studies on drivers of behaviour change, most recently to reduce food waste behaviours (Birau & Faure, 2018; Graham-Rowe *et al.,* 2015; Neubig *et al.,* 2020; Williams *et al.,* 2012). The Theory of Planned Behaviour (Ajzen, 1991) and the Behavioural Change Model (De Vries *et al.,* 2003) both state that decision-making is influenced by individual intent. Factors influencing whether a person will undertake behavioural change include 1. what the individual perceives as 'normal' or regular behaviour, 2. their attitude towards the behaviour (positive/negative), and 3. the degree the individual feels they have the ability to undertake that changed behaviour (Ajzen, 1991; de Leeuw *et al.,* 2015; De Vries *et al.,* 2003). Social influences or the quality of information messaging surrounding behaviour can also have a positive or negative effect on the outcome (Birau & Faure, 2018; Cialdini, 2003; De Vries *et al.,* 2003; Jiang *et al.,* 2024; Schwartz, 1973; Stobbelaar *et al*., 2021). Furthermore, perceptions of so called 'normal' or regular behaviour, can be categorised into descriptive norms and injunctive norms (Adu-Gyamfi *et al.,* 2022; Ajzen, 1991; Birau & Faure, 2018; Cialdini, 2003; Neubig *et al.,* 2020; Samus *et al.,* 2023). Descriptive (or personal) norms describe what people would typically do. Conversely, injunctive (or subjective) norms represent what people feel they ought to do, and that this behaviour is externally expected by others and could lead to approval or disapproval (Ajzen, 1991; Birau & Faure, 2018; Cialdini, 2003; Neubig *et al.,* 2020). For subjective or injunctive norms, how other people perceive our actions is a significant motivating factor (Birau & Faure, 2018; Cialdini, 2003; De Vries *et al.,* 2003). However, for descriptive norms, these can be viewed as acceptable even if they are negative behaviours or have negative outcomes, such as littering, if people feel that the majority also undertake this behaviour (Birau & Faure, 2018; Cialdini, 2003).

Environmental studies of litter or food waste reduction show that utilising these norms has influenced sustainability outcomes or practices (Cialdini, 2003; Neubig *et al.,* 2020). For example, advertisements to promote reduced littering were more successful when the images contained a clean environment rather than one with evidence of littering, as the latter unintentionally cemented littering as a descriptive norm despite it being a negative behaviour (Cialdini *et al.,* 1990). Using the descriptive norm to improve outcomes has also worked to encourage recycling (Cialdini, 2003) and reduce food waste at restaurants and at home (Birau & Faure, 2018; Neubig *et al.,* 2020).

1.8.2 Framing information to encourage pro-environmental behaviours

Literature on improving environmental practices (Birau & Faure, 2018; Cialdini, 2003; Kazemi *et al.,* 2023; Graham-Rowe *et al.,* 2015; Neubig *et al*., 2020; Phillips *et al.,* 2023; Sonntag *et al*., 2023; Stobbelaar *et al*., 2021) suggests that there are three main ways in which information intended to change people's actions is presented. These are:

1. System knowledge, which outlines the basic principles of the environmental problem.
2. Action-related knowledge, which includes how to potentially solve the environmental problem with behavioural change.
3. Effective knowledge, which highlights the resulting positive environmental benefits of the behaviour change (Frick *et al.,* 2004; Nuebig *et al.,* 2020) (Figure 1.1).

The latter two groups are key to improving pro-environmental choices and have been found to have a direct effect on outcomes, whereas system information alone has an indirect effect but can significantly influence action-related outcomes (Frick *et al.,* 2004; Heo & Muralidharan, 2019; Liu *et al.*, 2020a; Reynolds *et al.,* 2019; Samus *et al.,* 2023; Williams *et al.,* 2012).

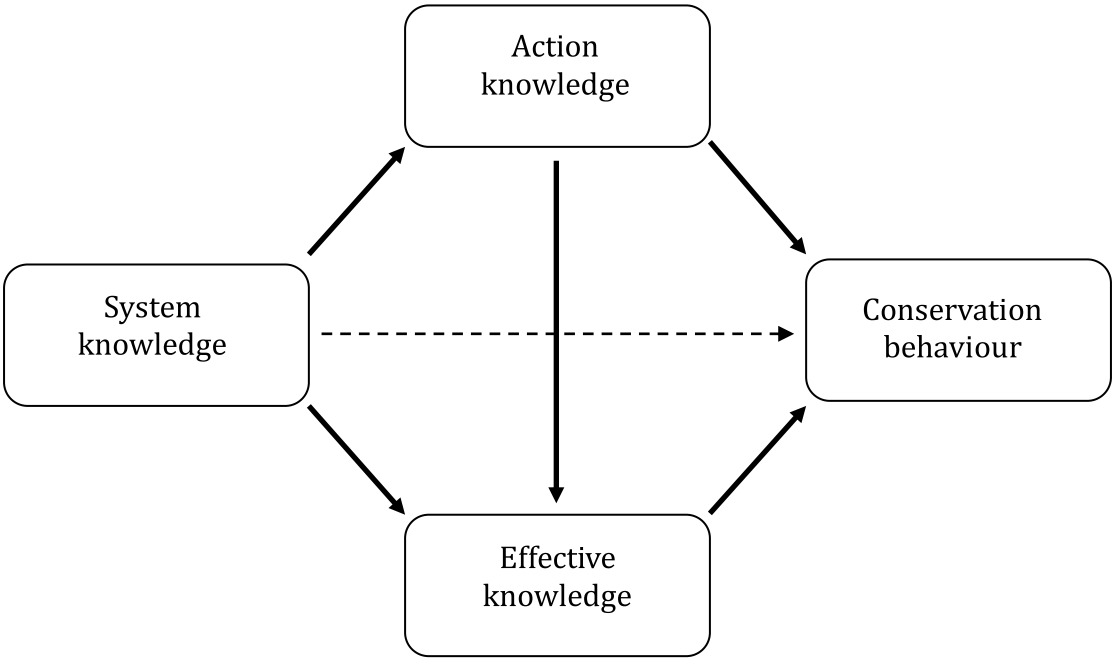


Figure 1.1: The Knowledge Structure Model, adapted from Frick *et al.* (2004). Solid arrows indicate direct influences. The dashed arrow indicates indirect effect.

This has been found with food waste studies, in which individual participants or households provided with action-related information (information and recommendations for how to correctly store food and recycle packaging) had significantly reduced intentions to waste food compared to control groups (Neubig *et al.,* 2020; Williams *et al.,* 2012). Focusing on urban greening, studies found pollinator-friendly seed purchases significantly increased (by 82%) when the environmental benefits information was prominent at the point of purchase, which was absent in control groups (Lange *et al.,* 2022). Furthermore, green infrastructure solutions (such as green facades and roofs, street trees, etc.) were viewed more favourably by neighbourhood residents in two different European surveys (Rotterdam, n = 200, Derkzen *et al.,* 2017; Brussels, n = 339, Phillips *et al.,* 2023) when their benefits (e.g. rainwater capture/flood mitigation, summer cooling) were emphasised compared to those provided with no information (Derkzen *et al.,* 2017; Phillips *et al.,* 2023).

1.8.3 Promoting positive behavioural outcomes

In addition to the type of information that could alter behavioural intentions, the way the information is framed can have positive or negative outcomes, depending on how people perceive it. Providing too much negative environmental information can result in worse environmental behaviours or no behavioural change, whereas highlighting the benefits of the behaviour has been shown to result in improved outcomes (Birau & Faure, 2018; Neubig *et al.,* 2020; Stobbelaar *et al*., 2021). The Theory of Planned Behaviour indicates that an important determinant of positive behaviour is whether the person feels capable of undertaking a specific behaviour (Ajzen, 1991). Consequently, framing environmental problems as easy to overcome leads to greater adoption of new, favourable, practices (Ajzen, 1991; Birau & Faure, 2018; Neubig *et al.,* 2020; Stobbelaar *et al*., 2021). Unintentional overemphasis on the normality of negative behaviour can lead to people denying their own responsibility (Birau & Faure, 2018). Additionally, messages that directly blame people for an outcome, such as increased food waste, can cause people to consider it more difficult to improve their behaviour because they feel the task is now more challenging to undertake and they are incapable of managing it (Birau & Faure, 2018; Cialdini, 2003). There is also a clear link between a positive attitude towards an intention and a greater probability of undertaking that behaviour (Neubig *et al.,* 2020). Moreover, stipulating the outcome benefits in addition to system knowledge can improve sustainability behaviours, and a recent study found emphasising the positive influence planting can have on flood reduction and drawing a link between flooding, paving, and vegetation encouraged greater positivity towards urban greening (Stobbelaar *et al*., 2021).

1.9 Research scope

The review of the literature indicates that perennial plants have the potential to provide runoff reduction ecosystem services, and this has been demonstrated in green roof and rain garden experiments (sections 1.4.1 and 1.4.2). However, both of these green infrastructure types create stressful growing conditions that not all plants can survive in, with green roofs being exposed to wind and extremes in temperature, and rain gardens frequently flooding, therefore results from these might not be transferable to a domestic garden setting. In addition, green roofs and rain gardens presently occupy smaller footprints in urban areas compared to domestic gardens, so their impact, however positive, might be limited. Domestic gardens in the UK context occupy a larger area and have a larger planting palette to utilise than rain gardens or green roofs, and there are potentially more plants that could be used to provide a range of ecosystem services. UK gardens, however, are also increasingly exposed to periods of heavy rainfall and flash flooding. That makes investigation into plant survival in waterlogged conditions and potential ecosystem service provision to alleviate surface water accumulation necessary and practically relevant.

Inferences can be made from the perennial plants used in other forms of green infrastructure, with previous research showing that plants with higher transpiration rates, larger leaf area, or hairy leaves can reduce runoff more efficiently than other plants or unvegetated surfaces (section 1.5). One of the aims of this research is to determine if this is also the case for a range of popular perennial garden plants. In chapter 3, plants' transpiration rates and stomatal conductance will be monitored over a period of substrate drying and exposure to different potential UK summer temperature scenarios.

The results of chapter 3 will provide baseline information on plants' physiological function (including transpiration rates) under a range of temperature scenarios. This will then be used in chapter 4 to combine plants with differing transpiration rates to investigate the impact of individual and combined planting on rainfall runoff reduction. With the exception of a small number of studies in a green roofs' context on companion planting or facilitation, there is limited research on the outcomes of combining plants for ecosystem service provision. Chapter 4 therefore aims to quantify whether combining plants with different leaf traits and transpiration rates can improve runoff reduction in a model garden setting.

In chapter 5, testing the value of garden plant combinations for survival and growth under stressful conditions will be applied to plant pairs with the aim to determine whether plants of high and low transpiration rates are able to tolerate short-term subtotal flooding and facilitate each other's growth and survival. Waterlogging tolerance and runoff reduction service provision are intrinsically connected, particularly in a domestic garden setting when plants are expected to survive the former and potentially provide the latter, however previous studies have rarely combined the two. Taking this approach and understanding plant pairings and their tolerance to waterlogging, as well as runoff reduction by rainfall within chapters 4 and 5 will provide a more rounded picture of how these plants might behave in a garden.

Previous research on people's planting preferences is extensive, particularly given that the aesthetics of a plant is linked with the delivery of cultural ecosystem services (section 1.8). Plant traits including foliage type have been linked with influencing people's plant preferences, therefore understanding this and how to encourage people to select plants for their environmental benefits - in addition to aesthetics - could be useful for improving the runoff reduction service provision of gardens. Chapter 6 will therefore survey participants with the aim to understand whether environmental information, or information and planting recommendations, could influence people to change their plant and planting preferences in favour of plants with traits that aid in runoff reduction.

1.9.1 Research aims

The key aims of this research were to understand 1. how to maximise rainfall runoff reduction ecosystem service delivery in a domestic garden using perennial plants, and 2. people's willingness to choose garden plants with environmental services' delivery in mind.

This would be achieved using plants (and their combinations) with greater potential for canopy rainfall retention (via evergreen or hairy leaves), and high evapotranspiration rates, which could improve the soil's capacity for rainfall storage. Additionally, a survey to test the potential of trait-based plant information to aid in plant selection of more environmentally beneficial garden plants will be carried out.

1.9.2 Context of experimental setup and plant selection

This research investigates plant traits, plant combinations, and people's preferences for plants, to identify perennial plants able to provide rainfall runoff reduction in a domestic garden setting. Previous research has mostly focused on using perennial plants for stormwater management service delivery in rain gardens or green roof settings (section 1.4), and this research using popular garden plants will be comparable to how these plants could behave in a domestic garden planting bed. Climate change has been affecting conditions for gardeners in the UK (IPCC, 2021; Kendon *et al.,* 2023; Webster *et al.,* 2017), with more erratic precipitation in summer and winter that can lead to both drought and waterlogging conditions (Webster *et al*., 2017), which can be stressful for some garden plants. The gardening media has championed several plant species for their ability to withstand drought and heat during the UK summer heat waves (Beth Chatto's Plants & Gardens, 2022a & 2022b; Wallington, 2022), although recent studies have also found that many of those 'drought-tolerant' plants, including herbaceous prairie species, are also able to tolerate increased moisture and even waterlogging (Bortolini & Zanin, 2019; Nasrollahpour *et al.,* 2022; Yuan & Dunnett, 2018). Previous research has identified plants with traits including leaf hairs and higher evapotranspiration rates as better able to aid with rainfall capture and runoff reduction (Kemp *et al.,* 2019; Lundholm *et al.,* 2010; Schrieke & Farrell, 2021; Vaz Monteiro *et al.,* 2017). Based on that context, six perennial plant species that all prefer full sun, well-drained growing conditions, and are all popular UK garden plants were selected. Prior research from the University of Reading indicated that one plant - *Stachys byzantina* - could already provide rainwater runoff reduction and cooling services (Blanuša *et al.,* 2013; Kemp *et al.,* 2019; Vaz Monteiro *et al.,* 2017) and was therefore chosen for comparison with other species. The plants had different growth forms, leaf shapes and surfaces, and were evergreen and deciduous, allowing comparison of a wide variety of perennial types commonly found in domestic gardens.

Experiments were carried out to enable investigation of plants as individuals and combinations, the latter of which used pots and model gardens. Experiments were conducted in controlled glasshouse conditions, or outside in the grounds of the Crops and Environment Laboratory (CEL) at the University of Reading in purpose-built model gardens. A peat-free growing medium was used for all experiments.

This research sits within a wider context of ecosystem service delivery and plant physiology. These experiments will be setup at the scale of individual plants up to combinations of nine plants in a model garden planting bed, and will investigate the extent of evapotranspiration of individual plants. Undertaking the research in this way enables close monitoring of the plants for individual physiological changes, and measurement of the plants at a level of detail to understand how their stomata react in different conditions and when their stomata are triggered to close due to waterlogging stress, which would be difficult to achieve on a larger scale. The ability of plants to retain water in their canopies or remove water from the substrate by transpiration will be measured on a small 'model' scale, with relatively small water quantities being applied and measured. The absolute value of runoff reduction service provision by these plants in a model garden context will be slight, particularly compared to trees or shrubs, or larger green infrastructure types such as rain gardens. However, when this research is scaled up to encompass greater areas, for example the large herbaceous planting beds found in bigger gardens, or the trend for swathes of perennial planting seen in designs by Piet Oudolf, Nigel Dunnett and James Hitchmough (section 1.7) the impact of these plants would increase. Domestic gardens account for approximately 30% of UK urban areas (Cameron *et al.,* 2012; Chalmin-Pui *et al.,* 2021a) and therefore the potential runoff reduction service provision of these plants could impact a relatively large area of most towns and cities. This research is informed by previous plant physiology research by Davies, Dodds, and Stoll to name a few (Davies *et al.,* 2002; Dodds *et al.,* 2007; Stoll *et al.,* 2000), planting design, ecology and companion planting by Grime, Rainer and West, and Butler and Orians (Butler & Orians, 2011; Grime, 1974; Rainer & West, 2015) and will sit alongside research on the ecosystem service delivery of individual plants or small combinations undertaken by Blanuša, Cameron, Dunnett and Lundholm (Blanuša *et al.,* 2013; Cameron *et al.,* 2014; Dunnett *et al.,* 2008; Lundholm *et al.,* 2010). It will hopefully then inform larger scale future research including plant ecology and modelling studies, as well as planting and garden design and urban planning.

Chapter 2

General materials and methods

This chapter will first provide an overview of the plants and equipment, and then a section on methods development that was necessary to undertake prior to experimentation.

2.1 Plant material

The plants used in this thesis (Table 2.1; Figure 2.1) were selected based on their contrasting traits, their contrasting potential or confirmed ecosystem service delivery, and their common popularity with the general public. Plant lists were compiled based on sales figures from five nationwide garden centre groups (unpublished data) to determine which plants the public bought frequently, as well as Royal Horticultural Society popular perennials lists. In addition to this *Salvia* 'Nachtvlinder', *Verbena bonariensis, Pseudodictamnus mediterraneus,* and *Erysimum* 'Bowles's Mauve' were given the Royal Horticultural Society award for garden merit, and *Erysimum* was also shortlisted for Chelsea Plant of the Centenary award. Genus title is used in this thesis as an abbreviated title and does not indicate the performance of all memebers of the genus. All plants selected have similar flowering periods, prefer full sun and moist to well-drained growing conditions, and are visited by a range of pollinators (Royal Horticultural Society, 2019).

Plant	Leaf traits	Reported services	Chapters and experiments	Supplier
Stachys byzantina	Evergreen; Large flat; Dense hairs	Localised stormwater management[3-6]; High evapotranspiration rate[3-7]; Flood tolerance[8]	Experiments 1 and 2, Chapters 3 and 6 (2021, 2023)	Provender Nurseries (Swanley, Kent, UK) in February 2021.
***Salvia* 'Nachtvlinder'**	Semi-evergreen[1]; Small; Hairless	Related *Salvia* species provided localised stormwater management[4] and flood tolerance[8]	Experiments 1 and 2, Chapter 3 (2021)	
***Erysimum* 'Bowles's Mauve'**	Evergreen; Narrow; Hairless		Experiments 1, 2, 3, 4, 5, 6, and 7, Chapters 3, 4, 5 and 6 (2021, 2022, 2023)	
***Oenothera lindheimeri* 'Whirling Butterflies'**	Deciduous; Narrow; Small hairs[2]	Related *Oenothera* species showed short-term tolerance to cyclical flooding[9] and localised stormwater management[10]	Experiments 1, 2, 3, 4, 5, 6, and 7, Chapters 3, 4, 5 and 6 (2021, 2022, 2023)	
Verbena bonariensis	Deciduous; Narrow; Hairless	Related *Verbena* species provided localised stormwater management[10]	Experiments 1, 3, 4, 5, 6, and 7, Chapters 3, 4, 5 and 6 (2022, 2023)	Manor Farm Nurseries (Northamptonshire, UK) in Autumn 2022.
Pseudodictamnus mediterraneus	Evergreen; Small round; Dense hairs		Experiments 1, 3, 4, 5, 6, and 7, Chapters 3, 4, 5 and 6 (2022, 2023)	

Table 2.1: Summary of experimental plants. Trait information and official names were taken from the Royal Horticultural Society.

[1] Advice from Principal Horticultural Advisor, Royal Horticultural Society;
[2] Baraldi *et al.,* 2019; [3] Blanuša *et al.,* 2013; [4] Kemp *et al.,* 2019; [5] Vaz Monteiro *et al.,* 2016; [6] Vaz Monteiro *et al.,* 2017; [7] Cameron *et al.,* 2014; [8] King *et al.,* 2012; [9] Yuan & Dunnett, 2018; [10] MacIvor *et al.,* 2018.

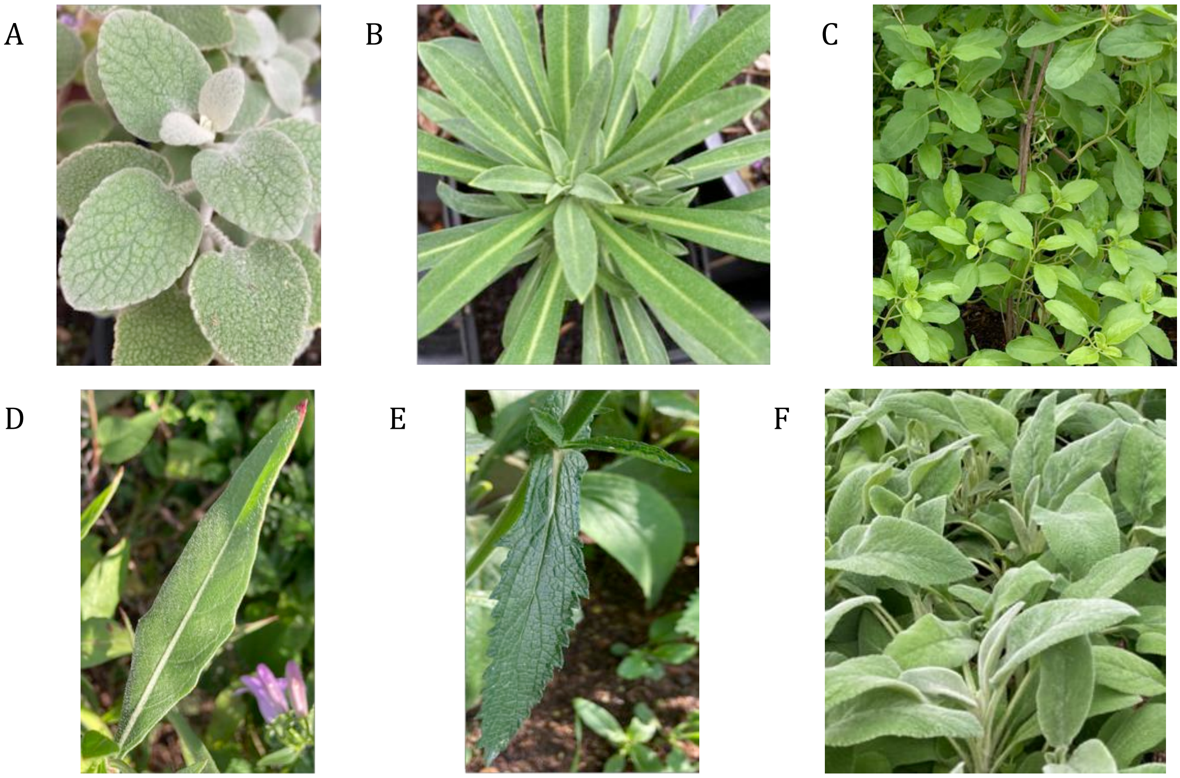


Figure 2.1: Photographs of plant foliage. A) *Pseudodictamnus*, B) *Erysimum*, C) *Salvia*, D) *Oenothera*, E) *Verbena*, F) *Stachys*.

Specifically, the selected group of plants allows a comparison of plants with evergreen versus deciduous foliage, leaf hairs (trichomes), and high versus low transpiration rates, which are traits that have been shown to explain variation in the provision of several ecosystem services including runoff reduction, air and substrate cooling, and air pollution mitigation. A higher evapotranspiration rate has been linked with greater runoff reduction and cooling services due to the increased water use removing water rapidly from the substrate (Berreta *et al.,* 2014; Kemp *et al.,* 2019; Stovin *et al.,* 2012). This has been particularly evident in green roof studies in comparison to lower transpiring *Sedum* plants (Blanuša *et al.,* 2013; Kemp *et al.,* 2019; Vaz Monteiro *et al.,* 2016 & 2017). Evergreen and deciduous foliage have been found to provide different rates of rainfall capture depending on the time of year, with evapotranspiration rates higher for deciduous compared to evergreen plants in spring and summer (Peters *et al.,* 2011; Tiwary *et al*., 2016) but some evergreen trees providing greater transpiration rates in April and November compared to deciduous plants and therefore reducing runoff at a time of year when deciduous plants are dormant (Peters *et al.,* 2011). Broadleaf evergreen trees also provide greater retention of rainfall within the canopy compared to deciduous species therefore delivering annual canopy retention (Xiao & McPherson, 2002). The presence of leaf hairs was shown in previous studies to enable capture of particulate matter pollution on the leaf surface (Blanuša *et al.,* 2020; Shao *et al.,* 2019; Weerakkody *et al.,* 2018a), reduce the albedo effect/provide higher reflectance that reduces leaf, soil and air temperatures (Blanuša *et al.,* 2013; Cameron *et al.,* 2014; Vaz Monteiro *et al.,* 2016 & 2017), and trap moisture therefore retaining rainfall within the canopy and reducing runoff (Kemp *et al.,* 2019). Water retention and other traits investigated in this thesis will likely vary among varieities and species as well as genus.

Following initial experimentation in 2021 on plant evapotranspiration rates and rainfall retention both *Salvia* 'Nachtvlinder' and *Stachys byzantina* were removed from further experiments with the focus on *Oenothera* and *Erysimum* due to their contrasting results. *Verbena bonariensis* and *Pseudodictamus mediterraneus* were introduced as additional plant varieties in 2023 to expand the investigation to include plants that are anecdotally reported to be tolerant of drought and heat, particularly in response to the 2022 summer heat wave, from which there were numerous articles in the media indicating that these plants would be suitable in UK gardens as we become further impacted by climate change (Beth Chatto's Plants & Gardens, 2019, 2022a & 2022b; Brown, 2022; Wallington, 2022).

Plants were paired in experiments due to their contrasting seasonal foliage and other traits such as leaf hairs or transpiration rates. For all paired experiments the combinations were *Salvia* and *Stachys, Erysimum* and *Oenothera*, and *Verbena* and *Pseudodictamnus*. *Oenothera, Erysimum, Stachys* and *Salvia* were repotted into larger containers using a peat-free growing medium before being used in chapter 3. It was observed that roots on some of the plant varieties purchased in 2021 were pot-bound and this was impacting some of the experimental results. As a result, all plants used in experiments 4, 5, 6, and 7 (chapters 4-5) were grown from cuttings in the Controlled Environments glasshouses at the University of Reading.

2.2 Experimental measurements

2.2.1 Substrate moisture content

Substrate moisture content (SMC) was measured in all experiments except for experiment 3, using a SM300 substrate moisture sensor connected to a HH2 Moisture Meter (Delta-T Devices Ltd., Cambridge, UK). In experiments 1, 2, 6 and 7, two measurements per pot were taken to give an average, and experiment 4 and 5 had five readings across each miniature model garden to give an average. Measurements were taken daily during experimentation.

2.2.2 Plant dimensions

Plant height and width were recorded as potential covariates in every experiment. Initial dimensions were taken at the beginning of every experiment and at the end before destructive harvests. The plant height was recorded as the measurement from the substrate layer to the end of the tallest stem, and two cross-section widths were also taken. In experiments 3, 4 and 5 individual plant heights were recorded and averaged per model garden. As plants grew together and overlapped in the model gardens individual widths were not possible so width was taken as two cross sections of plant growth across each garden container, regardless of whether the plants grew within the container or over the edges of it. In experiments 6 and 7 when plants were in pairs within a container the heights and widths of each individual plant in the container were recorded.

2.2.3 Leaf area

Leaf area (LA) was used to standardise water loss per unit of leaf surface area. Leaf area was measured using the WinDIAS 3 Image Analysis System (Delta-T Devices, Cambridge, UK). All leaves were removed from a plant, weighed, and then 10% of fresh mass was processed through the leaf area scanner, which was then used to calculate 100% of a plant's leaf area. In chapter 3 (experiment 1a and 2) two plants per species were destructively harvested to obtain an average leaf area for each species, however due to increased variability in plant sizes this replication increased in future experiments. Due to the size of the plants in the outdoor model gardens in chapter 3 (experiment 3) it was not feasible to harvest everything and therefore three of each species in each monoculture were harvested, and three of each species in each mixture (six plants per garden) were harvested. In the remaining experiments in chapters 3 and 4, and all experiments in chapter 5, every plant was harvested for leaf area.

Leaf area index (LAI) was used in chapter 4 as an explanatory variable to enable leaf density to be considered for canopy retention and storage of water droplets, calculated using equation 1 below.

Equation 1:

$$\text{LAI} = \frac{\text{Total LA per tray (m}^2\text{)}}{\text{Model garden area (m}^2\text{)}}$$

2.2.4 Evapotranspiration

Daily evapotranspiration of plants in chapters 3 and 5 (experiments 1, 2, 6, and 7) was determined by measuring mass loss from the containers every 24 hours for the course of the experiment length using a CBK 32 bench check-weighing scale (Adam Equipment Ltd., Milton Keynes, UK). Mass loss was equated to estimated evapotranspiration water loss from the plant and substrate between two consecutive measurements (Blanuša *et al.,* 2009; Kemp *et al.,* 2019). Substrate surface area was the same for all plants, enabling comparison.

2.2.5 Root and aboveground dry biomass

Plant dry root mass and aboveground biomass was recorded as potential covariates or indicators of treatment impact on plant growth in chapters 4 and 5 (experiments 3-7). Once plants had been stripped for leaf area, the shoots, woody stems, and leaves, collectively known as aboveground biomass, were dried in a ventilated oven at 70°C for 72 hours and subsequently weighed using an Ohaus Pioneer Precision Balance (Ohaus, Nänikon, Switzerland).

Plant roots and substrate removed from the plant pots were lightly shaken to remove loose substrate from the 'root ball'. The 'root ball' was then submerged in a bucket of water with a fine sieve and carefully washed to remove substrate from the roots. This was completed several times, with more substrate removed with each wash. Any broken roots that were collected in the sieve were also washed and added to the dry root mass recording. Substrate initially removed in the shaking stage was also washed using a sieve to collect any broken roots. The collection of roots for each plant was then dried in a ventilated oven at 70°C for 72 hours and weighed using the same method as the aboveground biomass.

All plant roots, shoots and leaves were harvested in experiments 4, 5, 6 and 7, and leaves and shoots from three of each variety (see leaf area above) were harvested from experiment 3's outdoor model gardens.

2.2.6 Leaf stomatal conductance

Leaf stomatal conductance was used as an explanatory variable for water loss in chapters 3 and 5 (experiments 1, 2, 6 and 7). Stomatal conductance (g_s) was measured as the rate of water vapour leaving a stomatal pore using an LCpro+ infrared gas analyser (IRGA; ADC BioScientific Ltd., Hertfordshire, UK) with an external light source set at 1000 mmol m^{-2} s^{-1} to account for light variability between the measurements that were conducted during daylight hours (8-14 hr). Three fully expanded healthy leaves were randomly selected per plant. In chapter 3 the IRGA was used on all experimental plants; in chapter 5, experiments 6 and 7a used three plants per layout, and experiment 7b used two leaves per plants but four plants per layout (Table 2.2). When a leaf filled the entire chamber of the IRGA the coverage was noted at 100%, however for leaves that were too small to cover this area the approximate coverage was noted at for example 60% and measurements multiplied at analysis stage to 100% coverage rates.

Chapter and experiment	Number of leaves used for stomatal conductance measurements	Number of plants used for stomatal conductance measurements
Chapter 3: Experiment 1 - differences in plant water use	3 leaves per plant	10 plants per species
Chapter 3: Experiment 2 - impact of temperature on plant water use	3 leaves per plant	10 plants per species
Chapter 5: Experiment 6 - spring overwatering	3 leaves per plant, 18 leaves per layout (monoculture or mixed)	Both plants in each pot, 3 pots per layout (monoculture or mixed)
Chapter 5: Experiment 7a - summer short-term subtotal flooding	3 leaves per plant, 18 leaves per layout (monoculture or mixed)	Both plants in each pot, 3 pots per layout (monoculture or mixed)
Chapter 5: Experiment 7b - spring short-term subtotal flooding	2 leaves per plant, 16 leaves per layout (monoculture or mixed)	Both plants in each pot, 4 pots per layout (monoculture or mixed)

Table 2.2: Summary of stomatal conductance collection data using an IRGA, including number of leaves and number of plants data was collected from in each relevant experiment.

2.2.7 Net CO_2 assimilation rate

Net CO_2 assimilation rate was used to assess plant's photosynthesis rates in experiment 7 (chapter 5). Assimilation rate was measured using an LCpro+ infrared gas analyser (IRGA) (ADC BioScientific Ltd., Hertfordshire, UK) with the same settings and data collection protocol as described in section 2.2.6 above (Table 2.2).

2.3 Environmental conditions

Experiments were conducted at the Crops and Environment Laboratory (CEL), Whitenights Campus, University of Reading, UK (51°26'10.31" N, 00°56'31.98" W). Experiments 1, 4, 5, 6 and 7 were carried out in an unheated ventilated glasshouse to allow for data collection without weather interference. Experiment 2 was undertaken in a temperature-controlled compartment and a natural photoperiod used (details of which are in chapter 3). Experiment 3 outdoor model gardens were built on the grounds of the CEL and were exposed to outdoor weather conditions. For all experiments except for the outdoor model gardens, air temperature and relative humidity were measured every 30 minutes using a Tinytag Plus 2 Data Logger (Gemini Data Loggers, Chichester, UK), shielded from direct sunlight. Outdoor model garden temperature data was collected from the University of Reading weather station (https://metdata.reading.ac.uk/cgi-bin/climate_extract.cgi). To plan suitable days for outdoor model garden data collection (when no rain was forecast and wind speed was low (under 10 mph)) the Met Office weather app was used.

2.4 Growing medium

All plants were grown in a peat-free growing medium (SylvaGrow Multi-purpose, Melcourt, UK). The main components were coniferous bark, wood fibre, and coir. Nominal particle size range was 0-6mm, moisture content by weight was 50%, and air-filled porosity was 21%. The growing medium had a pH of 6.5, and nutrient contents of 125 mg/L of nitrogen, 80 mg/L of phosphorus, and 300 mg/L of potassium. Nutrient contents were sufficient for the first 4-6 weeks of growth. Control pots containing this growing media without plants were included in every experiment.

During many of the experiments both in containers inside, and model gardens outside, the growing medium resulted in a variety of fungi that at times hindered the experimentation. Both Melcourt and the Royal Horticultural Society confirmed the small inkcap mushrooms that grew on the containerised growing media would not impact the experiments, but a rhizotron experiment designed to investigate whether root growth differed between plants grown in monocultures or mixed-species combinations was abandoned due to fungal growth that inhibited root identification and measurement (see Figure 2.2A & B). Large, flat fungi grew in the outdoor model gardens (Figure 2.2C-E), and were believed to be feeding on the wood content of the peat-free compost. These were manually removed prior to canopy rainfall experiments, but changed the moisture content of the beds and therefore prevented evapotranspiration testing.

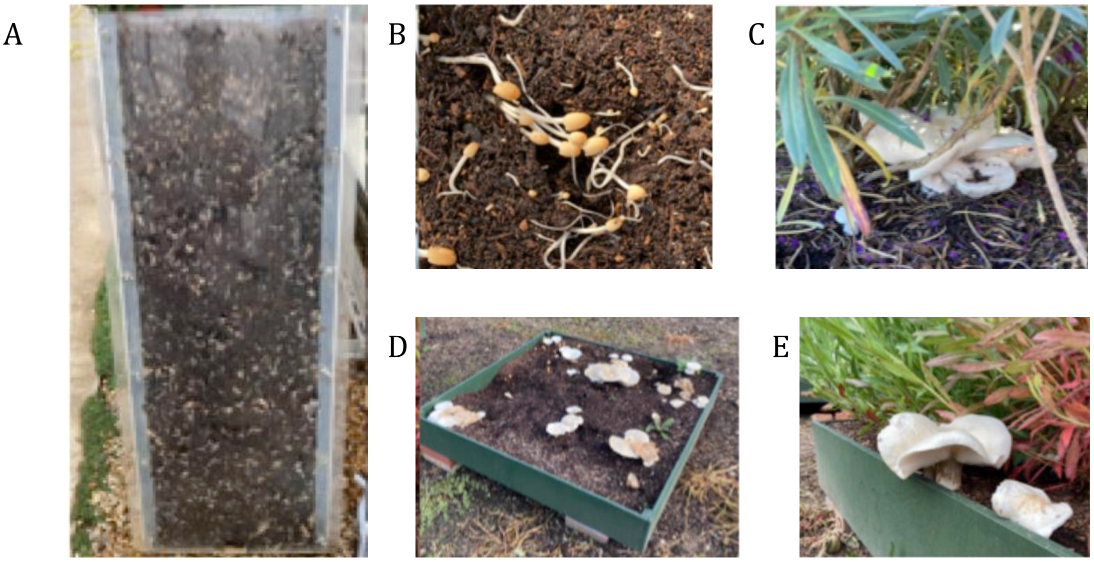


Figure 2.2: A-B) Fungal fruiting bodies growing in a rhizotron. C-E) Fungi in the outdoor model garden plots (C. *Erysimum* monoculture, D. bare substrate, E. *Oenothera* monoculture).

2.5 Rainfall applicator

To simulate natural rainfall a sprinkler applicator was used from Kemp *et al.* (2019). A Lechler 460 608 nozzle was attached to a 2 m length of hose (Tricoflex, Hozelock Ltd., Birmingham, UK), attached to an L-shaped timber structure (2.4 m high and 1 m across). Spray angle was 120°, bore diameter 2.11 mm, spray diameter at 30 psi is 1.27 m at 0.51 m in height. Flow pressure was set to 0.15 bars (15 kPa) using pressure gauges and filters to ensure consistent water flow and droplet size between replications. The rainfall spray diameter from the nozzle was approximately 190 cm. The applicator was connected to mains water supply. Raindrop size was tested in previous research and the majority (70%) of raindrop sizes were smaller than 1 mm in diameter, which was consistent with other studies, and the rain applicator was used in this setting for all experiments (Blanuša & Hadley, 2019; Kemp *et al.*, 2019).

The equipment was adapted with two main modifications. A solenoid control valve (Galcon Jewel BT 1” Valve Bluetooth Programming, Reading, UK) was added to the rain applicator for experiments 3, 4 and 5. This was installed after testing the rain applicator on plants in pots (section 2.7.3.1) found small variation in the water volume and using a programmed control valve improved uniform water output. The original wooden structure was damaged and replaced by a lightweight light stand (Calumet Air Cushioned Light Stand 3.9 m, Wex Photo Video, Norfolk, UK) for experiments 4 and 5, constructed to match the original dimensions of the rain applicator and ensure standardisation.

2.6 Experimental setup

Experiment	Chapter	Description	Data collected
Experiment 1 - differences in plant water use	3	Monitor plant water loss via transpiration and stomatal conductance using all plant varieties in individual containers	• Transpiration rate • Stomatal conductance • SMC • Leaf area • Plant dimensions
Experiment 2 - impact of temperature on plant water use	3	Monitor plant water loss via transpiration and stomatal conductance and determine the impact of temperature on plants in individual containers.	• Transpiration rate • Stomatal conductance • SMC • Leaf area • Plant dimensions
Experiment 3 - rainfall application on outdoor model gardens	4	Measure rainfall runoff volumes and retention of rainfall within the canopy of monoculture and mixed planting in outdoor model garden planting ‘beds’ in summer and winter.	• Rainwater runoff volume • Leaf area index • Plant dimensions • Aboveground dry biomass
Experiment 4 - rainfall application on miniature model gardens in the glasshouse	4	Measure rainfall runoff volumes, retention of rainfall within the canopy and plants’ evapotranspiration on the capacity to store rainfall in the substrate using monoculture and mixed planting in containers in the glasshouse in summer and winter.	• Rainwater runoff volume • Leaf area index • SMC • Plant dimensions • Root and aboveground dry biomass
Experiment 5 - rainfall application on miniature model gardens in the glasshouse - effect of pervious surfaces	4	Measure rainfall runoff volumes, retention of rainfall within the canopy and plants’ evapotranspiration on the capacity to store rainfall in the substrate using plants or pervious surfaces in containers in the glasshouse in summer.	• Rainwater runoff volume • Leaf area index • SMC • Plant dimensions • Root and aboveground dry biomass
Experiment 6 - spring overwatering	5	Investigate the impact of plant combinations and overwatering treatment on transpiration rates of monocultures and mixed planting in pots.	• Transpiration rate • Stomatal conductance • SMC • Leaf area • Plant dimensions • Root and aboveground dry biomass

Experiment 7 - spring and summer short-term subtotal flooding	5	Investigate the impact of plant combinations and short-term subtotal flooding treatment on transpiration rates of monocultures and mixed planting in pots.	• Transpiration rate • Stomatal conductance • Assimilation rate • SMC • Leaf area • Plant dimensions • Root and aboveground dry biomass
Experiment 8 - people's plant preferences survey	6	Investigate people's plant preferences using environmental information and planting recommendations to determine the impact of trait-based information and plant aesthetics on plant choice.	• Demographics • Plant preferences • Plant and environmental knowledge • Environmental concern

Table 2.3: Experimental setup and data collection summary.

2.7 Method testing and development

2.7.1 Testing alternative plant material using an IRGA

Introduction

When planning future experiments in Autumn 2022 it was decided that *Stachys* and *Salvia* would be removed from experimentation and replaced with two other plant species with the aim to introduce more plants with the same tested traits for comparison. This would enable experimentation to determine whether the trait is causing the difference in plant performance, and not the individual plant species. In October 2022 the stomatal conductance rates of six additional plant species were tested using an infrared gas analyser to determine whether it was possible to obtain gas exchange data from their leaves, and therefore their suitability for future experimentation. Between-reading variation in measurements would then be used to identify plants reliable for experiments. Once this was determined, the plants would be used alongside evergreen *Erysimum* and deciduous *Oenothera*, and therefore foliage type was also considered as part of the selection.

Methods and results

Plant species *Phlomis fruticosa, Achillea* 'Moonshine', *Pseudodictamnus mediterraneus, Verbena bonariensis, Helianthemum* 'The Bride', *Helianthemum*

'Ben Hope', and *Helianthemum* 'Fire Dragon' were selected from a plant long list. A single plant of each variety was obtained from a nursery (Hassett Plant Centre, Northamptonshire, UK; Manor Farm Nurseries, Northamptonshire, UK) and the individual plants were tested in the same 2 L pots and growing medium that they had when purchased from the nursery.

Plants were selected for their leaf traits, with focus on the presence or absence of leaf hairs, and evergreen or deciduous foliage. *Phlomis, Achillea*, *Pseudodictamnus,* and the three varieties of *Helianthemum* were all evergreen*; Phlomis, Achillea, and Pseudodictamnus* had leaf trichomes, and *Verbena* had deciduous leaves. Although *P. fruticosa* and *Helianthemum* are classified as shrubs they were included for consideration due to their small size or suitable leaf shape. Plants were also selected based for their potential to withstand drought and heat waves. All six plants prefer well-drained soil and full sun, and many are suitable for rock or gravel gardens. Following the 2022 UK heat wave, gardening media articles created lists of suitable plants to survive in these conditions and withstand drought, and *Helianthemum, Achillea, Verbena* and *Pseudodictamnus* were also selected based on this (Beth Chatto's Plants & Gardens, 2022a & 2022b). Related species of *Verbena* and *Achillea* have also been found in previous studies to provide greater stormwater retention as part of a mixed green roof planting scheme compared to *Sedum* (Ksiazek-Mikenas *et al.,* 2023; MacIvor *et al.,* 2018).

Testing was carried out on the 20th October 2022 in the CEL at the University of Reading Whiteknights campus. An IRGA with external light source was used on all plants (section 2.2.6), and plants were well watered prior to testing.

Two of the three *Helianthemum* varieties ('The Bride' and 'Fire Dragon') had leaves that were too small to clamp in the IRGA chamber, and no data was collected (data not shown). *Helianthemum* 'Ben Hope' had marginally larger leaves although these were still difficult to collect data and a decision was made after two attempts to remove this plant from the study, as it would be too challenging to use in future experimentation. *Verbena* was suitable for IRGA data collection and produced minimal variation between stomatal conductance readings. *Achillea*, with feathery grey foliage covered in small trichomes, was difficult to fix flat in the IRGA clamp, but readings were still obtained. Both *Pseudodictamnus* and *Phlomis* were suitable for IRGA use as they had flat leaves. After comparing results and ease of IRGA use, *Pseudodictamnus* and *Verbena* were selected for onward experimentation. *Verbena's* leaves were easy to use with the IRGA and there was little variability between readings. Comparing the hairy leaved plants, *Achillea* was too difficult to clamp into the IRGA, and although *Pseudodictamnus* and *Phlomis* were both suitable for IRGA data collection, as *Pseudodictamnus* is a perennial the decision was made to continue with this group of plants rather than introduce a single shrub species.

2.7.2 Porometer testing

Introduction

Leaf stomatal conductance is a key parameter to measure plant water regulation and is sensitive to moisture availability and temperature (Taiz & Zeiger, 2002; Toro *et al.*, 2019). There are two main types of instruments for collecting gas exchange data, an IRGA and a porometer, with variations in data collection and positive and negative considerations to each system. IRGAs are considered the more advanced of the two, with the ability to collect multiple variables including stomatal conductance and CO_2 diffusion at the same time (Lavoie-Lamoureux *et al.,* 2017; Toro *et al.,* 2019). Both devices are portable but IRGAs are heavy and data collection on each leaf takes longer than a porometer. IRGAs are also more expensive than porometers, and difficult to fix when problems occur, but porometers are lighter and easier to carry from plant to plant, cheaper, and faster to collect data (Toro *et al.,* 2019). Anecdotal evidence has also found porometers are not able to take readings from leaves with denser hair coverage. A comparison study by Toro *et al.* (2019) between a porometer and an IRGA consistently showed different readings on the same plants, with higher stomatal conductance readings using the porometer under water stress conditions compared to the IRGA, and the authors speculated that morphological differences in stomatal positions were a contributing factor.

A porometer reads only one side of the leaf, and it is therefore necessary to know the location of the stomatal pores to obtain readings. The number and size of stomata varies depending on plant species, and although many plants have stomata on both the upper and lower surfaces of the leaves (adaxial and abaxial respectively), some plants only have stomata on the abaxial side and this can impact using the porometer (Caird *et al.,* 2007; Driesen *et al.,* 2023; Kozlowski & Pallardy, 2002; Medrano *et al.,* 2009; Wall *et al.,* 2022). Leaf hairs can also disrupt this as they can block the porometer clamp. An IRGA clamps the leaf inside a chamber that then measures gas exchange within this space without it being necessary to know which side of the leaf has a higher concentration of stomata. This clamp also does not press down on the leaf surface within the chamber that enables it to work without leaf hairs blocking the mechanism and disrupting readings. This makes the IRGA more robust for a variety of different leaf morphologies.

Stomatal conductance data was collected using an IRGA in chapters 3 and 5 for experiments 1, 2, 6 and 7. A porometer (AP4, Delta-T Devices, Cambridge, UK) was tested to determine whether this could be used as an alternative for data collection in March 2023.

Methods and results

Plants *Erysimum, Oenothera, Pseudodictamnus* and *Verbena* (Table 2.1) were grown from cuttings and planted into individual 2 L plastic pots containing a peat-free growing medium in early March 2023. Plants were placed in a ventilated glasshouse at the University of Reading Whiteknights campus on the week commencing 21st March 2023. Temperature was not regulated. Average temperature for the week was 18.4°C inside the glasshouse, with an average minimum of 9.3°C and maximum of 27.4°C. On the day of experimentation (23rd March 2023) the average temperature was 20.2°C, with a minimum of 7.5°C and a maximum of 31.8°C. Plants were positioned in a random pattern across a glasshouse bench and watered to field capacity three days prior to porometer measurements. The leaves were tested in the porometer both adaxial side up (top of the leaf) and abaxial side up (underside of the leaf) on a range of leaf sizes, to determine the side with greatest stomatal density. The IRGA does not have a leaf side to determine and was used as recommended by the IRGA user manual. Number of leaves used for data collection is denoted in Table 2.4 below, and these vary for the porometer depending on whether it was possible to obtain any readings with the leaf in those positions. Some leaves have a low replication because the porometer was unable to fix a reading.

Pseudodictamnus, which had the most leaf trichomes of all species tested, took the longest time for the porometer to produce a reading, and both *Pseudodictamnus* and *Verbena* produced negative readings when the adaxial side of the leaf was in the porometer, which were excluded from the results. *Erysimum* produced unusually high readings using the adaxial side whilst *Oenothera* produced high readings when the abaxial side was in the porometer (Table 2.4). All results were more variable between leaves using the porometer compared to the IRGA counterparts (Table 2.4), with the exception of *Pseudodictamnus*, which had a lower standard error than the IRGA measurements from the same plant but the readings were far too low to be an accurate gas exchange rate. The *Oenothera* readings were more comparable to the IRGA when the adaxial side of the leaf was clamped in the porometer. Both *Erysimum* and *Verbena* had relatively similar stomatal conductance rates using the porometer and the IRGA (when excluding the adaxial results for *Erysimum*) and indicate the majority of stomatal openings on each of these species are located on the underside of the leaves. The range of results obtained for these four species indicate the morphology may be an influencing factor, particularly for *Pseudodictamnus*, whose leaf hairs could have prevented the porometer from clamping the leaf fully, leading to low readings. The large standard errors, or at times inability to obtain any readings from the porometer, may indicate measurement error rather than real changes in stomatal conductance rates.

Due to the varied and inaccurate data collected using the porometer, which for *Pseudodictamnus* stomatal conductance the values measured by the porometer were indicating almost closed stomata when it was environmentally unlikely that this was the case, and potentially due to the leaf hairs obscuring the equipement, and for *Oenothera* and *Erysimum* was too difficult to obtain and led to several incomplete reading attempts (data not shown), the decision was made to only use an IRGA in all experiments.

Plant	**Position of the leaf stomata in the porometer**	**Porometer stomatal conductance (mmol m^{-2} s^{-1})**	**IRGA stomatal conductance (mmol m^{-2} s^{-1})**
Pseudodictamnus	Abaxial	21.31 ± 3.35	163.33 ± 20.28
Verbena	Abaxial	217.20 ± 47.21	263.33 ± 17.64
Oenothera	Abaxial	3080.00 ± 881.82	226.67 ± 24.49
	Adaxial	339.00 ± 81.00	
Erysimum	Abaxial	185.33 ± 47.36	190.00 ± 11.55
	Adaxial	1460.00 ± 110.00	

Table 2.4: Average stomatal conductance rates of plants *Erysimum, Pseudodictamnus, Verbena* and *Oenothera* using a porometer and IRGA (± standard error). Position of the leaf in the porometer is denoted as abaxial (underside of the leaf) or adaxial (top of the leaf). The IRGA readings did not need a leaf side identified to enable use. IRGA n = 3 leaves per plant; Porometer: n = 8 (*Pseudodictamnus*), n = 5 (*Verbena*), n = 3 (*Oenothera* and *Erysimum* abaxial), n = 2 (*Oenothera* and *Erysimum* adaxial).

2.7.3 Model garden development

Prior to experimentation and data collection using model gardens and the rain applicator discussed in chapter 4, method development was trialled using plants in various design layouts and types of model gardens (summarised in Table 2.5 below). The aim of each model garden experiment was to trial a range of perennial species with varying traits, including leaf hairs and higher and lower transpiration rates (chapter 3).

Design 1 used plants in pots in configurations of monocultures, or mixed ‘chequered’ or ‘striped’ layouts in a glasshouse; Design 2 used plants in outdoor model gardens representing garden planting ‘beds’ in monocultures and mixed (‘chequered’) layouts; and Design 3 used plants in miniature model gardens in monocultures and mixed (‘chequered’) layouts in a glasshouse. Design and development are detailed in the subsequent sections. Final experimental design is detailed in chapter 4.

It was hypothesised that plants with larger leaf areas and the presence of leaf hairs would provide greater retention of rainfall within the canopy and produce less runoff. Plants with higher evapotranspiration rates, therefore higher water use, would also produce less runoff by reducing substrate moisture more and providing a greater rainfall storage capacity in the substrate before rainfall was applied. In mixed design layouts, runoff volumes would vary depending on the combination of plants with these traits.

Trials were conducted on all model gardens with the substrate either saturated or unsaturated, with the former measuring retention of rainfall within the canopies and the latter the plants’ evapotranspiration rate on the capacity to store rainfall in the substrate. Any differences in rainfall runoff produced by the plants when the substrate was saturated to field capacity would indicate rainfall was retained in the canopies of the plants and denote contribution of plant canopy and leaf traits. Differences in runoff generated from unsaturated substrate trials would indicate the contribution of the whole plant or model garden, including the contribution of the substrate to store rainfall and the plants’ evapotranspiration rates, with higher rates enabling more rapid removal of water from the substrate and restoration of the substrate water storage capacity. The aim was for all substrate moisture content for unsaturated experiments to be below 0.30 $m^3 m^{-3}$.

Model garden design	Plants used	Plant layouts	Number of plants per garden	Model garden location	Seasons trialled
Design 1: Potted plants and impact of planting design - nine individual plants in pots arranged within a tray and subjected to rainfall application.	• *Erysimum* 'Bowles's Mauve' (evergreen, hairless leaves) • *Stachys byzantina* (evergreen, leaf hairs) • *Salvia* 'Nachtvlinder' (semi-evergreen, hairless leaves) • *Oenothera lindheimeri* 'Whirling Butterflies' (deciduous, small leaf hairs)	Monocultures: *Erysimum*, *Stachys*, *Salvia*, *Oenothera*, Bare substrate Striped design: *Erysimum x Oenothera*, *Stachys x Salvia*, *Stachys x Oenothera* Chequered design: *Erysimum x Oenothera*, *Stachys x Salvia*, *Stachys x Oenothera*	9	Glasshouse	Summer
Design 2: Outdoor model gardens - individual garden 'beds' containing nine plants and peat-free growing medium subjected to rainfall application.	• *Erysimum* 'Bowles's Mauve' (evergreen, hairless leaves) • *Oenothera lindheimeri* 'Whirling Butterflies' (deciduous, small leaf hairs)	Monocultures: *Erysimum*, *Oenothera*, Bare substrate Mixed: *Erysimum x Oenothera*	9	Outside	Summer and Winter
Design 3: Miniature model gardens - containers planted with four plants and peat-free growing medium subjected to rainfall application.	• *Erysimum* 'Bowles's Mauve' (evergreen, hairless leaves) • *Pseudodictamnus mediterraneus* (evergreen, leaf hairs) • *Oenothera lindheimeri* 'Whirling Butterflies' (deciduous, small leaf hairs) • *Verbena bonariensis* (deciduous, hairless leaves)	Monocultures: *Erysimum*, *Pseudodictamnus*, *Oenothera*, *Verbena*, Bare substrate Mixed: *Erysimum x Oenothera*, *Pseudodictamnus x Verbena*	4	Glasshouse	Summer and Winter

Table 2.5: Summary of model garden designs.

2.7.3.1 Design 1 - Rainfall application on potted plants and impact of planting design

Introduction

Variation in rainfall retention between planting layouts, comprising plants with different traits, was quantified using individual potted plants arranged in designs within a tray and subjected to simulated rainfall using a rainfall applicator. Plants were arranged in either monocultures or mixed layouts to investigate the effect of planting design and combinations of different plant traits. The tray allowed different configurations of nine individual plants and this method was selected rather than permanently planted model gardens to enable quick and easy redesign of the planting schemes to determine their rainfall retention capacities. Each experimental layout was selected to compare plant traits or growth habits in layouts that are commonly used in domestic and public garden planting beds. Monocultures were used as control layouts to determine how the plant species behaved in isolation. In comparison, striped layouts were used to combine two plant species in a pattern seen in formal gardens or roadside displays, and chequered layouts were used as a smaller representation of matrix or naturalistic planting design, which weaves species together in cottage, prairie and wildlife gardens to create soft, textural planting. A chequered layout could also represent garden owner purchasing habits, with the purchase and planting of additional single plants into existing garden beds creating an unintentional chequered effect.

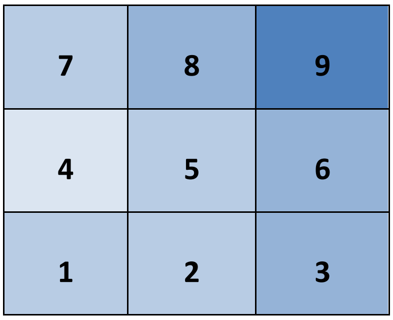
Method trials

Pots of nine individual plants or bare substrate were arranged in layouts within a plastic tray (80 cm x 80 cm x 12 cm) on a glasshouse bench for each rainfall application. Each trial involved subjecting the plants and tray to simulated rainfall. The volume of water delivered by the rain applicator was anticipated to be equal between trials, so any differences in water volume in the tray would be due to the plants themselves. Time for runoff to occur from the plant pots - noted as the time the pots began to leak water from their drainage holes, was also monitored.

Plants would be positioned 1.6 m below the rain applicator nozzle (Figure 2.3), which is within the range used in other rainfall simulator experiments, usually between 0.7 m and 3 m (Blanuša & Hadley, 2019; Humphry *et al.,* 2002; Fister *et al.,* 2012; Kemp *et al.,* 2019), and central to the middle of the tray. To identify spatial distribution of water droplets across the collection tray area, nine empty 5 L pots were positioned in the tray with pot drainage holes sealed with tape to ensure no water leakage. Water volumes in each pot were measured after 10 minutes of rainfall application, with three repetitions. Water volume was found to vary across the tray area, with the highest volume found on the right-hand side of the tray in pot numbers 9, 8, 6, and 3 (Figure 2.4). Tray volume outside of the pots was an average of 1.4 L. Kemp *et al*. (2019) noted the consistency of rainfall decreased further from the nozzle and immediate area. A second rainfall applicator was also tested for rainfall distribution and found to create a different pattern of rainfall that was not comparable to the first applicator (data not shown), and the decision was made to use only the first applicator for consistency of results.

Figure 2.3: Setup for rainfall application in a glasshouse with applicator and tray plants.

Pot number	Water volume (ml)
1	150-199
2	150-199
3	200-250
4	< 150
5	150-199
6	200-250
7	150-199
8	200-250
9	> 250



7	**8**	**9**
4	**5**	**6**
1	**2**	**3**

Figure 2.4: Spatial rainfall distribution trials and average water volumes for the rainfall applicator used. The applicator nozzle was positioned directly over the centre of pot 5. Mapped rainfall volume is shown via a colour gradient and table.

Rainfall runoff, assessed as observed time taken for the pot to leak water from the base, was tested on saturated and unsaturated monocultures of *Stachys, Salvia, Erysimum*, and *Oenothera*, to determine length of time to simulate rainfall. Saturated trials had a runoff time between 15-25 minutes, and unsaturated trials had a time between 25-60 minutes. As rainfall could only be applied to one tray at a time it was decided that rain application for 20 minutes for saturated trials, and 40 minutes for unsaturated trials would be employed to allow for multiple trials per day, similar to previous rain application trials (Blanuša & Hadley, 2019; Kemp *et al.*, 2019). In addition to tray volume, water was collected 30 minutes after rainfall application ceased to account for delays in runoff.

Method

Individual *Stachys, Salvia, Erysimum,* and *Oenothera* were purchased from Provender Nurseries (Swanley, Kent, UK) in 9 cm containers in February 2021 and repotted into 2 L containers. The plants were subsequently potted into 5 L plastic pots in Spring 2021 using a peat-free growing medium (SylvaGrow Multi-purpose, Melcourt, UK), allowing the plants to grow into their new containers for two months within a glasshouse.

The experiment was carried out in a ventilated glasshouse at the University of Reading Whiteknights campus on the week commencing 14th June 2021. Night temperatures were maintained to a minimum of 15°C and daytime temperature was not regulated. Air temperatures and relative humidity were measured every 30 minutes using a Tinytag Plus 2 Data logger (Gemini Data Loggers, Chichester, UK).

Impact of retention of rainfall within plant canopies (saturated media)

Prior to rainfall application, growing medium within each pot was saturated to field capacity on the morning of experimentation and allowed to drain for 1 hour. Substrate moisture content readings were taken using a substrate moisture sensor (SM300 sensor connected to a HH2 Moisture Meter, Delta-T Devices Ltd., Cambridge, UK), with two readings per pot after the drainage period, and pot mass was recorded. The rain applicator was applied for 20 minutes, pausing the applicator every 5 minutes to note water leakage from the base of the pots. To do this pots were lifted, keeping the plant upright to carefully ensure minimal disturbance to the canopy. When water droplets were visibly leaking from the pot drainage holes substrate water holding capacity was reached and the time interval was recorded. Rain application continued for the duration of the 20 minutes, and at the end of this period the applicator was stopped and plants were transferred to a drainage tray. Plants were left undisturbed for 30 minutes post-rainfall application. Water was collected from the rain application tray and water runoff volume recorded. After 30 minutes drainage time the substrate moisture content of the plant pots was recorded, and drainage tray water volume was also measured.

Impact of plants' evapotranspiration on the capacity to store rainfall in the substrate (unsaturated media)

Prior to rainfall application plants were watered to field capacity and then water was withheld 3 days until substrate moisture decreased to a significantly lower content than saturated media experiments. Each species was expected to have different substrate moisture contents due to varying transpiration rates, although the intention was for all readings to be below 0.30 $m^3 m^{-3}$. The substrate moisture content of the plants ranged from an average of 0.13 $m^3 m^{-3}$ (*Oenothera* monoculture) to 0.23 $m^3 m^{-3}$ (*Stachys* monoculture). The experiment setup was the same as the saturated media method (above) except that rain application was applied for 40 minutes.

Data analysis

Total runoff volumes were calculated as a combined total of tray runoff and drainage runoff, and expressed per layout and per standardised unit leaf area index (LAI) (section 2.2.3**,** Equation 1). Statistical analysis was undertaken in R (R Core Team, 2021) using one-way ANOVA to compare total runoff from each treatment (saturated or unsaturated) against plant layout. Total runoff volume from saturated trials per unit leaf area index was log-transformed prior to analysis. Additional post-hoc analysis using Tukey HSD tests were used to compare different layouts.

Results

Impact of retention of rainfall within plant canopies (saturated media)

There was an overall significant effect of plant layout on total runoff volume for saturated substrate per model garden ($p = 0.029$) and per unit leaf area index ($p = 0.019$) (data not shown). Per model garden the *Oenothera* monoculture layout generated the largest rainfall runoff volume compared to all other layouts including bare substrate, with an average of 7.95 L, 2.25 L more than bare substrate ($p = 0.073$). With the exception of *Oenothera,* all layouts had similar runoff volumes per garden. The lowest average runoff volume was produced by the *Erysimum x Oenothera* striped layout with an average of 5.22 L. Runoff volumes per unit leaf area index showed that all layouts were similar except *Stachys* produced a significantly larger runoff volume compared to the *Erysimum x Oenothera* striped layout ($p = 0.044$; 0.96 L more on average).

Impact of plants' evapotranspiration on the capacity to store rainfall in the substrate (unsaturated media)

There was an overall significant effect of plant layout on total runoff volume for unsaturated substrate per model garden ($p < 0.001$) and per unit leaf area index ($p = 0.04$). The *Oenothera* monoculture again produced the largest runoff volume compared to all layouts ($p < 0.001$; *Stachys x Oenothera* chequered layout p =

0.006) except bare substrate (Figure 2.5), and also had the lowest average substrate moisture content of the planted layouts prior to rainfall application (0.13 $m^3 m^{-3}$). Average substrate moisture content for all other plant monocultures ranged from 0.16 $m^3 m^{-3}$ (*Salvia*) to 0.23 $m^3 m^{-3}$ (*Stachys*), all chequered layouts ranged from 0.14 $m^3 m^{-3}$ (*Stachys x Oenothera*) to 0.16 $m^3 m^{-3}$ (*Stachys x Salvia*), and all striped layouts ranged from 0.15 $m^3 m^{-3}$ (*Erysimum x Oenothera*) to 0.22 $m^3 m^{-3}$ (*Stachys x Salvia*). The lowest average runoff volume was from the *Stachys x Salvia* striped layout at 4.37 L. The *Oenothera* monoculture layout had a significantly larger runoff volume compared to *Erysimum* ($p < 0.001$) but when the two plants were combined in both chequered and striped layouts the mixtures had significantly smaller runoff volumes than the *Oenothera* monoculture (5.07 L less and 5.73 L less respectively; $p < 0.001$) resulting in similar tray volumes to the *Erysimum* monoculture (Figure 2.5). As with the saturated layouts, runoff volumes per LAI found only *Stachys* was significantly different from the *Erysimum x Oenothera* striped layout ($p = 0.059$) (data not shown).

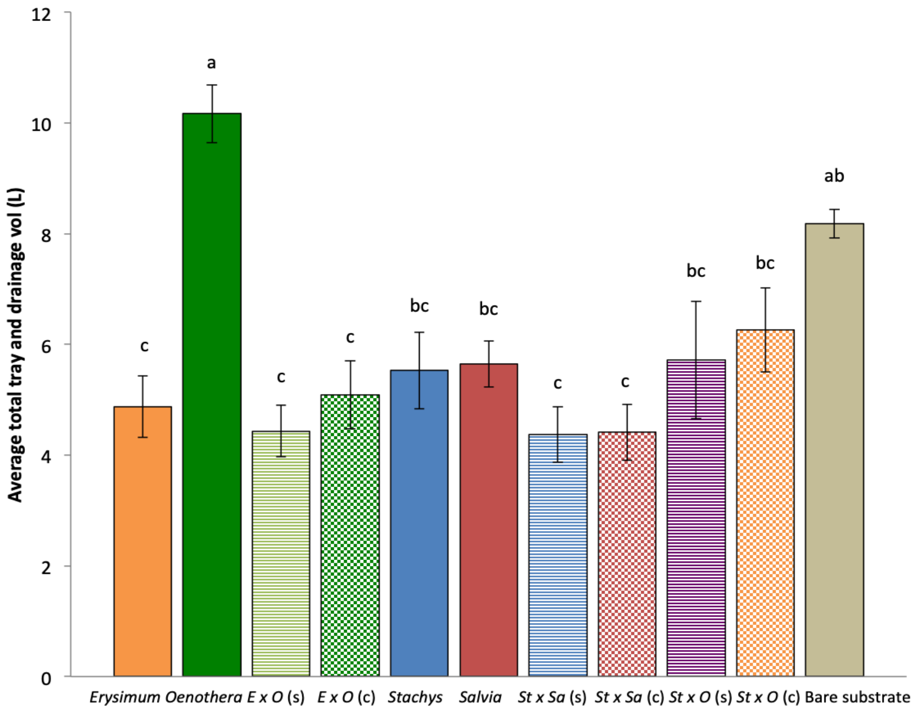


Figure 2.5: Mean total runoff volumes after rainfall application to unsaturated substrate per model garden with associated standard error of the means (n = 3 per layout). s = striped layouts, c = chequered layouts. Layouts sharing a letter above the bars were not significantly different from one another.

Conclusions and limitations

Comparison between striped and chequered layouts showed no significant difference in runoff volumes, and with the exception of *Oenothera* there was minimal difference in runoff volumes between the majority of mixtures and their monoculture counterparts. It was anticipated that *Stachys,* with its broad hairy leaves, would provide significantly greater rainfall retention, which has been observed in a previous study (Kemp *et al.,* 2019), however this was not found to be the case.

The *Oenothera* monoculture produced unexpected results, performing poorly compared to all layouts, and no better than bare substrate. This outcome may in part result from limitations in the methodology (see below). *Oenothera* plants had the largest leaf area index of all the plant layouts tested and the largest average plant canopy (data not shown), which in previous studies was beneficial for rainfall retention (Blanuša & Hadley, 2019; Nagase & Dunnett, 2012). However, water funnelling may have occurred, by the relatively large canopy projection of *Oenothera*, which extended beyond the collection tray, therefore exposing *Oenothera* to greater volumes of water than the other plants. *Thuja* hedge plants were observed to have a high surface runoff volume potentially due to their branch architecture as the 30-45° angle funnelled more water towards the trunk and base of the plants (Blanuša & Hadley, 2019).

When *Oenothera* was included in the mixed unsaturated layouts, the rainfall runoff was significantly reduced in comparison to the monoculture layout. Both the *Oenothera* and *Erysimum* monocultures had similar substrate moisture content readings (data not shown) and yet performed differently under 40 minutes of rainfall application. *Erysimum* was the dominant species in both the striped and chequered layouts (6/9 for the former, 5/9 for the latter), which could explain why the mixed layouts performed more similarly to the *Erysimum* monoculture. When *Oenothera* was mixed with *Stachys* this also reduced runoff volumes compared to *Oenothera* as a monoculture. However, both pairings only reduced how poorly *Oenothera* retained water in this experiment, and did not create a significantly better planting combination compared to either *Stachys* or

Erysimum as monocultures. Although this study does not take into account root level interactions or the role of substrate in a planting bed, and therefore cannot be considered representative of *Oenothera's* real-world performance and more research is needed.

Method limitations:

Although this rain application study was a temporary setup to allow for experimental screening of a larger number of design layouts than could typically be tested in planted model gardens, it may also have limitations that impacted results.

- As previously discussed, the results regarding the *Oenothera* monocultures were unexpected. Destructive sampling after the experiment indicated that *Oenothera* was pot-bound and had not grown from the equivalent of a 9 cm pot into the larger 5 L space available. This could have limited water uptake. Potentially *Oenothera* planted in the ground may have been more successful, and using plants grown from cuttings would alleviate any changes in root development that could result from nursery growing conditions.
- The rainfall applicator was found to not produce a consistent volume of water with each use, and this would have introduced error between the layouts. As such it cannot be concluded that there is no significance between monocultures and mixed planting, or between striped or chequered planting layouts, and the rain applicator design required improvement prior to reuse (see section 2.7.3.2 below).

2.7.3.2 Design 2 - Rainfall application on outdoor model gardens

Introduction

Outdoor model gardens were designed to quantify monocultures and chequered mixtures of *Erysimum* and *Oenothera* (referred to from here as Mixed layout) for their rainfall retention capacity in both summer and winter. Each model garden contained nine plants with 330 L peat-free growing media (SylvaGrow Multi-purpose, Melcourt, UK). *Erysimum* and *Oenothera* plants were transplanted from

5 L pots in December 2021, originally purchased from Provender Nurseries (Swanley, Kent, UK) in 9 cm containers in February 2021 and repotted into containers over the ten months before planting in model gardens.

Model gardens were built from treated plywood (1.2 m x 1.2 m x 20 cm) with drainage holes along the base. The gardens were located in a random pattern on the grounds of the CEL, University of Reading Whiteknights campus (chapter 4). The boxes were elevated at one end on bricks at a 10° angle to allow water to drain via the drainage holes.

Prior to experimentation both model garden design and the rainfall applicator were trialed to enable method development.

Method trials

Rainfall applicator trials

The spatial distribution and volume of water from the rain applicator was trialled outdoors using an empty model garden containing no substrate or plants in January 2022. Nine empty 10 L buckets were positioned in the model garden in the same position as the plants if the garden was populated. Eleven further buckets were positioned around the perimeter of the model garden to collect rainfall from the applicator that falls outside of the garden. After 10 minutes of rainfall application at fixed pressure setting of 15 kPa, water volume was measured for each bucket and the model garden box, with five repetitions (Figure 2.6). Due to the size of the model gardens only one garden could be trialled at a time.

Water volume was found to vary across both the internal model garden and the garden perimeter, with a range of 2.62 to 3.2 L falling within the buckets and garden box within the 10-minute time period (Figure 2.6). It was concluded that the wind blowing the rain away from the gardens and the slight output variability of the rain applicator itself led to the varied spatial distribution of the rain droplets and volume inconsistencies (scaled-up flow per hour 10.92 mm/ hr^{-1} - 13.33 mm/hr^{-1}, pressure 15 kPa). To combat this a solenoid control valve was added to the rain applicator, intended to control flow by controlling when rainfall began and ended. The valve was pre-programmed using Bluetooth to end water flow at exactly the time duration selected (e.g. 10 minutes), which aimed to reduce error introduced by manual turning off of the rain applicator. Rain gauges were also positioned in the model gardens (details below, Figure 2.7) that would allow for standardised runoff volumes to be calculated in relation to the actual rainfall quantity received on each garden.

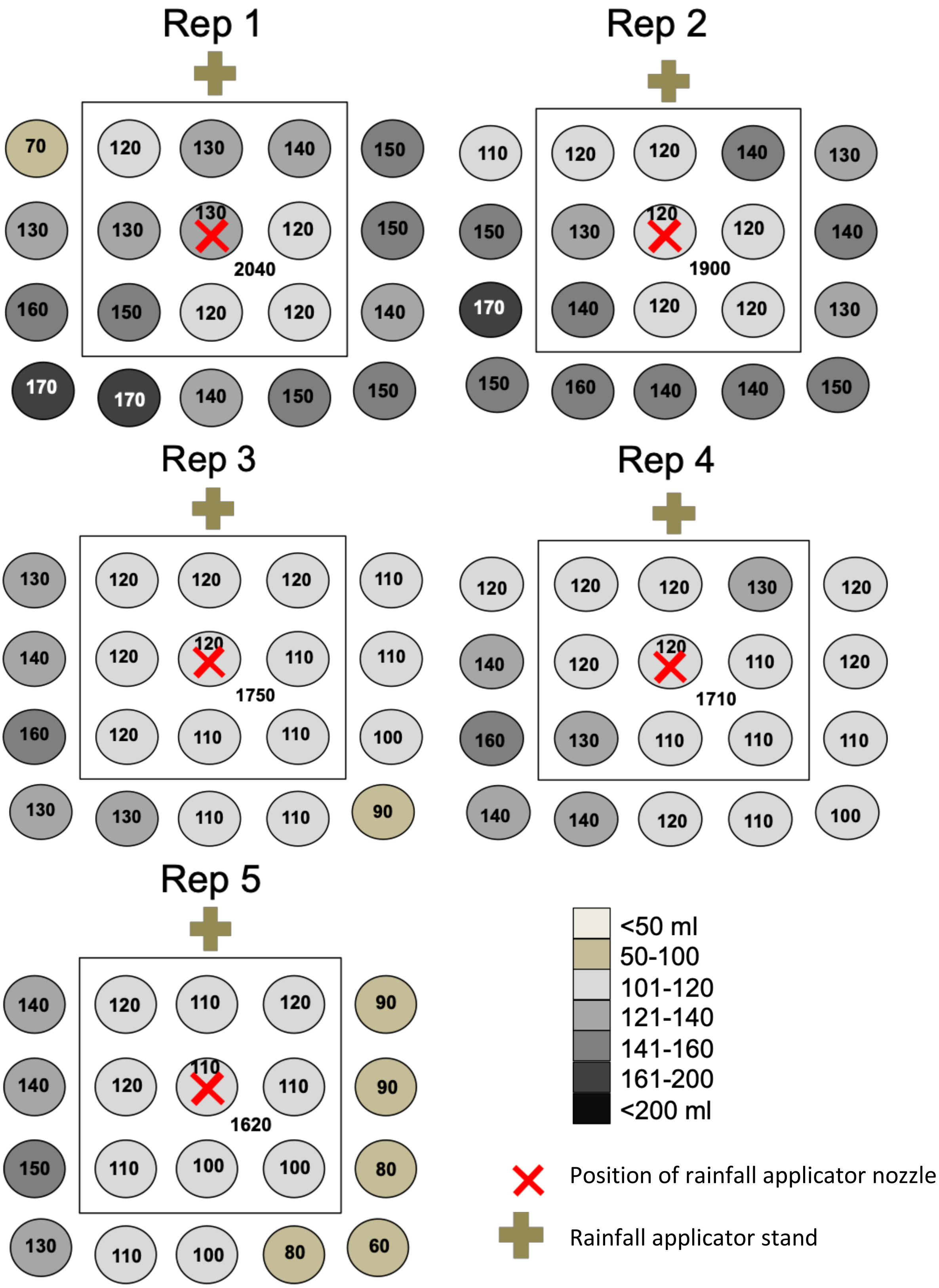


Figure 2.6: A spatial rainfall distribution trial using an empty model garden and buckets for the rainfall applicator used in Experiment 3 (not to scale). Nozzle was positioned directly above the centre of each model garden, shown as a red cross. Recorded rainfall volume is shown via a colour gradient and volume table.

Five rain gauge cups (Tildenet Gardenware, Bristol, UK) were positioned using garden stakes across each model garden, allowing them to be removed and emptied after each rainfall application (Figure 2.7). Rain gauges were placed on purpose-built stands 70 cm tall that would collect rainfall at the canopy heights of the plants. This setup, including solenoid valve, was trialled with five repetitions in May 2022 using an empty model garden tray in glasshouse conditions to remove the impact of weather variability. Standardised runoff volumes, which is a unitless measure of runoff to remove the effect of variable rainfall volumes between experimental trials, were calculated using the formula below:

Equation 2:

$$\text{Standardised runoff volume} = \frac{\text{Total runoff volume (ml)}}{\text{Total rain gauge volume (ml)}}$$

During the experiment (chapter 4) this would enable rainfall runoff volumes to be compared against rainfall applied to each individual garden, with experimental runs replicated three times (as there were three of each model garden layout), and the calculated standardised runoff figure allowed for comparison between different gardens despite varied water volumes produced by the applicator.

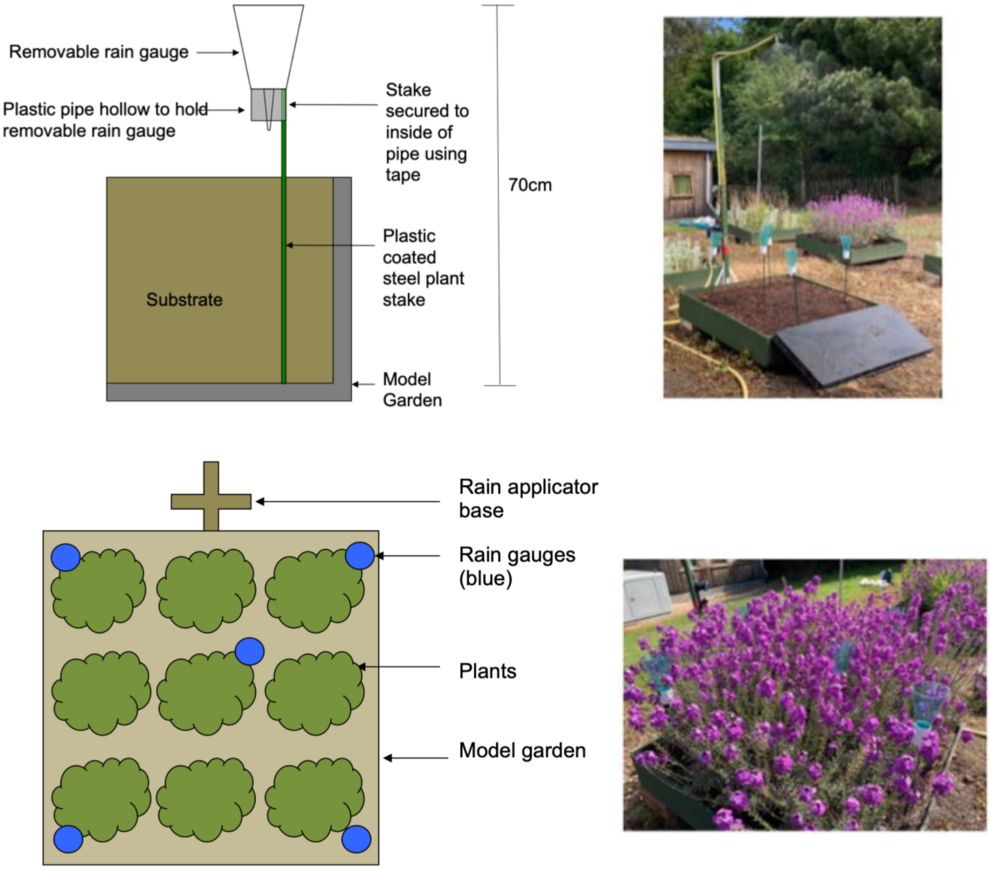


Figure 2.7: Rain gauge setup and layouts used for the outdoor model gardens (not to scale). Photographs show rain gauges positioned during experimentation in outdoor model gardens in a bare substrate garden (top right) and an *Erysimum* monoculture garden (bottom right).

Empty outdoor model garden trials

Rainfall was applied for 10 minutes with five replications. Total runoff volume was measured as the water collected in the empty tray after 10 minutes, and total rain gauge volume was the combined total volume from all five rain gauges. Rain gauge volumes ranged between 140-148 ml and accounted for 7.5-7.8% of total rainfall volume (Table 2.6). Runoff volume, measured as the water collected in the empty model garden tray, was marginally more variable and ranged from 1670-1800 ml (5.4-7.2%). The standardised runoff calculation ranged from 11.77-12.32. The amount of variation in rain gauge volume was similar to the variation in runoff volume and the standardized runoff volume was less variable than the runoff volume (Table 2.6), indicating that the standardisation implemented in the rain application for model gardens (the rain gauges and solenoid) helped counteract the variation in rainfall volume from the rain applicator.

Rep	Rain gauge total (ml)	Runoff volume (ml)	Standardised runoff volume	Rain gauge volume as percentage of total rainfall (%)
1	140	1670	11.93	7.73
2	147	1730	11.77	7.83
3	148	1800	12.16	7.60
4	144	1760	12.22	7.56
5	142	1750	12.32	7.51
Standard deviation	2.99	42.61	0.2	0.12
Coefficient of variation	0.0208	0.0245	0.0166	0.0154

Table 2.6: Preliminary trials using an empty tray and rain gauges, and calculated standardised runoff volumes.

Planted outdoor model garden trials

To determine how much water to apply and how much time was required before runoff was generated by each model garden layout trials were conducted on both saturated and unsaturated substrate, and detailed below.

Standardised rainfall runoff, measured as the water volume collected from the model garden drainage holes, was trialled in May 2022 on saturated gardens to determine canopy capacity to retain rainfall and unsaturated gardens for the contribution of evapotranspiration to reduce runoff. For retention of rainfall within the canopy, trial gardens were saturated to field capacity the morning of experimentation, achieved via watering using a hose until water was visibly dripping from the drainage holes. Five substrate moisture readings were taken per garden after saturation and drainage time, with an average of 0.37 m^3 m^{-3} across gardens. One model garden was trialled at a time. Rainfall was applied for 20 minutes, however the *Erysimum* monoculture only produced 5 ml of runoff during rainfall application and no runoff was generated from the *Oenothera* monoculture garden during this time or 30 minutes post rainfall application.

For trials of the plants' evapotranspiration contribution on the capacity of the model gardens to store water in the substrate the gardens were watered to field capacity 48 hours prior to testing and no further water applied (no irrigation, and no natural rain events). Average substrate moisture content on the morning of rainfall application was 0.22 $m^3\ m^{-3}$ for the *Erysimum* monoculture gardens, 0.24 $m^3\ m^{-3}$ for the *Oenothera* monoculture gardens, 0.27 $m^3\ m^{-3}$ for the Mixed gardens, and 0.28 $m^3\ m^{-3}$ for the bare substrate gardens. Rainfall was applied to each model garden for 40 minutes, as the substrate was drier than saturated trials and would therefore take a greater volume of water application for runoff to be generated. However, the initial rainfall time was extended until runoff was generated, which took 60 minutes for bare substrate, 85 minutes for *Oenothera*, and 110 minutes for *Erysimum* (Mixed was not tested). In addition to the extended trialling time, minimal runoff volumes were collected, with just 8 ml for the *Erysimum* monoculture. Due to the minimal volumes of water collected, standardised runoff was not calculated for this trial.

The variation in runoff times and volumes generated indicated that the plant layouts were impacting runoff, however the time taken was too long to make this method viable.

Impact of retention of rainfall within plant canopies

It was decided neither of these methodologies would work due to the time taken for them to be implemented and the large volumes of water applied. To conserve time and water, retention of rainfall within the canopy trials were altered to focus only on the aboveground rainfall collection via the placement of ten plastic dishes (750 ml total volume capacity, dimensions 193 x 132 x 60 mm) across the model garden that would sit on the substrate below the plant canopy (Figure 2.8). Rainfall would be applied for 15 minutes and the rainwater collected from these plastic dishes would equate to runoff because it would be the water volume that the plant canopy could not capture or retain. To calculate standardised runoff the total volume in the collection containers was equated to total volume in Equation 2 above. Three of each garden layout was trialled on two different days in May 2022 to ensure reproducibility.

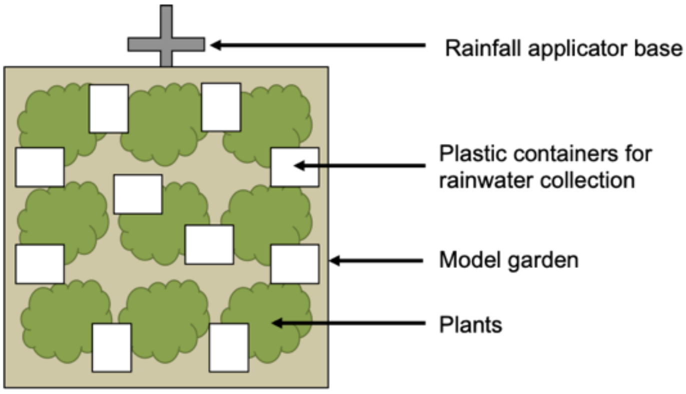


Figure 2.8: Plastic rainfall collection containers layout as used in outdoor model gardens (not to scale).

Statistical analysis of the results was undertaken using one-way ANOVAs in R and additional post-hoc analysis using Tukey HSD tests to compare multiple garden layouts.

Average standardised runoff volumes were significantly higher for bare substrate compared to the planted layouts ($p < 0.001$) (Figure 2.9). *Oenothera* and the Mixed layout had similar runoff volumes, with an average of 0.63 and 0.69 respectively, while *Erysimum* was significantly higher than *Oenothera* or Mixed layouts at 0.93 (*Erysimum* vs Mixed $p = 0.03$; *Erysimum* vs *Oenothera* $p < 0.001$). Although there was variation in rainfall depending on the severity of the wind blowing across the model garden site the rain gauges helped standardise this and the method was determined to be reliable for data collection of retention of rainfall within the canopy. This method enabled a smaller volume of water to be used in each trial and all twelve gardens to be trialled within a single day.

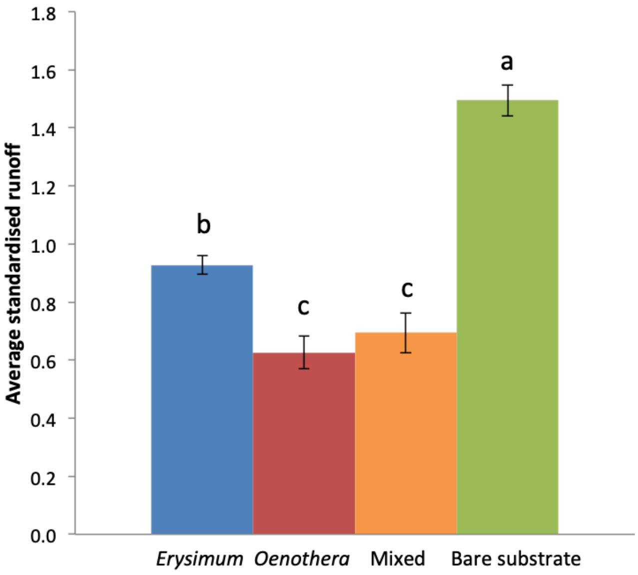


Figure 2.9: Retention of rainfall within the canopy trial per outdoor model garden. Mean standardised runoff volumes and associated standard error of the means (n = 6 per layout). Layouts sharing a letter were not significantly different from one another.

Impact of plants' evapotranspiration on the capacity of model gardens to store rainfall in the substrate

As an alternative unsaturated trial, substrate moisture content data was collected with the aim this would be a proxy to determine evapotranspiration related moisture usage. Model gardens were saturated to field capacity on day 0, determined as when water drips began from the garden drainage holes, and then on each day of testing twelve substrate moisture readings were taken across each garden and a mean of each model garden was calculated at each time point. This method could only be applied on periods of rain-free days, therefore the first trial lasted three days, and the second trial lasted five days. Three model gardens of each layout were tested in each trial. Statistical analysis of the results was undertaken using one-way ANOVAs and post-hoc Tukey HSD tests in R. The moisture deficit value could then be calculated using the following formula:

Equation 3:

Moisture deficit value (L) = (a - b) x c

a = substrate moisture at field capacity ($m^3\ m^{-3}$)
b = observed substrate moisture at time of measurement
c = volume of substrate in model garden

Results from the two trials were shown to contradict one another. In the first trial, bare substrate lost a larger volume of water compared to the planted layouts with an average of 80.71 L (Figure 2.10A), however in the second trial bare substrate lost the smallest volume of water evaporation. The planted layouts lost a greater volume of water in trial 2 in which they were not watered for a longer period of time. The water loss of the planted layouts were not significantly different from one another in either trial although in trial 1 *Erysimum* was on average shown to deplete the model garden of the largest volume of water in comparison to the other planted layouts (70.12 L) and in trial 2 after five days the opposite was the case, and *Oenothera* depleted the beds of the most water (104.15 L) (Figure 2.10B). All water loss differences were not large enough to be statistically significant, with the exception of water loss between bare substrate and the *Oenothera* monoculture in trial 2 which had a weak significant difference ($p = 0.069$), although this could be due to sampling error from the differences between the 12 substrate moisture readings per garden.

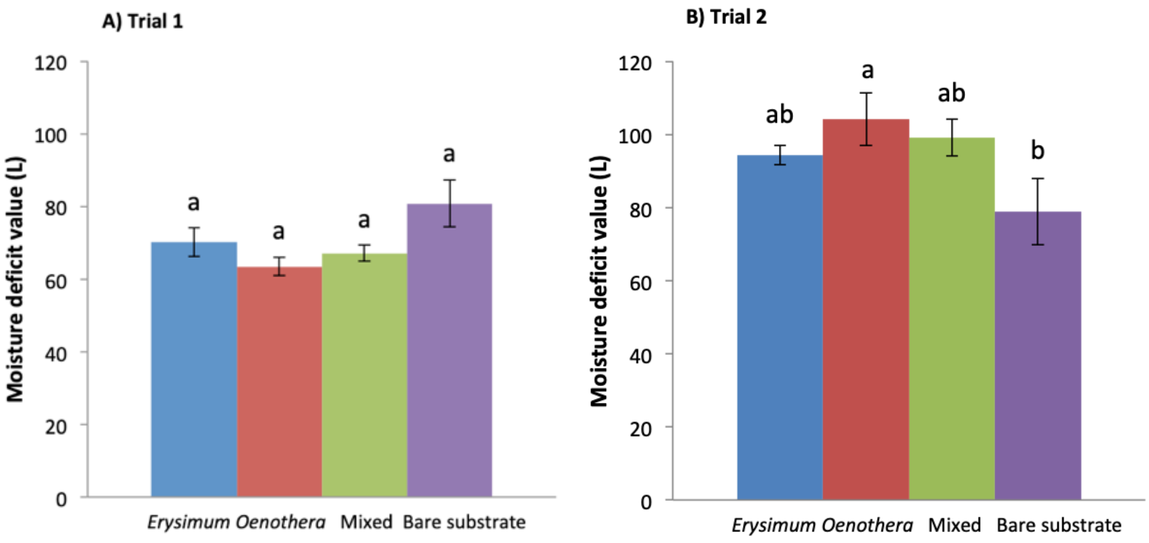


Figure 2.10: Moisture deficit trial results for the outdoor model gardens in summer 2022. Trial 1 (A) conducted over three rain-free days, and trial 2 (B) conducted over five rain-free days (n = 3, error bars are standard error). Layouts sharing a letter were not significantly different from one another.

Due to the fungal growth that occurred at this time (see section 2.4 above), as well as the limitations of data collection which relied on periods of weather without rain, and lack of statistical significance between layout water loss, it was decided to progress with only retention of rainfall within the canopy.

2.7.3.3 Design 3 - Rainfall application on miniature model gardens in the glasshouse

Introduction

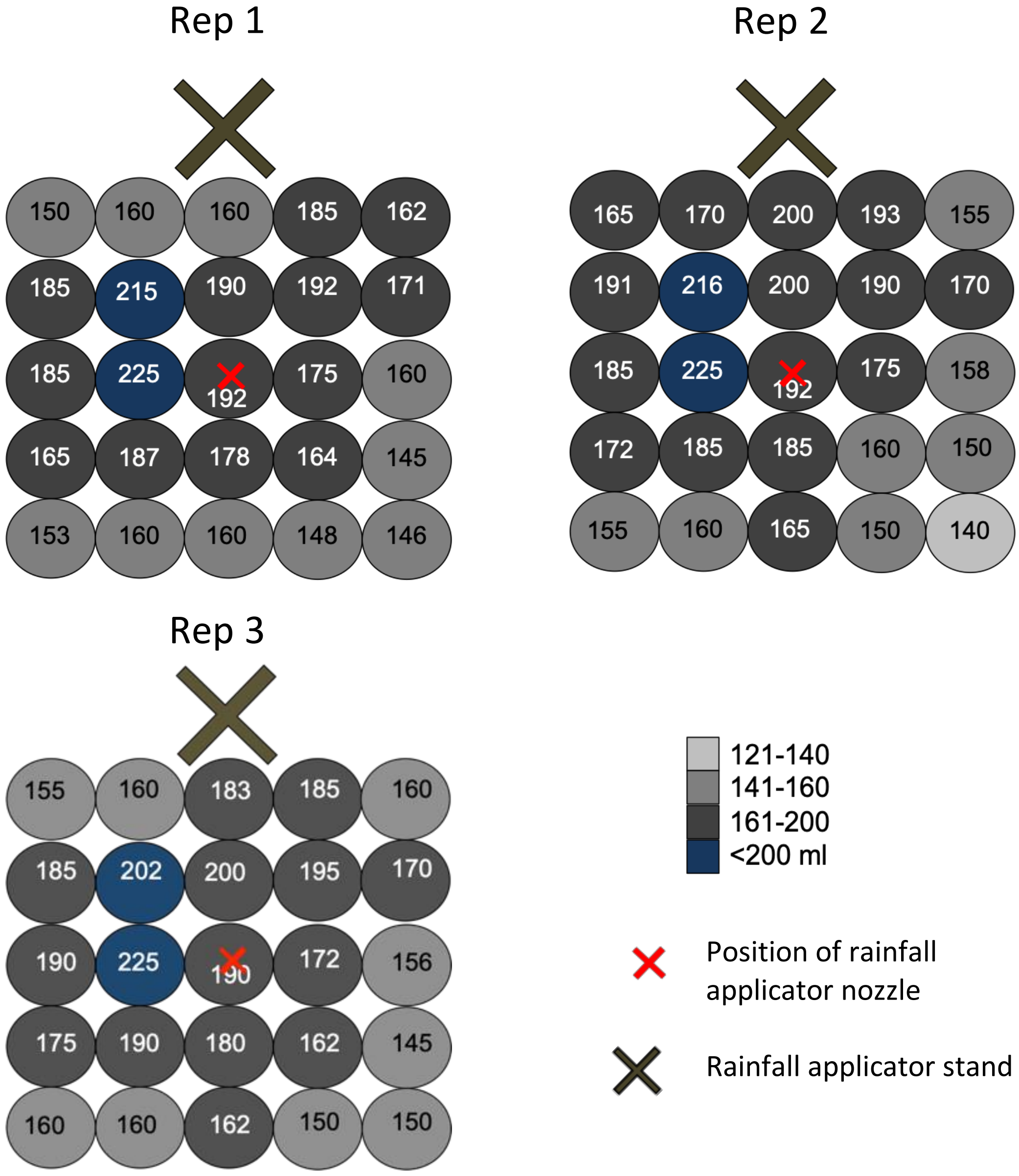
As described above, outdoor model gardens using larger plants were found to introduce some methodological limitations, including the larger volume of water required to conduct retention experiments, both with saturated and unsaturated substrate, as well as restriction to data collection days based on the weather. To overcome this, miniature model gardens were designed using plastic storage containers (400 mm wide x 280 mm depth x 200 mm height) with drainage holes drilled into the base of each. A limited selection of coloured containers was available and turquoise was selected rather than black or transparent to ensure the plants would not overheat within the former, or impact the root growth due to light levels with the latter. The miniature model gardens could each be planted with four plants and placed outside to expose them to seasonal growing conditions, but moved inside a glasshouse for experimentation, therefore overcoming the previous reliance on dry, wind-free weather. The smaller size of the gardens and the plants within them would enable rainfall retention within the canopy and retention of the substrate to be trialled easily and without an excess application of rainfall for each experiment. Prior to experimentation, the equipment and experimental setup were trialled inside a glasshouse at the CEL University of Reading Whiteknights campus in January 2023.

Erysimum, Oenothera, Pseudodictamnus and *Verbena* plants were grown from cuttings to overcome the problems introduced by nursery purchased plants with pot-bound roots (see Design 1 above). Cuttings were allowed to grow in a heated glasshouse before being potted into 9 cm containers after two months, and planted into miniature model gardens a month later (see chapter 4 for photographs of plants in situ). Prior to experimentation miniature model gardens and the rainfall applicator were trialed to enable method development.

Methods trials

Rainfall applicator trials

Prior to experimentation the spatial distribution and volume of water from the rain applicator was trialled inside an unheated glasshouse, which represented experiment conditions. As with the outdoor model gardens, a solenoid control valve and rain gauges were used. Water volume was measured in twenty-five 10 L buckets after 10 minutes of rainfall at fixed settings (15 kPa) with three replications (Figure 2.11). Water volume distribution was seen to vary across the space, with bucket volumes ranging from 140-225 ml, equating to 14-22.5 ml/min.



Rep 1

150	160	160	185	162
185	215	190	192	171
185	225	192	175	160
165	187	178	164	145
153	160	160	148	146

Rep 2

165	170	200	193	155
191	216	200	190	170
185	225	192	175	158
172	185	185	160	150
155	160	165	150	140

Rep 3

155	160	183	185	160
185	202	200	195	170
190	225	190	172	156
175	190	180	162	145
160	160	162	150	150

Figure 2.11: Spatial rainfall distribution trials using empty buckets (not to scale). Nozzle was positioned directly above the centre of the bucket configuration, shown as a red cross. Recorded rainfall volume is shown via a colour gradient and key.

It was decided four miniature model gardens could be trialled at one time with the addition of rain gauges to enable standardised runoff volumes to be calculated. Four empty model garden boxes were placed under the rainfall applicator with a single rain gauge in the centre of each. More rain gauges per garden were not possible, as they would obscure the plant canopies when the gardens were populated.

Water volume was found to vary with a range of 250-350 ml falling within the garden box within the 10-minute time period (Figure 2.12), but this was not deemed a concern as the presence of a rain gauge per garden box could be used to calculate standardised runoff for each layout. The position of the rain gauges for the miniature model gardens is shown in Figure 2.13.

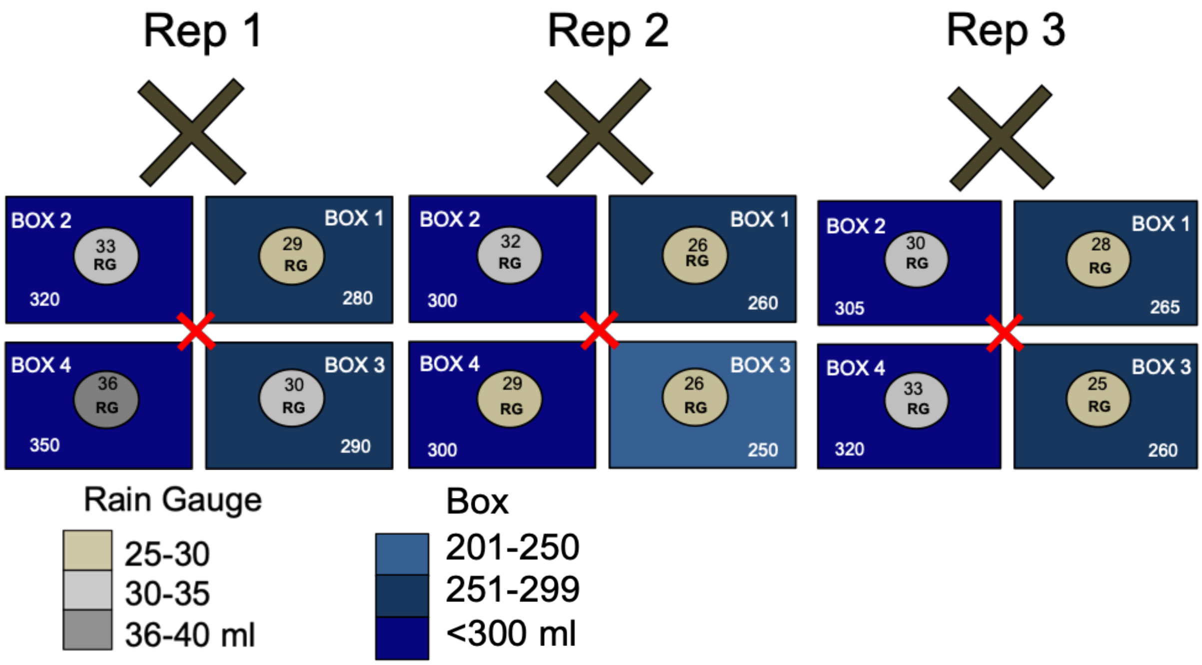


Figure 2.12: Spatial rainfall distribution trials using empty model garden boxes and rain gauges (not to scale). Nozzle was positioned in the centre of the four boxes, shown as a red cross, and rain gauges were positioned centrally in each garden box. Recorded rainfall volume is shown via a colour gradient and key.

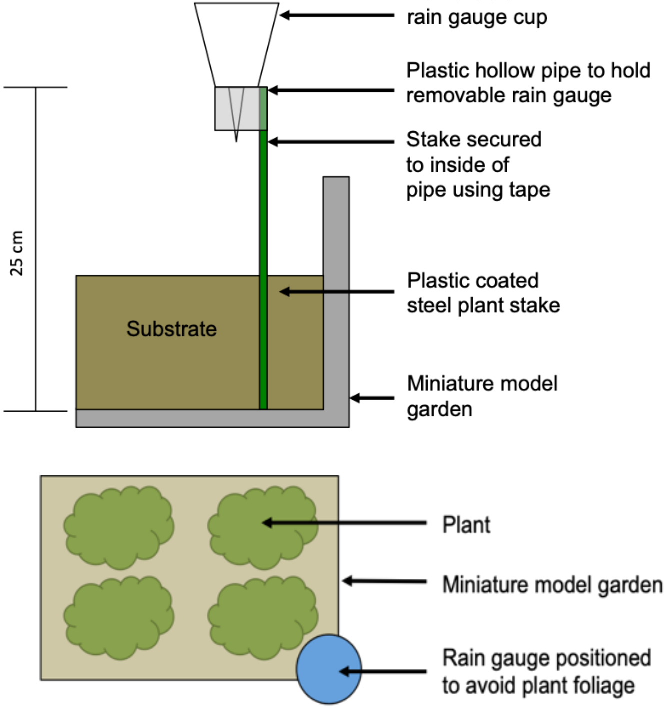


Figure 2.13: Rain gauge setup used for miniature model gardens (not to scale).

The model garden boxes had a capacity of 14 L however they were filled with a peat-free growing medium to a capacity of 7.2 L including plant root balls, as this was considered the maximum weight that could be safely lifted and moved after saturation. The miniature model garden containers were kept outside and exposed to winter or summer conditions before experimentation took place. A second empty container of the same size was placed underneath each miniature model garden to collect water runoff. The fit of the two containers ensured no water other than runoff from the individual gardens fell into the second container. The nozzle of the rain applicator was positioned 200 cm above the centre of the four model garden containers (individual plant species canopy heights varied) (Figure 2.14).

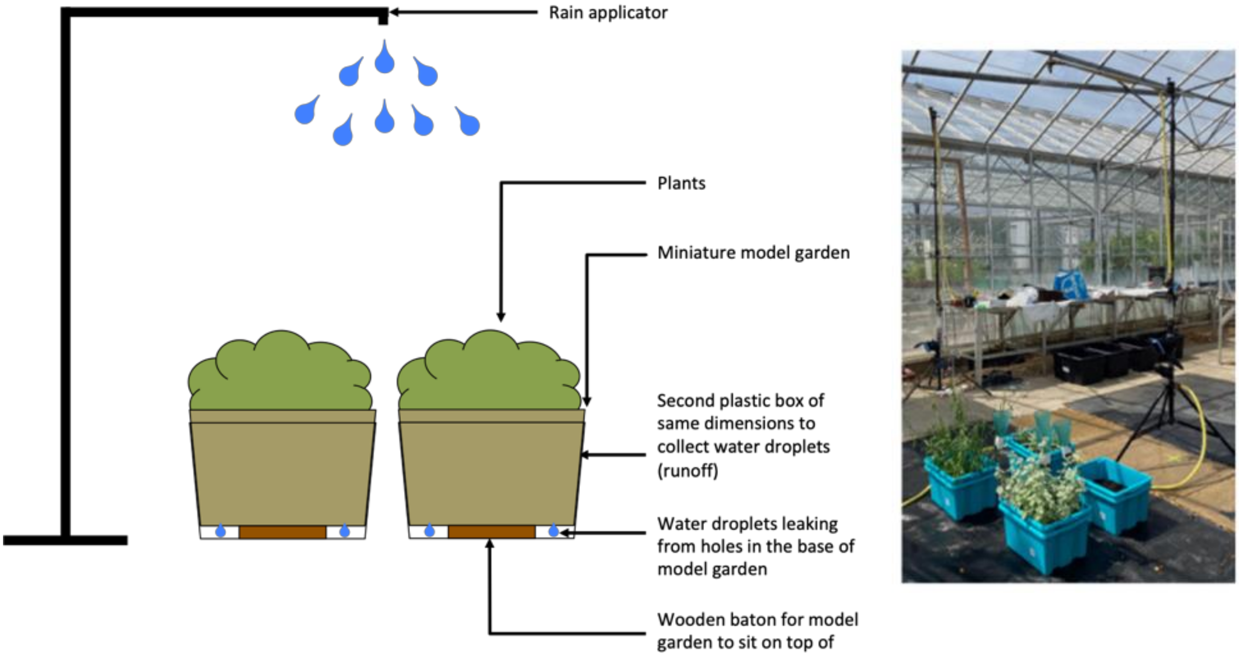


Figure 2.14: Diagram of the rain applicator and rain gauge setup used for Experiments 4 and 5 without the rain gauge in position (left) (not to scale). Photograph showing the rain applicator and four miniature model gardens with individual rain gauges.

Winter rainwater runoff, assessed as observed water volume collected from the model garden container drainage holes, was measured on saturated gardens for retention of rainfall within the canopy and unsaturated gardens for effect of plants' evapotranspiration and substrate rainfall storage, in January and February 2023. Statistical analysis was undertaken in R using one-way ANOVAs. Post-hoc analysis was conducted using Tukey HSD tests.

Impact of retention of rainfall within the canopy in winter

For retention of rainfall within the canopy trials, boxes were saturated to field capacity the morning of experimentation, achieved via watering using a hose for a count of 10 seconds until water was visibly dripping from the drainage holes and then placing the boxes in a tray of water for 5 minutes. Model gardens were then removed from the water and allowed to drain for 1 hour. Five substrate moisture readings were taken per garden after saturation and drainage time, with an average of 0.55-0.58 m^3 m^{-3} across gardens. Rainfall was applied for 10 minutes, as the model gardens are smaller than used in previous experiments.

Two replications of each layout were analysed due to incomplete data from additional reps.

All gardens produced runoff volumes within the 10 minutes of applied rainfall, although no differences between layouts were statistically significant (p = 0.152) (Figure 2.15). The *Verbena* monoculture produced the lowest standardised runoff volume with an average of 7.5 and the *Erysimum x Oenothera* mixed layout produced the greatest volume with an average of 11.11.

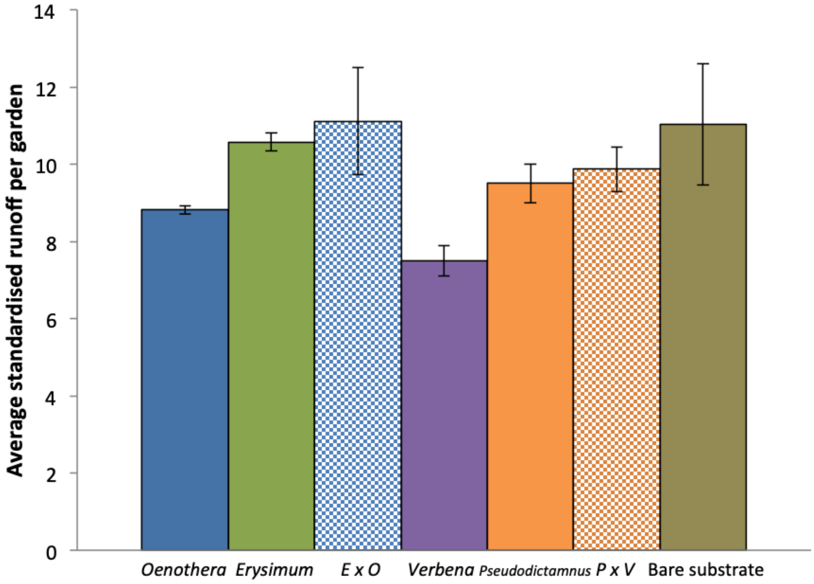


Figure 2.15: Winter retention of rainfall within the canopy trial per miniature model garden. Mean standardised runoff volumes and associated standard error of the means (n = 2 per layout).

Impact of plants' evapotranspiration on the capacity of model gardens to store rainfall in the substrate in winter

The unsaturated trials were undertaken nine days after the boxes were saturated to field capacity and substrate moisture sufficiently decreased. Due to the cold conditions, the substrate failed to dry without assistance and it was decided that heating would be applied to the glasshouse on day 7 for two days to sufficiently decrease the substrate moisture (Figure 2.16).

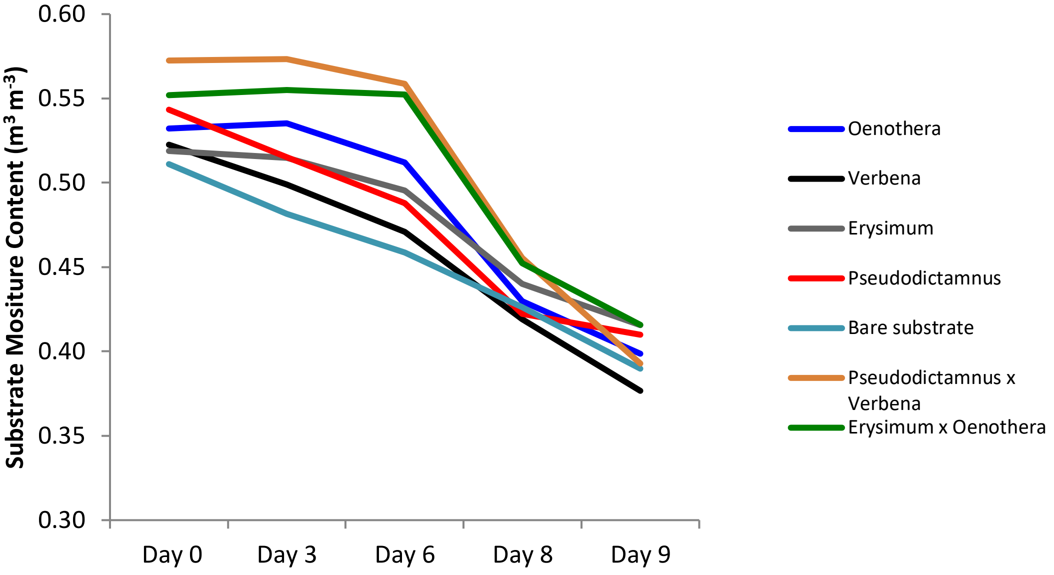


Figure 2.16: Average substrate moisture decline trial for each miniature model garden layout in the winter after nine days without additional water. Glasshouse heating was applied on days 7-9.

Average substrate moisture content prior to trial rainfall application was highest for the *Pseudodictamnus* monoculture and *Erysimum x Oenothera* mixed layout at 0.416 m^3 m^{-3}, and lowest for the *Verbena* monoculture at 0.377 m^3 m^{-3}. This was higher than anticipated, however it was decided that this would be suitable for winter trialling due to there being a significant decrease between saturated and unsaturated substrate moisture contents ($p < 0.001$, data not shown) and the cold temperatures preventing a larger decrease. Average temperatures inside the glasshouse on the unheated days ranged from 7.8-11.7°C with lows of 1.3°C.

Rainfall was applied for 10 minutes, and following this, additional increments of 5 minutes until all boxes produced runoff. As the *Verbena* monoculture took the longest time to drip, the rainfall time was set at 30 minutes for these winter trials. Three replications of each layout were trialled. *Verbena* had the lowest average standardised runoff volume compared to all other layouts at 3.23 and the *Erysimum x Oenothera* mixed layout had the largest volume at 7.26, larger even than bare substrate (Figure 2.17). However, no differences between layouts were statistically significant.

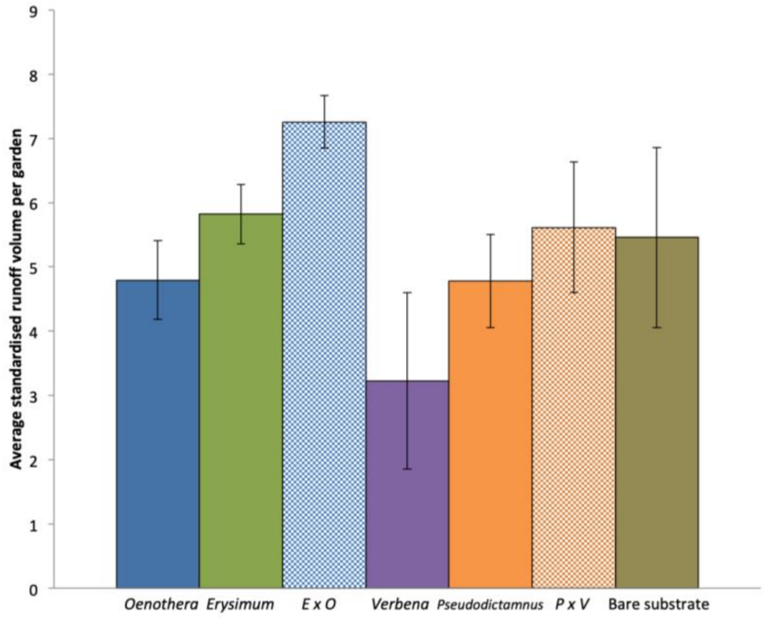


Figure 2.17: Trial winter mean standardised runoff volumes per miniature model garden for unsaturated substrate and associated standard error of the means (n = 3 per layout).

After this trial, for data collection of unsaturated substrate experiments (see chapter 4 for results) glasshouse heating was applied due to the cold weather prior to unsaturated rainfall application, and the substrate moisture content decline is shown in Figure 2.18 below. Two unsaturated data collection attempts took place during this season, both using 45 minutes of rainfall application preceded by three/four days of glasshouse heating (rep 1 and rep 2 respectively) (Figure 2.18). It was decided that applied heating, although not representative of what was happening naturally to the plants and substrate was necessary to undertake data collection because otherwise the substrate remained too saturated. Artificially drying the substrate could replicate unsaturated substrate after a period when no rainfall has occurred, and would therefore represent the runoff reduction these plant varieties could achieve if rainfall fell after a period of no rainfall.

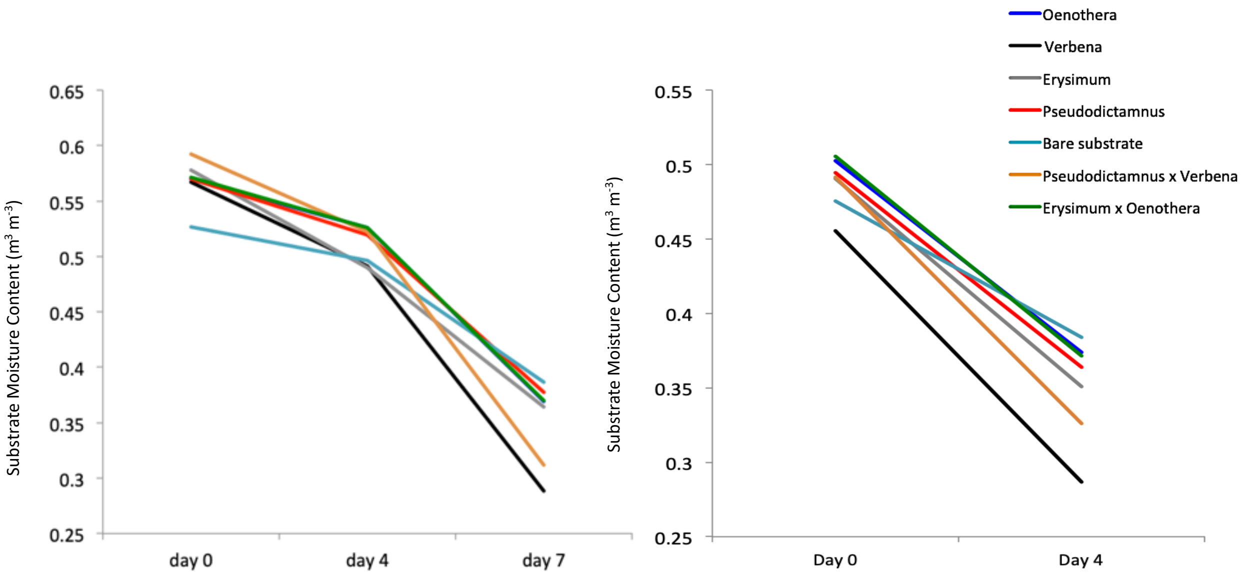


Figure 2.18: Average winter substrate moisture decline for miniature model gardens during unsaturated experimentation. Rep 1 (left) had heating applied to the glasshouse on day 4 and rep 2 (right) had heating applied on day 0.

Impact of plants' evapotranspiration on the capacity of model gardens to store rainfall in the substrate in summer

During the summer, rainfall application for the unsaturated layouts was applied for 45 minutes to enable comparison with winter results, and also increased to 1 hour to determine whether runoff volumes could be increased. Gardens were not watered for three days prior to rainfall application with average temperatures in the glasshouse ranging between 21.4-23.4°C but daily highs between 28.8-42.7°C.

After 1 hour of rainfall, average standardised runoff was significantly larger for the bare substrate layout compared to all planted layouts (bare substrate vs *Pseudodictamnus, Oenothera*, and *Pseudodictamnus x Verbena* $p < 0.001$; vs *Verbena* $p = 0.008$; vs *Erysimum* $p = 0.004$; vs *Erysimum x Oenothera* $p = 0.003$) (Figure 2.19). All other layouts did not produce significantly different runoff volumes. The *Pseudodictamnus x Verbena* mix produced the lowest average standardised runoff volume at 0.68. All other planted layouts ranged between 2.31-3.77. It was concluded that increasing the rainfall application time did not have a significant impact on runoff volumes generated between planted layouts and therefore 45 minutes would be sufficient.

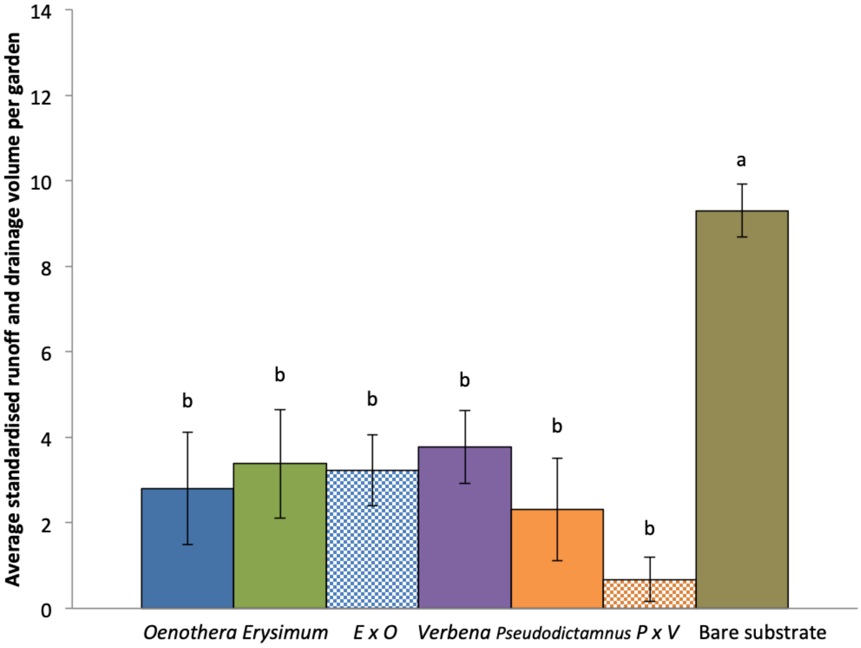


Figure 2.19: Summer runoff volumes trial per miniature model garden for one hour of rainfall on unsaturated substrate. Mean standardised runoff and associated standard error of the means (n = 5 per layout). Layouts sharing a letter were not significantly different from one another.

Chapter 3

Plant water loss - Impact of species choice and temperature on evapotranspiration of perennial garden plants

3.1 Introduction

Climate change is anticipated to alter UK precipitation patterns and seasonal temperatures, with an increase in irregular, heavy rainfall events and average temperatures in all seasons (IPCC, 2021; Webster *et al.,* 2017). The UK is also predicted to experience, and to an extent has already experienced, increased extreme weather events including flash flooding (Beidokhti & Moore, 2021; IPCC, 2021; Kendon *et al.,* 2023; Webster *et al.,* 2017). Approximately 3 million UK homes are at risk of flooding (Kendon *et al.,* 2023), and the replacement of vegetation with impervious surfaces only exacerbates the problem by increasing runoff (Kelly, 2016; Perry & Nawaz, 2008; Warhurst *et al.,* 2014). Intense summer rainfall means garden plants will need to remove this water quickly from the substrate by transpiration to prevent surface water accumulation, and it is necessary to explore how well different perennial species can do this in a range of summer temperature scenarios.

Plant species can restore the soil's water retention capacity via evapotranspiration and this is particularly useful when heavy rainfall leads to rapid substrate saturation (Berretta *et al.,* 2014; Stovin *et al.,* 2012). The rate of evapotranspiration and therefore the ability of individual plants to restore the soil's water retention capacity and contribute to localised flood alleviation varies (Kemp *et al.,* 2019). Plant evapotranspiration rates are maintained by a steady water supply from the growing substrate and sustain constant higher rates when water is abundant (Taiz & Zeiger, 2002). Higher temperatures will increase evaporation from the leaf surface and therefore increase transpiration rates (Gourdji *et al.,* 2013; Hatfield & Prueger, 2015), but a decline in substrate moisture content will result in leaf stomata closing and transpiration rate decreasing or ceasing (Hsiao, 1973; Jones, 1998; Stovin *et al.,* 2012; Toro *et al.,* 2019).

Genera chosen for this experimental study (*Erysimum, Salvia, Oenothera, Stachys, Pseudodictamnus* and *Verbena)* have all been noted by the Royal Horticultural Society to prefer 'well-drained' substrate, and the gardening media have included many of the species and cultivars within them on lists of plants that survive in gardens during summer heat events (Beth Chatto's Plants & Gardens, 2022a & 2022b; Horton, 2023; Wallington, 2022) (see section 2.1, Chapter 2 for more information on plant selection). Therefore, it is anticipated that these plants can survive in reduced water availability, but their ability to provide a runoff reduction service is unknown. The exception to this is *Stachys byzantina*, which was found in previous research to have a high transpiration rate that increased runoff reduction (Kemp *et al.,* 2019). Plants that prefer growing in drier substrate and require lower volumes of water have been found to employ water conservation strategies in periods of decreased water availability (Raimondo *et al.,* 2015; Taiz & Zeiger, 2002), whereas higher transpiring plants can quickly deplete the limited substrate moisture and subsequently wilt if provided with no additional irrigation (Chu & Farrell, 2022; Shrieke & Farrell, 2021). However, plants with higher transpiration rates have also been shown to reduce localised flooding in comparison to lower transpiring plants or unvegetated surfaces (Berretta *et al.,* 2014; Kemp *et al.,* 2019; Lundholm *et al.,* 2010), so there may be a balance required between reducing runoff and ensuring the plant can survive the resultant lower water availability.

An investigation into transpiration rates of perennial garden plants over short cycles of substrate 'drying' in a range of UK ambient temperatures could provide a ranking of plant transpiration rates in different UK summertime climatic conditions, which could then indicate useful plants for localised runoff reduction.

3.2 Study Aims and Hypotheses

The aim of this series of experiments was to investigate the role of transpiration in reducing substrate moisture content. In addition, it was to explore the impact of UK summer temperatures on plant evapotranspiration rates. Three temperature settings over three weeks would expose plants to typical UK summer temperatures, with week 1 testing the coolest daytime temperature of 15°C, week 2 testing the 'medium' temperature of 22°C, and the warmest temperature of 28°C tested in week 3. Previous studies have shown that increased temperature leads to higher evapotranspiration rates (Gourdji *et al.,* 2013; Hatfield & Prueger, 2015), therefore it was hypothesised that:

- Plants with higher transpiration rates would be more efficient at reducing substrate moisture content.
- Increased temperatures would result in increased transpiration rates in all species, although the rates between species would be different, with some transpiring greater volumes of water than others in a shorter period of time. This would enable a ranking of species, from highest to lowest transpiration rates in each temperature setting.

3.3 Methodology

Experiment 1 measured spring plant water loss of individual potted plants in a glasshouse setting. Experiment 2 measured summer water loss of individual potted plants in a temperature-controlled glasshouse compartment to determine the impact of a range of summer temperatures on transpiration rates.

3.3.1 Experiment 1 - Differences in plant water use between *Erysimum, Oenothera, Salvia, Stachys, Verbena* and *Pseudodictamnus*

Plants were monitored over the course of 1 week in March 2021 (referred to as experiment 1a), and new plants in March 2023 (referred to as experiment 1b) to establish their water loss via evapotranspiration. The plants were watered to field capacity on the first day of the experiment (day 0) and provided with no additional irrigation after this. Mass loss was measured daily and equated to plant evapotranspiration, in conjunction with measured leaf stomatal conductance.

Plant Material

In March 2021 (experiment 1a) plant species *Stachys byzantina*, *Salvia* 'Nachtvlinder', *Oenothera lindheimeri* 'Whirling Butterflies', and *Erysimum* 'Bowles's Mauve' were used in individual 2 L plastic pots in a peat-free growing medium (SylvaGrow Multi-purpose, Melcourt, UK). Plants were grown from 9 cm nursery plants purchased in February 2021 (Figure 3.1A). In March 2023 (experiment 1b) *Pseudodictamnus mediterraneus, Verbena bonariensis, Oenothera lindheimeri* ‘Whirling Butterflies’, and *Erysimum* ‘Bowles’s Mauve’ were propagated from cuttings taken in Autumn 2022 (Figure 3.1B). Experiment 1a used 10 plants per species and 3 control bare substrate pots, and experiment 1b used 10 plants per species and 10 control bare substrate pots.

Figure 3.1: Photographs of one experimental plant per species used for experiment 1. For scale height dimensions are provided using a metre stick placed on the pot substrate. A: Experiment 1a, from left to right - *Salvia, Erysimum, Stachys, Oenothera*. B: Experiment 1b, from left to right - *Verbena, Erysimum, Pseudodictamnus, Oenothera.*

Experiment setup and conditions

Experiment 1a was carried out in a ventilated glasshouse at the University of Reading Whiteknights campus on the week commencing 22nd March 2021 for five days, and experiment 1b on the 21st March 2023 for five days. Temperature was not regulated. Daily average minimum and maximum temperatures inside the glasshouse for experiment 1a was recorded using the in-built glasshouse temperature regulation system with an average minimum over the week of experimentation of 12.2°C and a maximum of 22.8°C. Daily air temperatures and relative humidity within the glasshouse for experiment 1b were measured every 30 minutes using a Tinytag Plus 2 Data Logger (Gemini Data Loggers, Chichester, UK), which was positioned in a shady location in the centre of the bench of plants at the same height as the plants being monitored. Daily average temperature for the week of experimentation was 14.6°C (± 5.60 SD), with an average minimum of 9.3°C and maximum of 27.4°C. Plants were set out in a random pattern across a glasshouse bench, with 20 cm spacing between plants.

Data collection

Plants were placed in the glasshouse three days prior to experimentation, and prior to this were maintained in a neighbouring glasshouse with similar environmental conditions. At the start of the experiment (day 0) all pots were saturated to field capacity, achieved via thoroughly watering each pot with a hose for 1 minute, and then placing pots in a bucket of water for 5 minutes. Plants and control pots were then removed and left to drain for approximately 1 hour, after which their weight and substrate moisture content was recorded and no additional irrigation applied until the experiment end. Substrate moisture content (two readings per pot) and pot weight was recorded daily (see section 2.2.1, Chapter 2). Stomatal conductance was collected using an IRGA on days 1-4, commencing on day 1 (24 hours after watering) using three leaves per plant and ten plants per species (method noted in section 2.2.6, Chapter 2). After data collection on the final experimentation day (day 4) the plants were watered until saturated.

3.3.2 Experiment 2 - Impact of temperature on plant water use in *Erysimum, Oenothera, Stachys* and *Salvia*

Plants were monitored over the course of three weeks in July 2021 to establish their water loss by evapotranspiration at different temperatures. Three temperature settings were tested, ‘control’ temperature in week 1, ‘medium’ temperature in week 2, and ‘warm’ temperature in week 3 (Table 3.1 below). Plants were watered to field capacity on the first day of each temperature experiment (day 0) and provided with no additional irrigation after this until day

4 when they were re-watered to field capacity. Mass loss and stomatal conductance was measured daily.

Plant Material

Plant species *Stachys byzantina*, *Salvia* ‘Nachtvlinder’, *Oenothera lindheimeri* ‘Whirling Butterflies’, and *Erysimum* ‘Bowles’s Mauve’ were used in individual 2 L pots, propagated from cuttings in Spring 2021 and grown in a peat-free growing medium (SylvaGrow Multi-purpose, Melcourt, UK) (Figure 3.2). Ten plants per species and 10 control bare substrate pots were used for all weeks tested.

Figure 3.2: Photographs of plants and layout for experiment 2 in a temperature-controlled glasshouse compartment.

Experiment setup and conditions

Experiment 2 was carried out in a glasshouse compartment at the University of Reading Whiteknights campus on the week commencing 5th July 2021 for three weeks. The compartment was temperature-controlled, with plants exposed to daily light levels from the sun outside. Air temperatures and relative humidity within the compartment were measured every 30 minutes using a Tinytag Plus 2 Data Logger (Gemini Data Loggers, Chichester, UK).

Each week of the experiment the compartment was set at a temperature defined as ‘control, ’medium’ or ‘warm’ (Table 3.1). The ‘control’ temperature of 15°C was used as a comparison to the spring temperatures of Experiment 1, with increasing temperatures representing a range of realistic summer temperatures experienced in the UK. The new temperature was set at the completion of each week's data collection and three days prior to the subsequent experimental week commencing. The lowest temperature the compartment could consistently sustain was 15°C, which is why it has been listed for the night temperatures of week 1 and 2. Actual temperatures, recorded via Tinytag data logger, were higher than the set temperatures due to the heat wave experienced across the UK at time of experimentation, and are also included below.

Week Number	Temperature category	Daytime Temperature setting (°C)	Night Temperature setting (°C)	Average recorded temperature (day/night) (°C) (± SD)	Average recorded minimum/ maximum temperatures (°C)
1	'Control'	15	15	22.1 (± 3.4)/ 16.5 (± 0.9)	14.8/28.7
2	'Medium'	22	15	26.9 (± 2.9)/ 19.6 (± 1.9)	16.4/32.7
3	'Warm'	28	18	34.8 (± 4.4)/ 25.6 (± 1.1)	22.7/43.0

Table 3.1: Experiment 2 day and night temperatures, and actual temperature range data collected from a Tinytag Plus 2 Data Logger (± standard deviation). Day and night was represented by 12 h photoperiods (day - 7am-7pm, night 7pm-7am).

Data collection

Plants were laid out randomly across two compartment benches. At the start of the experiment (day 0) all pots were saturated to field capacity (see section 3.3.1 above). Substrate moisture content (two measurements per pot) and pot weight was recorded daily. Stomatal conductance was collected using an IRGA on days 1-4, commencing on day 1 (24 hours after watering) using three leaves per plant and ten plants per species (see section 2.2.6, Chapter 2 for details). During each week plant species were 'removed' from the study when substrate moisture content became too low for guaranteed plant survival (chosen from past experience as < 0.05 $m^3 m^{-3}$ (Blanuša *et al.,* 2009)). *Oenothera* was removed at the end of day 3 on Week 1; *Oenothera* and *Salvia* were removed at the end of day 2 on Week 2; *Oenothera* and *Salvia* were removed at the end of day 2, and *Stachys* on the end of day 3 on Week 3.

3.3.3 Data analysis

Data was analysed with R (R Core Team, 2021). Mixed linear regressions were used to take into account the same plants used for each experiment and the potential for errors this could introduce. The interaction term comparing day and species was checked using Akaike Information Criteria (AIC) comparison, and was included in all code except for experiment 1b stomatal conductance data, which included a reduced number of days and used the following code:

```
Average gs ~ relevel(as.factor(species) + (1|plantref) + (1|day))
```

All residual plots were checked for normality assumptions.

3.4 Results

3.4.1 Experiment 1 - Differences in plant water use

1a. Daily water loss per pot - *Stachys, Salvia, Erysimum* and *Oenothera*

All plants had signifcantly greater water loss per pot than bare substrate control over the course of the week ($p < 0.001$) (Figure 3.3A). Each plant species also had a signficantly different rate of water loss compared to the other species over the week ($p < 0.001$), with the exception of *Stachys* and *Salvia* (Figure 3.3A), where there was a closer association between the rates of *Stachys* and *Salvia* over the five days. *Oenothera* lost significantly more water than other plant species per pot, averaging 19.5 ml per day more than *Stachys* and *Salvia* and 47 ml more than *Erysimum*, which lost the least water during the week.

1b. Daily water loss per pot - *Verbena, Pseudodictamnus, Erysimum* and *Oenothera*

Evapotranspirational water loss over the course of a week was again signficantly different per pot for all plants compared to bare substrate ($p < 0.001$), and only *Verbena* and *Oenothera* were not signficantly different from each other ($p = 0.178$) (Figure 3.3B). *Verbena* and *Oenothera* both lost significantly more water per pot than the other species over five days ($p < 0.001$), but themselves lost similar quantities of water. *Erysimum* lost significantly less water over the week than all other plant species ($p < 0.001$), losing on average of 9.5 ml (20%) less than *Pseudodictamnus* per day, 18.9 ml (36%) less than *Oenothera* and 21.3 ml (40%) less than *Verbena*.

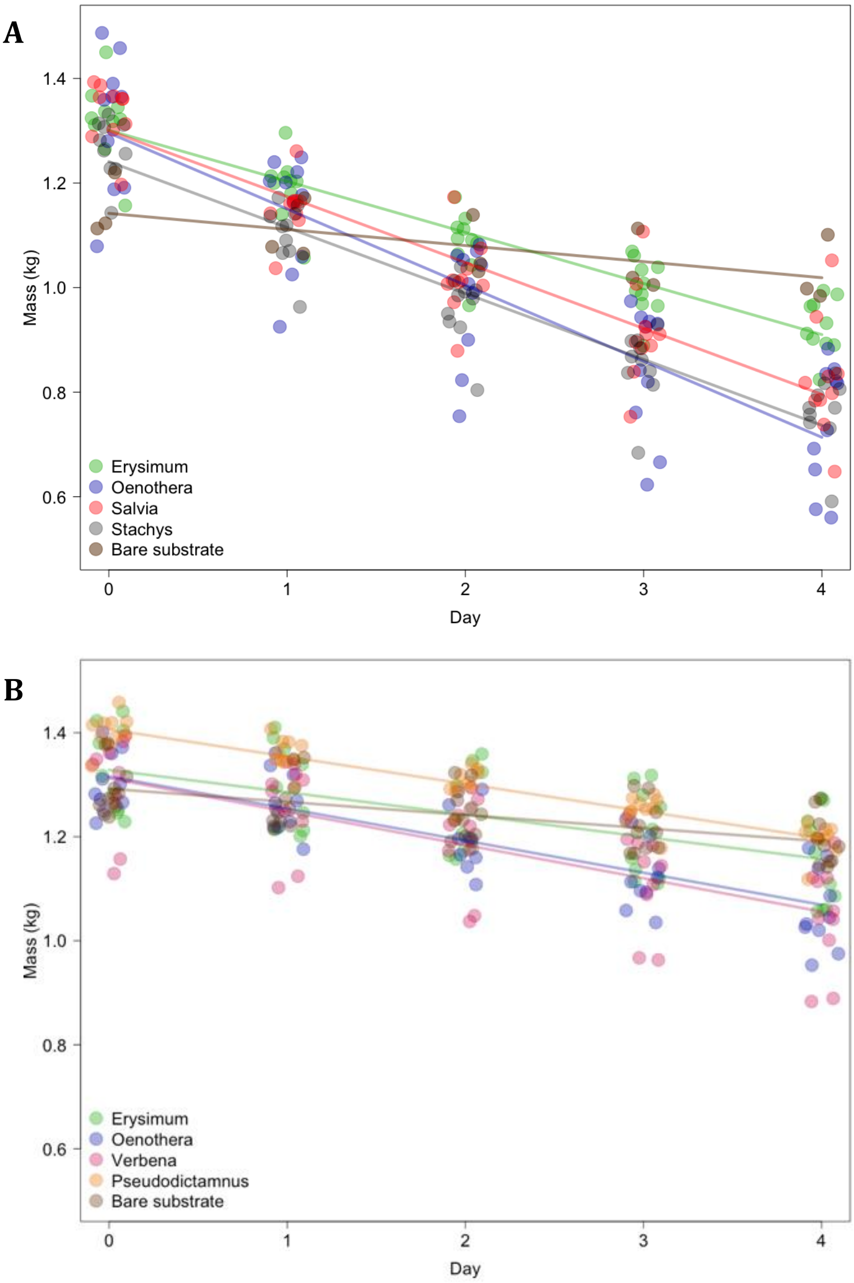


Figure 3.3: Distribution of daily water loss per pot for *Erysimum, Oenothera, Stachys, Salvia, Pseudodictamnus* and *Verbena* over 5 days after watering. Lines represent linear regressions fitted to each species. A: Experiment 1a, n = 10 for all plant species, n = 3 for bare substrate. B: Experiment 1b, n = 10 for all plant species and bare substrate.

1a. Daily water loss per leaf area - *Stachys, Salvia, Erysimum* and *Oenothera*

Water loss per standardised unit of leaf area showed a different ranking of species compared to per pot. Both *Salvia* and *Erysimum* lost significantly more water per unit leaf area over the week than *Oenothera* and *Stachys* ($p < 0.001$), which is the opposite of water loss per pot. The rate of water loss was similar for *Erysimum* and *Salvia* over the week ($p = 0.387$) but ultimate volume of water loss per m^2 of leaf area was greater for *Erysimum* ($p < 0.001$) (data not shown).

1b. Daily water loss per leaf area - *Verbena, Pseudodictamnus, Erysimum* and *Oenothera*

Water loss per unit of leaf area was significantly greater in *Verbena* and *Oenothera* over the week compared to other plant species ($p < 0.001$). Those two species were similar to each other in their rates of water loss. *Erysimum* lost significantly less water than the other plants ($p < 0.001$; *Pseudodictamnus* $p = 0.009$) (data not shown).

1a. Stomatal Conductance - *Stachys, Salvia, Erysimum* and *Oenothera*

Oenothera had a signficantly higher stomatal conductance rate than the other plants over the week ($p \leq 0.004$) (Figure 3.4A), and was the only species observed to increase in rate between day 1 and day 2 despite decreasing water availability, on average increasing from 0.24 mol m^{-2} s^{-1} to 0.32 mol m^{-2} s^{-1}. *Stachys* had a significantly higher stomatal conductance rate than *Erysimum* over the week. *Erysimum* had an average rate of 0.28 to 0.24 mol m^{-2} s^{-1} over the four days but the *Stachys* rate fluctuated and then increased between day 3 and 4 from an average of 0.22 to 0.27 mol m^{-2} s^{-1}. *Salvia* had the lowest average stomatal conductance over the week compared to the other species ($p \leq 0.01$) (Figure 3.4A), with an average rate of 0.12 to 0.14 mol m^{-2} s^{-1}, which was on average 0.12 mol m^{-2} s^{-1} lower than *Erysimum* and *Stachys*, and 0.16 mol m^{-2} s^{-1} lower than *Oenothera* across the week.

1b. Stomatal Conductance - *Verbena, Pseudodictamnus, Erysimum* and *Oenothera*

The stomatal conductance rates of each plant species were found to pair together in a similar pattern to the water loss section above. *Verbena* and *Oenothera* stomatal conductance rates were not significantly different from one another ($p = 0.758$) and neither were *Pseudodictamnus* and *Erysimum* ($p= 0.545$) (Figure 3.4B). *Verbena* and *Oenothera* had a significantly higher rate compared to *Pseudodictamnus* and *Erysimum* ($p < 0.001$). The latter two were seen to decrease over the week to 0.15 mol m^{-2} s^{-1} and 0.12 mol m^{-2} s^{-1} respectively by day 4. *Verbena*'s stomatal conductance, although higher, was also seen to begin to decline after day 2 with an average decrease from 0.29 to 0.24 mol m^{-2} s^{-1} by day 4. *Oenothera* was the only plant not seen to decrease its stomatal conductance rate over the week despite no additional irrigation provided, with an average rate of 0.26 mol m^{-2} s^{-1} on day 1, increase to 0.27 mol m^{-2} s^{-1} on day 2, and further increase to 0.28 mol m^{-2} s^{-1} on day 4.

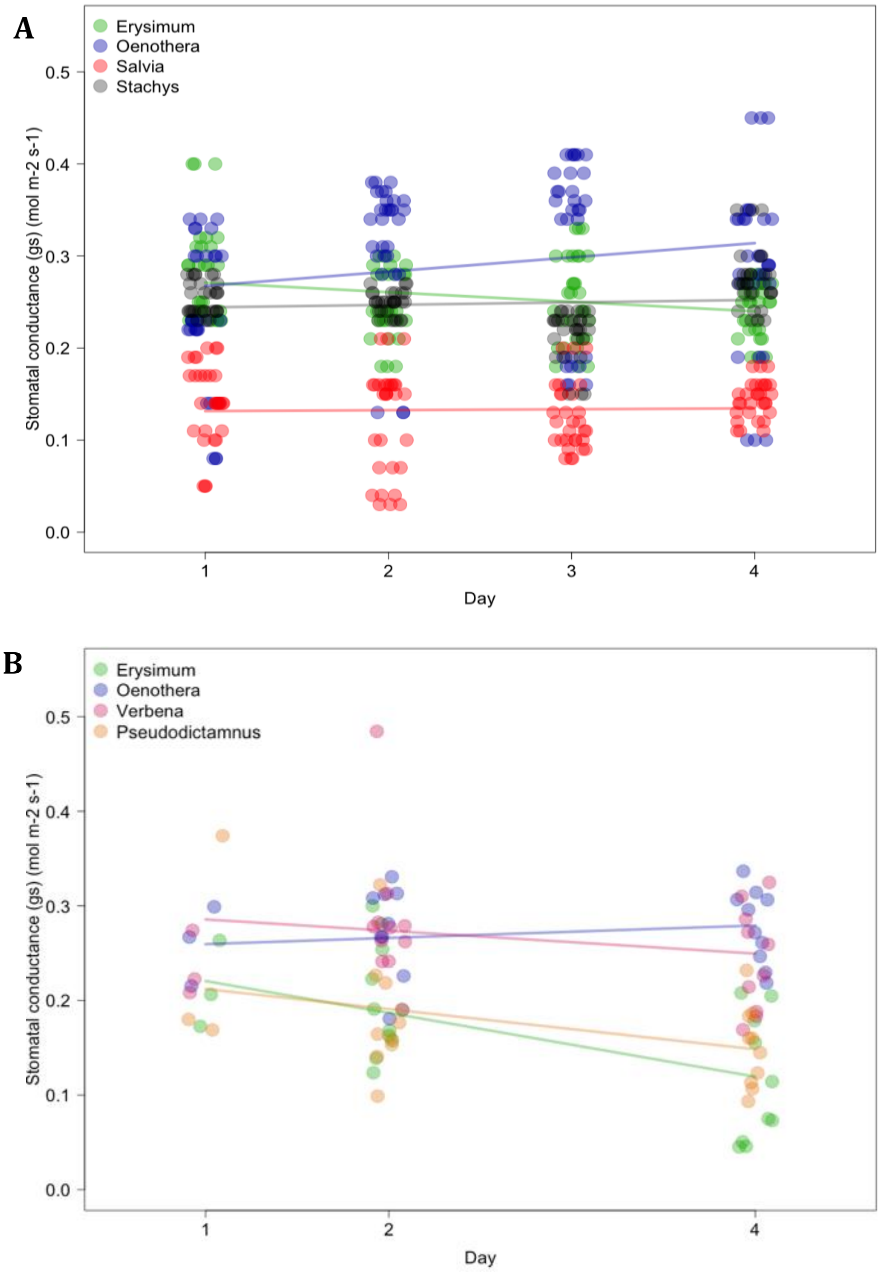


Figure 3.4: Distribution of stomatal conductance for *Erysimum, Oenothera, Stachys, Salvia, Pseudodictamnus* and *Verbena* over 4 days after watering. Lines represent linear regressions fitted to each species (n = 10). A: Experiment 1a and B: Experiment 1b.

3.4.2 Experiment 2 - Impact of temperature on plant water use

Daily water loss per pot - *Stachys, Salvia, Erysimum* and *Oenothera*

Plants lost signficantly more water per pot over each week compared to bare substrate at all temperatures tested ($p < 0.001$) (Figure 3.5) and the temperature increase led to signficantly higher volumes of water loss for all plants ($p < 0.001$). *Oenothera* and *Salvia* had similar rates of water loss for ‘medium’ and ‘warm’ temperatures ($p = 0.555$ and $p = 0.202$ respectively), and lost significantly more water than *Stachys* and *Erysimum* ($p < 0.001$). *Oenothera* and *Salvia* both rapidly decreased the substrate moisture content in the ‘warm’ temperature, with an average reduction of 0.26 $m^3\ m^{-3}$ and 0.28 $m^3\ m^{-3}$ between day 1 and 2, resulting in average pot moisture of 0.05 $m^3\ m^{-3}$ for both species on day 2 (data not shown). *Erysimum* lost signifcantly less water than the other plant species per pot ($p < 0.001$; *Stachys* ‘control’ temperature $p = 0.029$), and during the warmest temperature experiment *Erysimum* lost on average 0.041 L (17%) less than *Stachys*, 0.119 L (44%) less than *Oenothera*, and 0.138 L (49%) less than *Salvia* per day. *Erysimum* was also the only plant during the ‘warm’ temperature that was able to continue to be measured to the final day of the experiment (day 4), whereas *Stachys, Salvia*, and *Oenothera* were all removed due to low substrate moisture content and visible wilting.

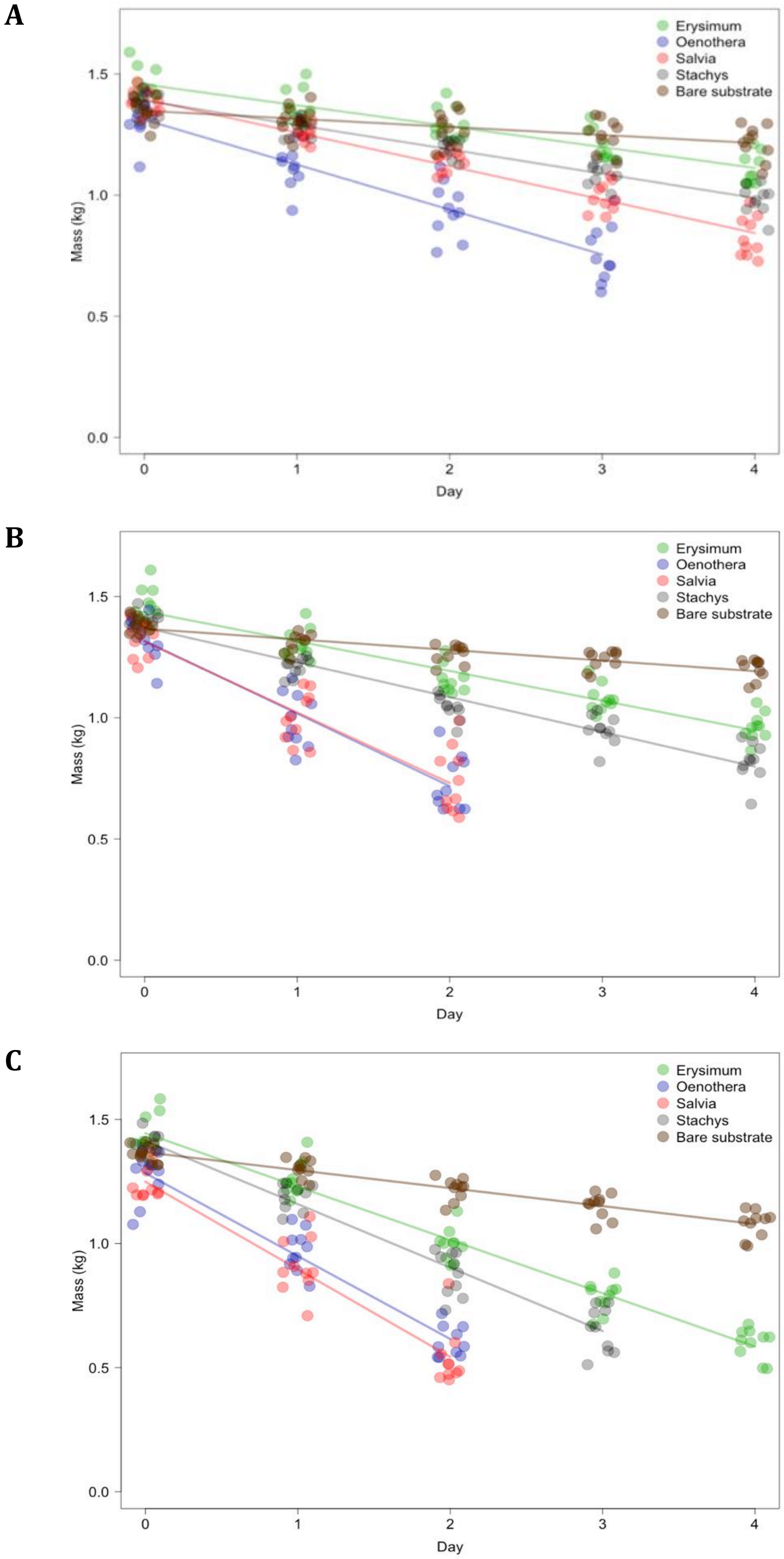


Figure 3.5: Distribution of daily water loss per pot for *Erysimum, Oenothera, Stachys,* and *Salvia* over 5 days after watering. Lines represent linear regressions fitted to each species (n = 10). A: Control temperature (22.1/16.5°C day/night). B: Medium temperature (26.9/19.6°C day/night). C: Warm temperature (34.8/25.6°C day/night).

Daily water loss per leaf area - *Stachys, Salvia, Erysimum* and *Oenothera*

Oenothera transpired signficantly more per standardised unit of leaf area at all three temperatures compared to the other plant species ($p < 0.001$) (data not shown). *Stachys, Salvia*, and *Erysimum* all transpired at similar rates at 'control' temperatures per unit of leaf area, however they each had significantly different intercepts with water loss on day 0 ranging from 9.94-16.84 L per m^2 (*Salvia* and *Erysimum* respectively) ($p < 0.001$). The warmest treatment resulted in signficantly higher volumes of water loss for all plants compared to their other temperature treatment counterparts ($p < 0.001$, except for *Oenothera* 'warm' vs 'medium' $p = 0.012$, and *Salvia* 'warm' vs 'medium' $p = 0.010$). All plants, with the exception of *Erysimum,* were removed early from the warmest temperature yet despite this *Stachys* lost signifciantly less water than *Erysimum* during that week per unit of leaf area ($p = 0.001$).

Stomatal Conductance - *Stachys, Salvia, Erysimum* and *Oenothera*

In the 'control' temperature all species has similar stomatal conductance (g_s) rates over the week, with the exception of *Oenothera* and *Salvia* ($p = 0.015$) (Figure 3.6A). *Oenothera* experienced a greater decline in g_s than *Salvia*, whose rate actually increased on average towards the end of the week by 0.05 mol m^{-2} s^{-1}. *Stachys* and *Erysimum* had similar steady stomatal conductance rates over the week ($p = 0.798$).

In the 'medium' temperature *Salvia* and *Oenothera* were comparable ($p = 0.264$) (Figure 3.6B), although only *Salvia* had a signficantly steeper decline in stomatal conductance than either *Erysimum* or *Stachys* ($p = 0.006$ and $p = 0.008$ respectively). Both *Stachys* and *Erysimum* had a small increase in average conductance rate towards the end of the week, with *Stachys* increasing on average from 0.23 on day 2 to 0.28 mol m^{-2} s^{-1} and *Erysimum* increasing on average from 0.28 on day 2 to 0.31 mol m^{-2} s^{-1} (Figure 3.6B).

In the 'warm' temperature the stomatal conductance rate of *Oenothera* and *Salvia* was again not signficantly different and they were both removed after day 2 (Figure 3.6C). *Stachys* was also removed early from the experiment on day 3 after some plants showed wilting, and although its average stomatal conductance declined from 0.27 to 0.23 mol m^{-2} s^{-1} between day 2 and 3, several plants had a stomatal conductance between 0.08-0.15 mol m^{-2} s^{-1}. *Erysimum* was the only plant species to remain without visible signs of stress for the entirety of the week in the warmest temperature, and was signficantly different from all plant species ($p \leq 0.02$; *Erysimum* vs *Stachys* $p = 0.047$), but the stomatal conductance rate noticeably decreased between day 1 and 4 by an average of 0.13 mol m^{-2} s^{-1}. It appeared overall that only the 'warm' temperature resulted in stomatal closure for *Erysimum* and *Stachys*, but 'control' and 'medium' did not.

Oenothera and *Salvia* g_s rates signficantly reduced from the 'control' to 'warm' temperature setting ($p < 0.001$) and 'medium' to warmest temperature ($p \leq 0.008$). *Erysimum* also had a signficantly reduced stomatal conductance rate between the 'warm' and 'control', and 'warm' and 'medium' temperature ($p < 0.001$). Stomatal conducatance rates was similar for *Stachys* plants in all tested temperature regimes ($p = 0.607$ 'control' vs 'warm', $p = 0.392$ 'medium' vs 'warm').

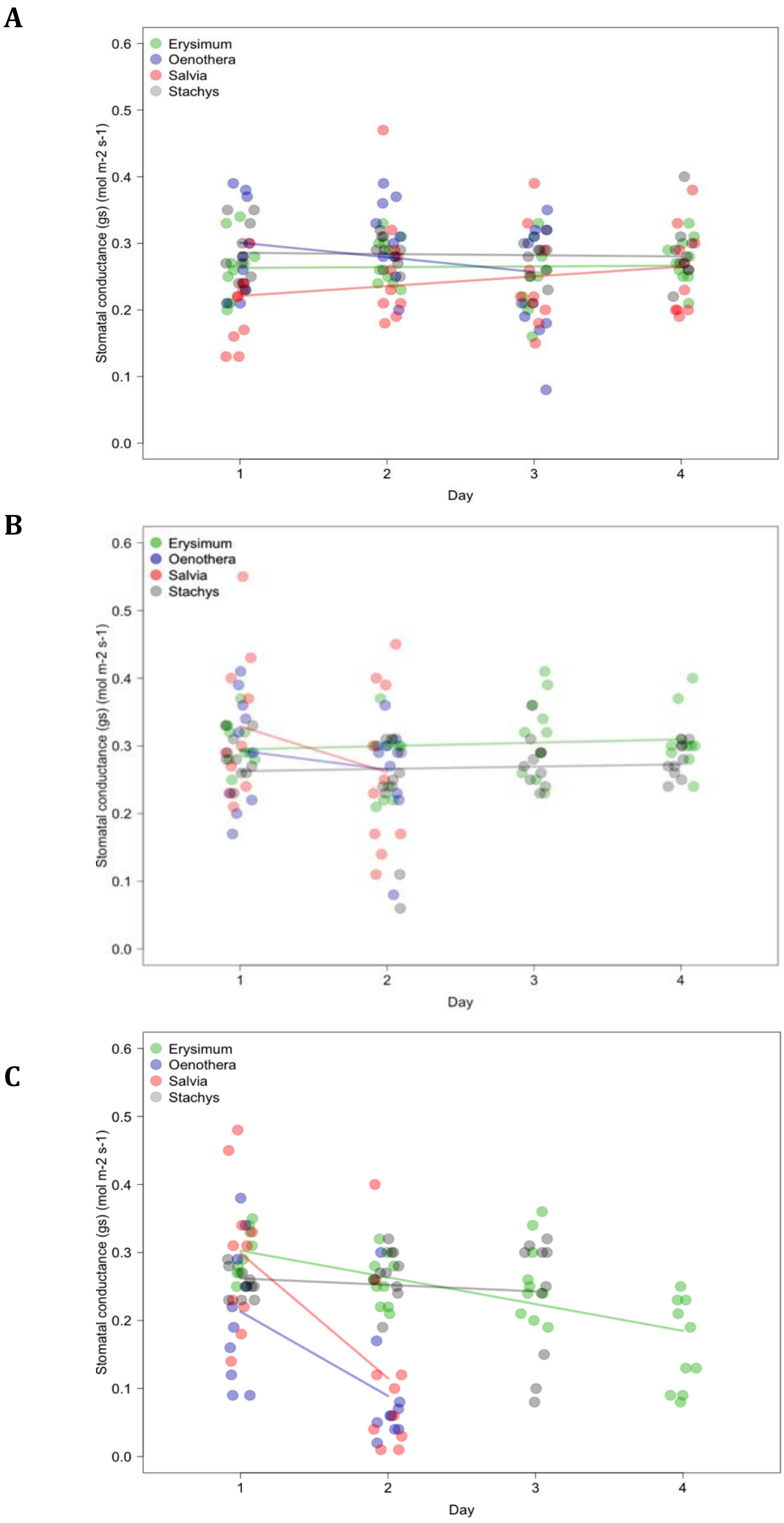


Figure 3.6: Distribution of daily stomatal conductance for *Erysimum, Oenothera, Stachys,* and *Salvia* over 4 days after watering. Lines represent linear regressions fitted to each species (n = 10). A: Control temperature (22.1/16.5°C day/night). B: Medium temperature (26.9/19.6°C day/night). C: Warm temperature (34.8/25.6°C day/night).

3.5 Discussion

Experiments conducted on popular garden perennials under glasshouse conditions in spring and summer identified differences in transpirational water loss between species, indicating that the plants would vary in their capacity to reduce soil/substrate moisture content and therefore provide a rainfall runoff ecosystem service provision.

Differences in plant water use between *Erysimum, Oenothera, Salvia, Stachys, Verbena* and *Pseudodictamnus*

During experiment 1a *Oenothera* had the highest water loss per pot, and in experiment 1b *Verbena* and *Oenothera* both had the highest water loss per pot. When water loss was expressed relative to leaf area/size of plant, to compare how efficiently water was used (and how much irrespective of the plant size), *Oenothera* in experiment 1b again had the highest rate of water loss and *Erysimum* had the lowest water loss. Conversely in experiment 1a *Erysimum* had a higher water loss per unit of leaf area than *Oenothera* and *Stachys.* Expressing water loss relative to plant size enables ‘mathematical’ comparison between the different species as the water loss is standardised over the same unit area, but in a garden context water use of the plants in sizes likely to be encountered in practice could be more helpful.

The variation in results could be due to differences in air temperature at the time of the two experiments, with a maximum of 24°C during experiment 1a (March 2021), whereas experiment 1b (March 2023) had an average maximum of 27.8°C across the week inside the glasshouse, with one day reaching a maximum of 31.8°C. These differences and their likely impact on evapotranspiration rates make a direct comparison difficult. An additional explanation could be the plants themselves. Experiment 1a used plants from a nursery that were repotted into larger containers, but the plants used in experiment 1b were grown from cuttings in the Controlled Environments glasshouses. This enabled complete control of the growing process and avoided any issues relating to pot-bound roots, something that was noted to impact the growth of the nursery plants in

2021 (see section 2.7, Chapter 2 for further information) and consequently their function too.

Impact of temperature on plant water use between *Erysimum, Oenothera, Stachys* and *Salvia*

Within a temperature-controlled environment in experiment 2, *Oenothera* transpired larger volumes of water than *Stachys* and *Erysimum* per pot and per standardised unit of leaf area across all three temperature scenarios. *Salvia* and *Oenothera* had similar rates of water loss per pot in the 'medium' and 'warm' temperatures. *Oenothera* and *Salvia* also transpired until there was very little water available, decreasing substrate moisture content to under 0.05 $m^3 m^{-3}$. Their rapid uptake of water could increase capacity for the substrate to store water after subsequent heavy rainfall events (Berretta *et al.,* 2014; Stovin *et al.,* 2012). In contrast, *Erysimum* and *Stachys* transpired at lower rates even at higher temperatures.

This experiment was conducted in short cycles of five days to monitor water use in drying substrate under a range of ambient temperatures. In the 'warm' temperature treatment, this effectively exposed the plants to water deficit due to the rapid water use. Therefore, it is also necessary to discuss drought tolerance because *Oenothera* and *Salvia* depleted the substrate moisture to low levels in a two-day period, and the gardening literature indicates these plants grow well in droughted conditions (Beth Chatto's Plants & Gardens, 2019 & 2022b; Wallington, 2022).

Drought tolerance strategies

All six studied species are categorised by the Royal Horticultural Society as preferring full sun and 'well-drained' soils (Royal Horticultural Society, no date, e, f, g, h), which, in horticultural practice, usually refers to soil that allows water drainage without drying out too quickly. *Oenothera lindheimeri* 'Whirling Butterflies' also tolerates 'dry soils' (Royal Horticultural Society, no date, e) and *Salvia* 'Nachtvlinder' is specifically referred to as 'drought-tolerant' (Royal Horticultural Society, no date, h). There are both scientific and gardening classifications for drought tolerance. From the scientific perspective tolerating drought is divided into two main types - desiccation postponement/avoiders or desiccation tolerance (Chapman & Augé, 1994; Kozlowski & Pallardy, 2002; Szota *et al.,* 2017; Wiström *et al.,* 2023). Desiccation postponement allows plants to maintain tissue hydration and therefore delay the negative effects of drought, usually by decreasing water use or seeking out additional water using deep roots. Desiccation tolerance allows plants to tolerate dehydration and continue to function because of adapted traits such as small, thick leaves that reduce water loss (Chapman & Augé, 1994; Farrell *et al.,* 2013; Nazemi Rafi *et al.,* 2019; Tabassum *et al.,* 2021). In gardening and horticultural practice, however, drought tolerance usually refers to plants that can tolerate and grow with limited soil moisture and still produce attractive floral displays in a garden setting (BBC Gardeners' World Magazine, 2024). *Oenothera* and *Salvia* both experienced wilting in this experiment, and this visible reduction in turgor pressure is a physically recognisable early response to insufficient water supply (Farooq *et al.,* 2012; Matthews *et al.,* 1984). Plants can recover with rehydration unless they reach the permanent wilting point after which they cannot regain turgor pressure even after stomatal closure, therefore wilting and substrate moisture content were both used as indicators of the plant's inability to continue in this experiment (Poë *et al.,* 2015; Szota *et al.,* 2017). This reaction was more rapid in both of these plant varieties than it was in either *Stachys* or *Erysimum*, the latter of which did not wilt during the experimental period (even with an average substrate moisture content of 6.6% on the final day of experimentation) regardless of temperature tested, and does not tally with the gardening literature classifying *Oenothera* or *Salvia* as drought tolerant.

Discrepancy with the horticultural literature

A recent study by Tabassum *et al.* (2021) found that horticultural classification of Australian drought tolerant plants overall did not agree with their experimental analysis of drought tolerance. To address inconsistencies with the horticultural classifications they used five plant traits including leaf water potential at turgor loss point, and leaf thickness and mass, to help identify the drought strategies of over 100 plant varieties. They found that the majority of the studied species classified in horticulture as drought tolerant were actually dehydration avoiders, employing a desiccation postponement strategy, rather than tolerating desiccation. Considering *Oenothera* originates from the dry North American prairies of Texas and Louisiana (Burnett & van Iersel, 2008; Ksiazek-Mikenas *et al.,* 2021; Royal Botanic Gardens Kew, 2007), and *Erysimum* is commonly known as wallflowers, named because they are found growing between the stones of garden walls and a large proportion of the species grow on mountains (Moazzeni *et al.,* 2014), drought tolerance in both species was expected, but the response from *Oenothera* in our experiments did not indicate tolerance. However, breeding plants for their ornamental qualities has been found in some cases to reduce the new cultivar's stress tolerance to waterlogging and drought, with aesthetics replacing survival traits (Lewis *et al.,* 2019), which may make comparisons between wild parents and bred varieties speculative only. Drought tolerance is also not always related to the climate of plant origin or ecological history (Cameron *et al.,* 2006; Schrieke & Farrell, 2021; Tabassum *et al.,* 2021; Watkins *et al.,* 2020) but instead to the plant traits, particularly leaf water potential and turgor pressure, stomatal closure response, leaf area and shape, and root architecture (Chu & Farrell, 2022; Farrell *et al.,* 2013; Nazemi Rafi *et al.,* 2019; Tabassum *et al.,* 2021; Toro *et al.,* 2019). This experiment highlights the gap between science or trait-based classifications and the practical literature, and indicates more work is required to incorporate science with gardening information, considering the majority of gardeners would select plants based on recommendations from the latter. Selecting a plant for its drought tolerance using only the gardening literature may not result in plants that thrive in those environmental conditions.

Transpiration rate and stomatal closure in response to drought

Plants with high transpiration rates, whilst able to deplete substrate moisture more quickly, also display physical symptoms of drought stress including loss of turgor pressure and wilting when water availability is low (Szota *et al.,* 2017). Both *Salvia* and *Oenothera* responded to lower substrate moisture on day 2 in the 'medium' and 'warm' temperatures (average substrate moisture content for *Salvia* was 13.5% and 4.8% in 'medium' and 'warm' respectively, and *Oenothera* was 10.8% and 5.3% respectively) by decreasing their stomatal conductance rates to 0.11 mol m^{-2} s^{-1} and 0.09 mol m^{-2} s^{-1} respectively. Environmental factors including relative humidity and air temperature impact stomatal conductance (Toro *et al.,* 2019), and as water availability decreases plants respond by closing their stomata to conserve moisture and reduce loss via transpiration (Davies *et al.,* 2002; Hsiao, 1973; Jones, 1998). But for *Oenothera* and *Salvia* this stomatal closure was at a point when their water loss was potentially too great to survive the remainder of the week without additional irrigation, based on the decreased substrate moisture content. The stomatal closure also appeared to be too late to allow the plants to conserve water in higher temperatures (Figure 3.6). Previous research found that deciduous shrub *Forsythia* maintained relatively high stomatal conductance even in severely water-stressed leaves, potentially to use available light for photosynthesis even when experiencing water deficit (Cameron *et al.,* 2006), which could possibly explain the observed responses of *Oenothera* and *Salvia* 'Nachtvlinder' as they continued to rapidly transpire even when water availability became limited. Related species *Salvia officinalis* was observed employing an anisohydric drought strategy during water stress, maintaining high stomatal conductance but only until substrate water was depleted (Raimondo *et al.,* 2015), which did not appear to be the case with *Salvia* 'Nachtvlinder'.

Ornamental plants can adapt to reduced watering by implementing stomatal control but this results in smaller, compact plants over time (Blanuša *et al.,* 2009; Cameron *et al.,* 2006) or a significant increase in flowering after water is reinstated (Demotes-Mainard *et al.,* 2013; García-Navarro *et al.,* 2003). Related species *Salvia dolomitica* and *Salvia sinaloensis* tolerated reduced water availability at 60% of the volume given to control plants, but reduction of 40% and 20% inhibited leaf growth, caused visual/aesthetic damage to foliage, and in some cases plant death (Caser *et al.,* 2012). Water restriction of *Oenothera* 'Siskiyou Pink' resulted in reduced shoot dry weight (Burnett & van Iersel, 2008). Plant adaptation to reduced watering could therefore occur in taxa related to the *Oenothera* and *Salvia* used in this experiment, but requires further investigation to determine if this is the case, and no adaptation occurred during the course of this experiment. Although when water is abundant or waterlogging occurs, plants with high transpiration rates in other studies, including *Oenothera, Stachys* and *Salvia* species, have reduced substrate moisture and also tolerated short-term waterlogging (Kemp *et al.,* 2019; King *et al.,* 2012; Yuan & Dunnett, 2018), which could indicate that plants with higher transpiration rates could survive inundation and aid in the reduction of surface water over a small area.

Plant traits linked to drought tolerance

Certain plant traits have been associated with increased drought tolerance (Heim *et al.,* 2023; Klein *et al.,* 2013). Plants with smaller leaf area have been shown to experience less vulnerability to drought (Kozlowski & Pallardy, 2002; Nagase & Dunnett, 2010), which may be a factor attributed to *Erysimum's* response across the temperature gradients tested, however *Oenothera* also had a low leaf area in these experiments and experienced wilting, therefore more than leaf area must be a factor for these plants. Chu and Farrell (2022) investigated the concept of 'fast' and 'slow' plant traits, which develop in response to resource availability. 'Fast' traits, including larger shoot dry mass, was more common in plants exposed to resource-rich environments to enable 'rapid resource acquisition', whereas 'slow' traits, including smaller dry shoot mass, were linked to water conservation. They found that plants with a higher allocation of slow traits and greater drought tolerance employed an anisohydric strategy, closing their stomata later in water deficit conditions and therefore continuing to use water (Chu & Farrell, 2022), which was something that was observed with *Erysimum* in the 'warm' temperature experiment. Other traits in combination including leaf trichomes, leaf orientation and greater rooting depth, have also been shown to aid drought tolerance (Farrell *et al.,* 2013; Kozlowski & Pallardy, 2002; Nazemi Rafi *et al.,* 2019; Tabassum *et al.,* 2021; Wasson *et al.,* 2012), although *Oenothera* has leaf trichomes and this did not appear to aid drought tolerance in this experiment. Greater root mass has also been linked with greater plant water use (Markesteijin & Poorter, 2009; Larson & Funk, 2016) but this was not the case for Chu and Farrell (2022) due to root growth restricted by plant containers that stopped plants behaving as they would in the field.

Although roots were not assessed in this experiment, root restriction could be one of the explanatory factors for *Oenothera's* response.

Oenothera's **response to low water availability in experiment 2**

In this experiment *Oenothera* lost significantly more water than *Erysimum* and *Stachys* but then appeared negatively impacted when its high transpiration rate depleted substrate moisture below 5%, leading to a significant decline in stomatal conductance rate and eventual wilting. Shrieke and Farrell (2021) observed a similar response in a green roof setting using *Lolium perenne*, which had the highest transpiration rate in their study in well-watered and water deficit conditions, and although it responded to water deficit by reducing its transpiration rate this still led to desiccation. However, a potential difference that limits comparisons between these two species is the type of root system. *Lolium* has fibrous roots (CABI Digital Library, 2013), whereas *Oenothera* has been noted in some literature to have a taproot, particularly as a seedling or younger plant (Mahr, no date), although root morphology is plastic and can differ depending on substrate type and oxygen levels, leading to ramified roots instead. Within desiccation-tolerant drought strategies there are plants that are known as water spenders that consume large volumes of water even when availability is reduced, facilitated by a deeper rooting system (Nazemi Rafi *et al.,* 2019; Wiström *et al.,* 2023). This experiment was conducted in pots, which would have restricted root growth and access to water (Chapman & Augé, 1994; Chu & Farrell, 2022; Farrell *et al.,* 2013), however in the field *Oenothera's* long roots have the potential to access water deeper in the substrate and this could aid its survival when water is in deficit. This was also observed with 'drought-tolerant' species *Helianthus angustifolius*, the roots of which were limited by a pot experiment, and this plus slower stomatal closure led to leaf desiccation (Chapman & Augé, 1994). It could be speculated that *Oenothera*, as a plant noted in the gardening literature to grow in drought conditions (Beth Chatto's Plants & Gardens, 2019 & 2022b; Wallington, 2022), may employ a water-spending desiccation strategy, whereas *Lolium* uses available resources, tolerates desiccation, and then recovers quickly upon rehydration. In contrast, *Erysimum* appeared to tolerate lower substrate moisture content even at higher temperatures and could be a suitable garden plant in areas of lower rainfall, as it may not require as much additional irrigation as *Oenothera*.

Evergreen versus deciduous experimental plant species

Despite the literature (Royal Horticultural Society, no date, e, f, g, h) indicating all the chosen species have comparable growing conditions, evergreen *Stachys, Erysimum*, and *Pseudodictamnus* had lower water loss than their deciduous counterparts. Previous research found *Stachys* had a higher transpiration rate than *Sedum*, which made it useful for removing water from the substrate of a green roof (Blanuša *et al.,* 2013; Kemp *et al.,* 2019). However, *Sedum* is a CAM plant with a low transpiration rate (Basu *et al.,* 2016; Kemp *et al.,* 2019; Vaz Monteiro *et al.,* 2017), and in experiment 1 and 2 *Stachys* had a lower transpiration rate than both *Oenothera* and *Salvia*, therefore the rankings of plant transpiration rates change depending on the species they are tested against. *Pseudodictamnus* and *Stachys* both have comparable traits (silver leaves, trichomes), which could potentially explain their performance in experiment 1. However, *Erysimum* does not have either of those traits and had a significantly lower transpiration rate than *Stachys* and *Pseudodictamnus*. The commonality between these three species, other than growing conditions, is they all retain their leaves in the winter months; therefore, their evergreen nature could be one of the traits separating them from *Oenothera, Salvia*, and *Verbena*. Previous research comparing evergreen and deciduous plants is vast, however there is usually a focus on broad-leaved deciduous plants versus needle-leaved evergreen plants (both usually trees) (Beidokhti & Moore, 2021; Geldenhuys, 1993; Markesteijin & Poorter, 2009; Peters *et al.,* 2011; Richardson *et al.,* 2010; Tiwary *et al.,* 2016; Xiao & McPherson, 2002), which makes inferences with experiment 1 and 2 difficult. Despite this, studies have suggested that variations in leaf phenology are driven by temperature rather than moisture availability even in cases of drought exposure (Richardson *et al.,* 2010; van Ommen Kloeke *et al.,* 2012), which may explain why the evergreen plants were better at conserving substrate moisture in increased temperatures compared to deciduous *Oenothera* and *Salvia*.

The literature considers evergreen plants to be more drought-tolerant than deciduous plants by the nature of possessing specific traits (lower photosynthesis and transpiration rates, low specific leaf area) that promote water conservation (Givnish, 2002; Markesteijin & Poorter, 2009; Tomlinson *et al.,* 2013). Deciduous shrubs and herbs have been found to maintain a high stomatal conductance under well-watered conditions to enable rapid water extraction from the substrate and fast growth in spring (Farrell *et al.,* 2013; Givnish, 2002; Medrano *et al.,* 2009). However, for Mediterranean species, research by Medrano *et al.* (2009) indicated that although woody evergreen shrubs had higher water use efficiency under water stress conditions, all plants, including deciduous species, increased both their leaf area mass (linked to drought tolerance) and water use efficiency in response to drought progression, therefore the capacity to withstand water stress was not related to specific growth forms for plants in this region. There is the potential that drought-tolerant species, regardless of evergreen or deciduous leaf habits, may be able to control or reduce water uptake during drought conditions, therefore experiment 2 results may be due to drought tolerance strategies used by the individual species more than because of leaf type.

3.6 Limitations

- Although the glasshouse compartment used for experiment 2 had set temperatures, during week 3 when testing ‘warm’ temperatures the UK experienced a heat wave with outside temperatures surpassing 30°C in Reading, and this resulted in poorer temperature control and daytime compartment temperatures above the set 28°C. Recorded temperatures inside the compartment were 34.1°C on average during the daytime (Table 3.1). This, although unintended, has had an impact on transpiration rates. However, as heat waves and heat stress are becoming more common during the UK summers (with a subsequent heat wave in 2022 with temperatures reaching 40°C) testing plants in these conditions is not unrepresentative of conditions in a UK changing climate.

3.7 Key conclusions

Oenothera, Salvia and *Verbena* exhibited relatively high transpiration rates in comparison to *Stachys, Pseudodictamnus*, and *Erysimum*, and *Oenothera* and *Salvia* in the ‘warm’ temperature quickly depleted the substrate moisture content. This could potentially help them provide a ‘rainfall management’ ecosystem service, although additional irrigation may be required when water availability is low. The plant responses did not however match the classifications given to them in the gardening literature, and their resistance to lower substrate moisture content, and potentially drought, is uncertain. In these experiments the plants’ ability to quickly reduce excess substrate moisture did not coincide with an ability to continue to function in those resulting conditions, therefore choosing garden plants for their tolerance in specific climatic conditions or for their potential ecosystem service provision based on the gardening literature alone may not result in suitable selections. However, tested plants in potted experiments may not represent how plants behave in nature and therefore further research to compare gardening classifications with experimental plant responses in the field is required.

Chapter 4

Impact of planting combinations and time of year on plants' evapotranspiration and retention of rainfall within the canopy

4.1 Introduction

Overall, there has been a decrease in the amount of vegetation in UK gardens, replaced by impermeable surfaces for uses such as driveways and patios, as well as artificial grass replacing living lawns (Chalmin-Pui *et al.,* 2019; Simpson & Francis, 2021; Warhurst *et al.,* 2014). Increase in the areas of impermeable surfaces and subsequent decrease of vegetated areas, leads to increased surface water accumulation and flooding (Kadavergu *et al.,* 2021; Kelly, 2016; Perry & Nawaz, 2008). Incorporating carefully selected planting schemes into domestic gardens has the potential to attenuate rainfall by reducing the volume of rainwater runoff and therefore mitigate the negative impacts of urbanisation (Kemp *et al.,* 2019; MacIvor & Lundholm, 2011; Stovin *et al.,* 2015).

Plants can reduce surface water and mitigate rainfall events by intercepting and storing rainwater in their canopies, therefore reducing the volume of water falling to the ground, and removing water from the growing substrate or soil using the mechanism of evapotranspiration (Berretta, *et al.,* 2014; Lundholm *et al.,* 2010; Kemp *et al.,* 2019). Substrate is considered the most significant rainwater storage 'pool', with interception of rainfall by plant canopies contributing only an additional 4% of storage (MacIvor & Lundholm, 2011). However, substrate has a maximum volume of water it can retain before runoff is generated (Stovin *et al.,* 2015). A plant's ability to remove water quickly from the substrate via a high transpiration rate enables more rapid restoration of the substrate water storage capacity and ability to take on more rainfall (Berretta *et al.,* 2014; Kemp *et al.,* 2019; Stovin *et al.,* 2012). Previous research has also found that plants with larger canopies, greater leaf area, and traits including hairy leaves, are better at retaining water in their canopies (Blanuša & Hadley, 2019; Kemp *et al.,* 2019; Nagase & Dunnett, 2012), and several traits in combination, for example leaf hairs, larger leaf area, and greater evapotranspiration rate can provide the most effective rainwater management (Blanuša & Hadley, 2019; Kemp *et al.,* 2019; Lundholm *et al.,* 2010).

Within domestic gardens, aesthetics, style and planting design are important factors that can drive planting decisions, the latter of which features the mixing of different plant types to create visually interesting garden beds (Chalmin-Pui *et al.,* 2019; Kendal *et al.,* 2012; van den Berg & van Winsum-Westra, 2010). There is a positive relationship between people's wellbeing and aesthetic preferences within a garden (Hoyle *et al.,* 2017b) and aesthetics is also one of the most important factors facilitating people valuing a plant's ecosystem services (Frantzskaki*,* 2019), which makes planting choice an influential factor to consider for how it impacts both people and the environment.

As planting design has developed, contemporary planting theory has included trait-based plant selection to create aesthetically pleasing displays, a method also used when identifying plants for ecosystem service delivery (Cameron & Blanuša, 2016). Ecological theories of plant behaviour, competition for resources and survival strategies have been applied to planting design, with inspiration taken from naturally occurring plant communities, with the aim that the newly created planting groups would thrive with little intervention or management (Hansen & Stahl, 1993; Kühn, 2011; Grime, 1974; Rainer & West, 2015). Grime (1974) developed the CSR theory of plant interactions using plant traits and behaviours to categorise all species into competitors, stress tolerators or ruderals, which has been adapted and applied to green roof planting communities to develop more robust planting schemes (Lönnqvist *et al.,* 2023; Rivière *et al.,* 2024). This theory has been developed further and used within planting design by Rainer and West (2015) who created planting layers and categorised plants based on their traits and use within a design to create attractive beds. Mixing plants with specific traits to better suit spatial niches allowed different competitive abilities in environmental conditions to coexist (Rainer & West, 2015). Their theory also incorporated ecosystem service delivery in a relatively simplistic way, but this can be used as groundwork to create more complex schemes that merge design and service delivery.

A small body of previous research on a range of regulating ecosystem services, including rainwater retention and runoff reduction, has also found using carefully selected planting combinations with specific traits can provide improved outcomes compared to individual species (Heim *et al.*, 2023; Lundholm *et al.,* 2010; Nagase & Dunnett, 2012; O'Carroll *et al.,* 2023). Both rainwater retention and cooling services were provided on a green roof using planting combinations of herbaceous forbs, grasses, and succulents (Lundholm *et al.,* 2010); a garden bed of mixed perennial planting was able to provide greater rainwater retention than lawn (Nagase & Dunnett, 2012; Yuan *et al.,* 2017), and a combination of deciduous perennials and shrubs reduced soil temperatures in summer compared to other planting designs (Nazemi Rafi & Kazemi, 2021).

Planting design can impact some ecosystem service delivery and therefore has an important role to play in domestic gardens. The selection of popular plant combinations with different traits, including evergreen or deciduous growth habits, hairy or smooth leaves, and fast and slow transpiration rates, can now be tested for rainwater runoff reduction. This will help inform planting choices in a garden setting to provide localised environmental benefits, and determine whether service provision can be improved when mixing plants with different traits, with impact explored in both summer and winter rainfall conditions.

4.2 Study Aims and Hypotheses

Despite perennial plants being a common feature in public and private green spaces (Oudolf & Kingsbury, 2013; Rainer & West, 2015), limited research has been done into their environmental benefits in a garden setting, including the reduction of rainfall runoff, with research in the field dominated by larger plants (trees and shrubs (Beidokhti & Moore, 2021; Ginebra-Solanellas *et al.,* 2020; Pataki *et al*., 2011; Xiao & McPherson, 2011)), rain gardens (Laukli *et al.,* 2022b; Nocco *et al.,* 2016; Yuan & Dunnett, 2018), and green roofs (Heim *et al.,* 2017; Lundholm *et al.,* 2010; Nagase & Dunnett, 2012; Stovin *et al.,* 2015). Plant traits including leaf hairs and high transpiration rate have been shown to reduce rainfall runoff but the impact of retention of rainfall within canopies in different seasons has not been investigated in domestic gardens with regards to service delivery potential. In addition to this, the vast majority of studies have focused on plant ‘monocultures’ rather than plant combinations and their potential interactions, but as planting combinations play a significant role in how a garden is designed this is an important aspect to explore. These experiments investigate planting combinations in experimental conditions rather than in a garden, however the findings can be indicative of the potential of these plants at reducing rainfall runoff. The objectives of this chapter were to:

- Investigate the impact that combinations of different plants with varying traits and different designs have on rainfall runoff reduction, and determine whether specific trait combinations can result in better service provision. It was hypothesised that combinations of plants with hairy leaves would store greater volumes of rainfall within the canopy and produce less runoff compared to those with smooth leaves. It was also hypothesised that plants with higher transpiration rates/higher water use would produce less rainfall runoff compared to those with slower rates, as they would reduce substrate moisture content more prior to rainfall application and therefore increase substrate rainfall storage capacity.
- Investigate the seasonal differences in runoff reduction by different planting combinations via both rainfall retention in the canopy and evapotranspiration. It was hypothesised that evergreen plants would provide greater rainwater retention in winter compared to deciduous plants.

4.3 Materials and Methods

Model gardens and plant combinations in monocultures and mixtures were tested for their ability to reduce rainfall runoff. Experiment 3 used outdoor model gardens to test retention of rainfall in the canopy in summer and winter; experiment 4 used miniature model gardens to test retention in the canopy and plants’ evapotranspiration in summer and winter; and experiment 5 used miniature model gardens to test plants compared to pervious surfaces for retention in the canopy and plants' evapotranspiration in summer. Details about each experiment can be found in Table 4.1 and sections below.

Experiment	**Season**	**Type of model garden**	**Species/ materials**	**Retention of rainfall in the canopy**	**Plants' evapo-transpiration rate**	**Replicate number**
3 - Rainfall application on outdoor model gardens - effect of planting combinations and time of year and impact of retention of rainfall within the canopy	Summer, winter	Outdoor model gardens	• *Erysimum* • *Oenothera* • Mixed *Erysimum x Oenothera* • Bare substrate	Yes	No	3 gardens per layout
4 - Rainfall application on miniature model gardens in the glasshouse - effect of planting combinations and time of year and impact of plants' evapo-transpiration and retention of rainfall within the canopy and substrate	Summer, winter	Miniature model gardens	• *Erysimum* • *Oenothera* • *Pseudodictamnus* • *Verbena* • Mixed *Erysimum x Oenothera* • Mixed *Pseudodictamnus x Verbena* • Bare substrate	Yes	Yes	5 gardens per layout
5 - Rainfall application on miniature model gardens in the glasshouse - effect of pervious surfaces compared to the impact of plants' evapotranspiration and retention of rainfall within the canopy and substrate	Summer	Miniature model gardens	• *Pseudodictamnus* • Mixed *Pseudodictamnus x Verbena* • Bare substrate • Bark chippings • Gravel	Yes	Yes	5 gardens per layout

Table 4.1: Experiments 3, 4 and 5 data collection summaries.

4.3.1 Experiment 3 - Rainfall application on outdoor model gardens - Effect of planting combinations and time of year and impact of retention of rainfall within the canopy

The effect of planting combinations and time of year were tested using outdoor model gardens in summer and winter 2022. Monocultures and mixed planting combinations of *Erysimum, Oenothera*, and bare substrate (control) were tested with a rainfall applicator for the capacity of the canopy to retain rainfall, with three replicate model gardens of each layout randomly positioned outside on the grounds of the Controlled Environments Laboratories (University of Reading, Reading, UK) (Table 4.1; Figure 4.1). Model gardens were made from treated plywood built into an open box 1.2 m x 1.2 m x 20 cm with four drainage holes along the base of one side of the box only. Each garden contained nine large plants, originally planted in December 2021 from 5 L containers that were allowed to grow over the year of experimentation, and 330 L of peat-free growing medium (SylvaGrow Multi-purpose, Melcourt, UK) including from the individual plant root balls. Four rainfall simulation tests were conducted per season on each garden. A summary of the rain applicator and prior experiment trials can be found in Chapter 2.

Planted model gardens each contained either a monoculture of *Erysimum* or *Oenothera*, or ‘chequered’ mixed planting layout of the two plant varieties, referred to as the Mixed layout throughout experiment 3 (Figure 4.1). Chequered rather than striped layouts were chosen after a preliminary experiment indicated no significant difference in performance between the different mixed designs (see section 2.7.3, Chapter 2), and chequered therefore allowed for a more even distribution of the two plants.

BS

E7	E8	E9
E4	E5	E6
E1	E2	E3

O7	O8	O9
O4	O5	O6
O1	O2	O3

E4	O4	E5
O2	E3	O3
E1	O1	E2

Figure 4.1: Block layout of the model gardens positioned on the grounds of the University of Reading (not to scale) (left), and model garden photographs (right) from top to bottom show summer *Erysimum* monoculture, *Oenothera* monoculture, Mixed, and winter *Erysimum* monoculture *and Oenothera* monoculture. Planting layouts of plants for experiment 3 (bottom): E = *Erysimum*, BS = Bare substrate, O = *Oenothera*, n = 3 gardens per layout.

Data collection was carried out on rain-free days with minimal wind; weather data was collected from a miniature weather station on site. Weather data can be found in Table 4.2 below. The rain applicator was attached to the mains water supply and positioned above the model garden with the nozzle above the centre of each bed. Ten plastic containers (750 ml total volume capacity, dimensions 193 x 132 x 60 mm) and five rain gauges were positioned on the garden plot to be tested (see section 2.7.3, Chapter 2 for details). Model gardens were tested in randomised blocks of replicates with all twelve gardens tested in one day. Rainfall was applied for 15 minutes, after which the rain applicator was turned off and water volumes recorded for the rain gauges and plastic containers.

Data collection date	**Season tested**	**Average daily recorded temperature (°C)**	**Minimum daily recorded temperature (°C)**	**Maximum daily recorded temperature (°C)**	**Daily wind speed (mph)**
7.06.2022	Summer	14.5	11.2	20.9	2-10
14.06.2022	Summer	15.5	6.9	24.1	4-8
22.06.2022	Summer	18.1	9.1	27.1	7-9
5.07.2022	Summer	14.4	7.2	21.6	7-10
30.11.2022	Winter	7.5	4.9	10.1	4-5
1.12.2022	Winter	2.3	-1.0	5.5	2-4
2.12.2022	Winter	3.6	-0.3	7.5	5-8
3.12.2022	Winter	5.2	2.9	7.4	10-13

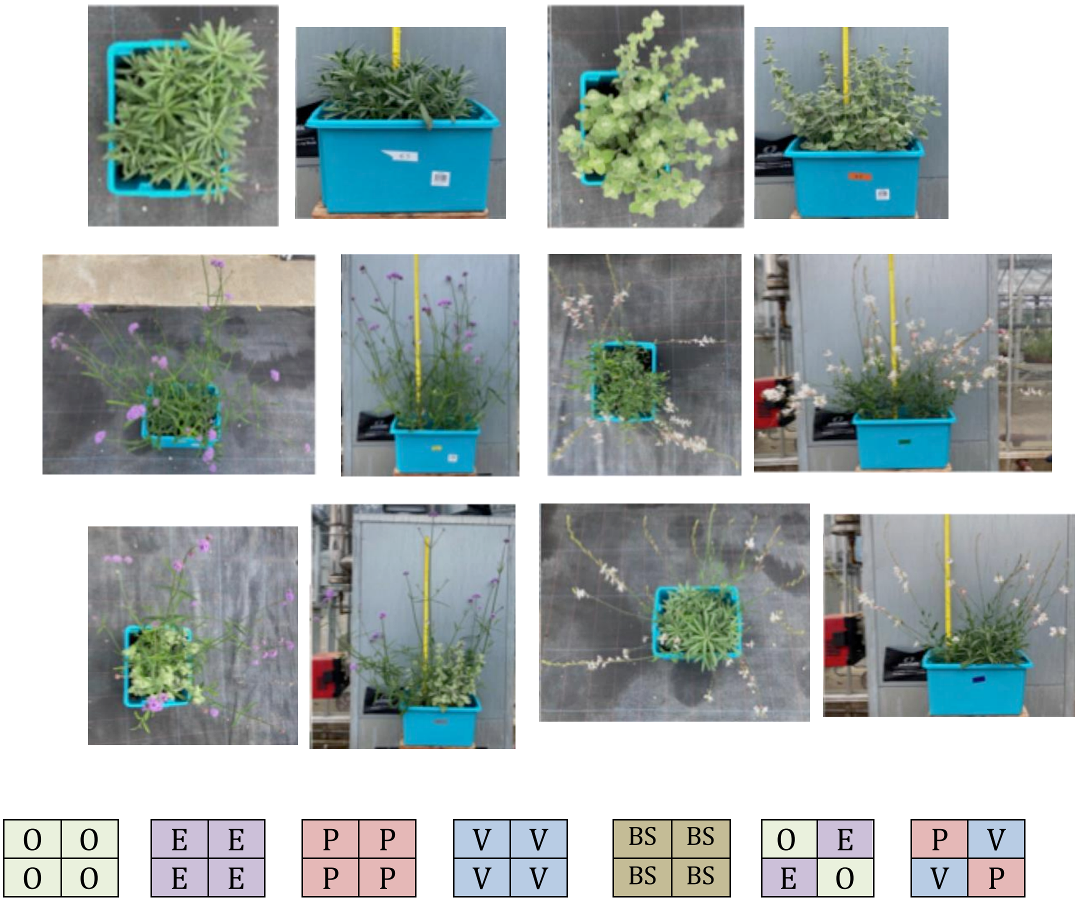
Table 4.2: Average daily, minimum and maximum temperatures and wind speed range for data collection days for experiment 3. Recorded from Reading University Weather Station.

4.3.2 Experiments 4 and 5 - Rainfall application on miniature model gardens in the glasshouse - Effect of planting combinations and time of year and impact of plants' evapotranspiration and retention of rainfall

Miniature model gardens were used to test planting combinations in winter and summer of 2023 using a rainfall applicator, and in September 2023 to test plants compared to non-vegetative pervious surfaces (Table 4.1). Retention of rainfall within the canopy and evapotranspiration impact was tested using a similar methodology to experiment 3. Miniature model gardens were created using 14 L plastic container boxes (400 mm wide x 280 mm depth x 200 mm height) (full design and setup can be found in section 2.7.3, Chapter 2), planted before each seasonal experiment began and destructively harvested at the end of each experiment, therefore new plants were used for winter, summer, and pervious surfaces.

4.3.3 Experiment 4 - Rainfall application on miniature model gardens in the glasshouse - Effect of planting combinations and time of year and impact of plants' evapotranspiration and retention of rainfall within the canopy and substrate

All plants were grown from cuttings in a heated glasshouse at the Controlled Environments Laboratories at the University of Reading Whiteknights campus. For the winter experiment plants were potted into 9 cm containers in December 2022, transplanted into miniature model gardens on the 20th January 2023 and relocated outside. Summer plants were potted into 9 cm containers in May 2023, planted into miniature model gardens on the 30th May 2023 and moved to an unheated glasshouse. Each planted layout contained four plants and a peat-free growing medium (SylvaGrow Multi-purpose, Melcourt, UK), which including plant root balls totalled 7.2 L of substrate. Plants were arranged in monocultures of *Erysimum*, *Oenothera*, *Pseudodictamnus*, *Verbena* or bare substrate control, or a chequered mixed planting layout of either *Erysimum* and *Oenothera* or *Pseudodictamnus* and *Verbena* (Figure 4.2). Each experimental layout was replicated five times based on the results of a power analysis to determine suitable repetition required (data not shown). Plant layouts were the same in both winter and summer although canopy size was larger in summer for all layouts (Table 4.3).



O	O
O	O

E	E
E	E

P	P
P	P

V	V
V	V

BS	BS
BS	BS

O	E
E	O

P	V
V	P

Figure 4.2: Summer miniature model garden canopy and side profile comparison photos. From top left *Erysimum, Pseudodictamnus, Verbena, Oenothera, Pseudodictamnus x Verbena* mix, *Erysimum x Oenothera* mix. Layout diagrams of experiment 4 plants. O = *Oenothera,* E = *Erysimum*, P = *Pseudodictamnus,* V = *Verbena,* BS = Bare substrate.

Plant layout	Height (winter)	Height (summer)	Spread (width x length) (winter)	Spread (width x length) (summer)
Erysimum	17.6	24.6	32.2 x 39.6	37.0 x 44.4
Pseudodictamnus	22.1	41.5	31.6 x 39.6	46.0 x 52.8
Verbena	32.4	77.8	38.0 x 40.0	77.2 x 72.0
Oenothera	22.0	52.0	33.8 x 45.8	103.0 x 77.4
Pseudodictamnus x Verbena mix	24.8	64.6	34.0 x 39.0	90.8 x 79.0
Erysimum x Oenothera mix	19.2	37.0	30.4 x 39.4	74.4 x 79.4

Table 4.3: Average dimensions in centimetres at the end of experimentation (n = 5 gardens per layout).

4.3.3.1 Impact of retention of rainfall within the canopy in summer and winter

Prior to rainfall application, growing medium within model gardens was saturated to field capacity and allowed to drain for 1 hour. Winter daily average temperature inside the glasshouse on day of experimentation (13th February 2023) was 11.5°C (± 6.48 SD) with a minimum of 4.0°C and a maximum of 25.2°C; summer daily average (19th July 2023) was 24.6°C (± 4.94 SD) with a minimum of 13.5°C and a maximum of 31.9°C (recorded using a Tinytag Plus 2 Data Logger (Gemini Data Loggers, Chichester, UK)). Five substrate moisture content readings (SM300 sensor connected to a HH2 Moisture Meter, Delta-T Devices Ltd., Cambridge, UK) per container were taken after this drainage period and container mass was recorded. Each individual model garden was positioned above a collection container in an unheated glasshouse. The rain applicator was attached to the mains water supply and positioned above the model gardens. A rain gauge was positioned in each model garden container to be tested (see Chapter 2 for details). Model gardens were tested in randomised blocks of replicates, with four miniature model gardens rained on at one time and all five replicates tested in one day. Rainwater was applied for 10 minutes after which time the rain applicator was turned off and rainwater volumes recorded from the rain gauge and collection container using measuring cylinders. Miniature model gardens were allowed to drain for 30 minutes post rainfall application, after which time this drainage volume was measured, container mass recorded, and five substrate moisture content readings taken again.

4.3.3.2 Impact of winter plants' evapotranspiration on the capacity of model gardens to store rainfall in the substrate

Prior to rainfall application, model gardens had been watered to field capacity and then not watered for 6 days, including 2 days of heating applied to the glasshouse. Daily temperature inside the glasshouse was recorded using a Tinytag Plus 2 Data Logger (Gemini Data Loggers, Chichester, UK) (Table 4.4). Plants were allowed to dry in an unheated glasshouse for four days, after which heating was applied on the afternoon of the 17th February, just over two days prior to rainfall application, to assist the drying of the substrate (see section

2.7.3, Chapter 2 for more details). Substrate moisture readings for each layout needed to be significantly lower than their saturated counterparts, and below 0.40 $m^3 m^{-3}$. Five substrate moisture content readings per container were taken after this period and container mass was recorded. The experimental setup was the same as for retention of rainfall within the canopy (section 4.3.3.1 above). Model gardens were tested in randomised blocks of replicates, with four miniature model gardens rained on at one time, and all five replicates (35 model gardens) tested over one day. Rainwater was applied for 45 minutes after which the rain applicator was turned off and rainwater volumes recorded from the rain gauge and collection container using measuring cylinders. Miniature model gardens were allowed to drain for 30 minutes post rainfall application, after which time this drainage volume was measured, container mass recorded, and five substrate moisture content readings taken.

Date	**Average temperature (°C) (± SD)**	**Daily maximum temperature (°C)**	**Daily minimum temperature (°C)**
14.02.2023	9.1 (5.63)	23.2	3.5
15.02.2023	11.0 (8.42)	25.9	2.3
16.02.2023	12.9 (4.59)	27.9	8.2
17.02.2023	19.5 (4.17) (heating applied in the afternoon)	28.3	14.7
18.02.2023	23.8 (1.41) (heating applied)	27.4	21.0
19.02.2023	24.9 (2.20) (heating applied)	30.2	22.6

Table 4.4: Internal glasshouse temperatures prior to unsaturated rainfall application recorded on a Tinytag Plus 2 Data Logger (Gemini Data Loggers, Chichester, UK) in February 2023.

4.3.3.3 Impact of summer plants' evapotranspiration on the capacity of model gardens to store rainfall in the substrate

The summer method was the same as winter experimentation with the exception of the number of irrigation-free days. Plants were not watered for two days before experimentation. Daily average temperature inside the glasshouse on day of experimentation (26th July 2023) was 22.3°C (± 5.12 SD) with a minimum of 9.9°C and a maximum of 30.2°C, recorded using a Tinytag Plus 2 Data Logger (Gemini Data Loggers, Chichester, UK). Rainfall was applied for 45 minutes, allowing comparison with winter results. Substrate moisture readings needed to be significantly lower than their saturated counterparts, with the aim that all model gardens would be below 0.30 $m^3 m^{-3}$.

4.3.4 Experiment 5 - Rainfall application on miniature model gardens in the glasshouse - Effect of pervious surfaces compared to the impact of plants' evapotranspiration and retention of rainfall within the canopy and substrate

Replicating the same miniature model garden design as in experiment 4, applied rainfall runoff volumes were compared between non-vegetated pervious surfaces and planted layouts. Pervious surfaces (gravel, bark chippings) were chosen as there was a gap in the literature with regards to these commonly used garden materials, with the majority of previous research focusing on impervious surfaces and their generated rainwater runoff (Kadavergu *et al.,* 2021; Kelly, 2016; Perry & Nawaz, 2008; Simpson & Francis, 2021; Warhurst *et al.,* 2014). Gravel and bark chippings were selected as non-vegetated pervious surfaces as these are used in domestic gardens for driveways, paths, and planting beds. Both materials were sourced from unused bags at the Controlled Environments Laboratories to reduce waste. Gravel size was approximately 10 mm (Travis Perkins, Northampton, UK), and bark chippings were approximately 10-100 mm. Peat-free growing medium was laid as a base for the gravel and bark miniature model gardens (Figure 4.3). To replicate how the materials would be laid in a domestic garden, a layer of Mypex was placed over the growing medium, and the pervious surface placed on top. The gravel layer was 40 mm deep and bark chippings were 50 mm deep, similar to depths used when laid in a garden setting, therefore ratios in each container were 60:40 gravel/bark to compost. To compare generated runoff volumes to non-vegetated pervious surfaces, *Pseudodictamnus* was used as the planted monoculture layout, and *Pseudodictamnus* and *Verbena* plants were used in a mixed layout, and selected due to their effective performance in experiment 4. Plant cuttings were potted into 9 cm containers in May 2023 and replanted into miniature model gardens in early August 2023 (Figure 4.4). Planted layouts were the same as seen in experiment 4. Bare substrate (SylvaGrow Multi-purpose, Melcourt, UK) was also still used as a control layout. Each experimental layout was replicated five times.

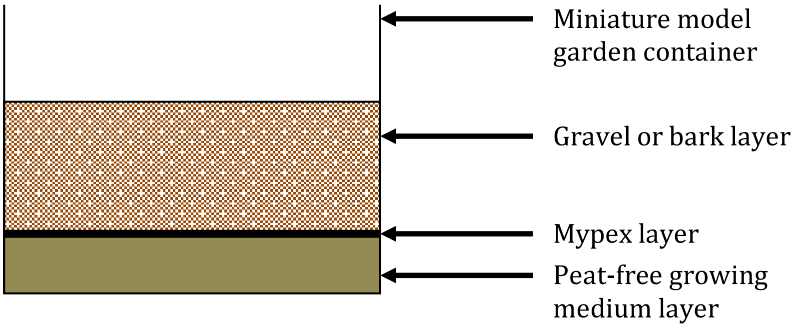


Figure 4.3: Miniature model garden with pervious surface layers for experiment 5 (not to scale).

Figure 4.4: Planted miniature model gardens used in experiment 5 - *Pseudodictamnus* (left) and *Pseudodictamnus x Verbena* mix (right).

4.3.4.1 Impact of retention of rainfall within the canopy and plants' evapotranspiration on the capacity of model gardens to store rainfall in the substrate

Experiment methodology was the same as experiment 4 (section 4.3.3.3), however to test evapotranspiration impact model gardens were not irrigated for five days prior to rainfall application. Daily average temperature inside the glasshouse on day of retention of rainfall within the canopy experimentation (21st August 2023) was 26.3°C (± 4.28 SD) with a minimum of 15.7°C and a maximum of 32.9°C; daily average temperature inside the glasshouse on day of unsaturated substrate experimentation (29th August 2023) was 21.0°C (± 3.05 SD) with a minimum of 11.8°C and a maximum of 27.2°C (recorded using a Tinytag Plus 2 Data Logger (Gemini Data Loggers, Chichester, UK)).

4.3.5 Data analysis

The volume of the water collected as runoff in experiments 3, 4 and 5 was converted to unitless standardised runoff volumes by dividing the total water collected in the containers (experiment 3) or the total collected in the tray during rainfall application and after 30 minutes of drainage time (experiments 4 and 5) with the volume of water in the rain gauges (Eq. 2, section 2.7.3.2, Chapter 2). This was to overcome any small variability in rainfall volumes produced by the rain applicator and enable each garden's rainfall application to be assessed on an individual basis depending on the water in each rain gauge. Runoff volumes were expressed per garden and per standardised unit of leaf area index in all experiments. Data was analysed using R (R Core Team, 2021). Runoff volumes were analysed using one-way and two-way ANOVAs to compare standardised runoff with layout and season. Additional t-tests and linear regressions were used for experiments 4 and 5 to analyse the impact of substrate moisture content on runoff volumes. All data satisfied normality assumptions, with the exception of the miniature model garden dried roots data, which was log-transformed prior to analysis.

4.4 Results

4.4.1 Experiment 3 - Rainfall application on outdoor model gardens - Effect of planting combinations and time of year and impact of retention of rainfall within the canopy

Impact of retention of rainfall within plant canopies per garden

All planted layouts had a significantly higher rainfall retention of the canopy compared to bare substrate in both summer and winter ($p < 0.001$), and each planted layout had a significantly lower runoff volume in summer compared to winter (*Erysimum* p = 0.045, *Oenothera* p < 0.001, *Erysimum x Oenothera* mix p < 0.001) (Figure 4.5).

Summer: The *Oenothera* monoculture in summer had the significantly lowest standardised runoff volume at 1.70 (*Oenothera* summer compared to all winter layouts p < 0.001; *Oenothera* summer compared to *Erysimum* summer p = 0.006, and Mixed summer p = 0.005). The summer Mixed planting was not significantly different from the evergreen *Erysimum* monoculture (p = 1.000), both producing on average 0.37 and 0.36 more standardised runoff respectively per garden than the deciduous *Oenothera*.

Winter: The Mixed winter layout, consisting of 50% evergreen planting, had the highest average standardised runoff volume of all the planted layouts at 2.58, on average 0.36 more standardised runoff than *Oenothera* (p = 0.008) and 0.22 more than *Erysimum* (p = 0.339).

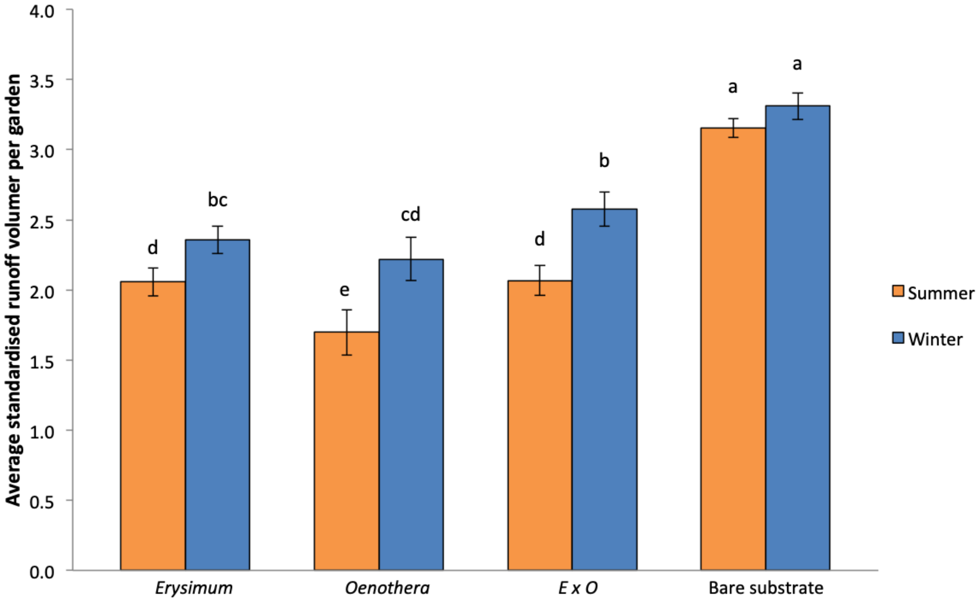


Figure 4.5: Seasonal comparison of retention of rainfall within the canopy per outdoor model garden. Mean standardised runoff volumes after 15 minutes of rainfall and associated standard error of the means (n = 12). Layouts sharing a letter were not significantly different from one another.

Impact of retention of rainfall within plant canopies per LAI

Leaf area index (LAI) was calculated using Eq. 1, section 2.2.3, Chapter 2. There was a significant decline in leaf area index between the summer and winter seasons for all plant layouts (p < 0.001). *Oenothera* had the largest decrease in leaf area index between the two seasons, however it also had the largest leaf area index of all the layouts (4.004 in summer compared to 1.638 in winter). In contrast to values expressed per model garden, comparing seasonal runoff volumes at leaf area index level found all layouts were significantly different from each other ($p < 0.001$). *Oenothera* monoculture layout had the lowest average runoff volume regardless of season tested ($p < 0.001$) and the Mixed planting had a significantly lower average runoff volume in both summer and winter compared to the evergreen *Erysimum* monoculture (summer $p = 0.007$, winter $p < 0.001$) (Figure 4.6).

Summer: The *Oenothera* summer monoculture had the significantly lowest standardised runoff volume at 0.42, retaining an average standardised volume of 0.68 more than *Erysimum* and 0.50 more than the Mixed layout in its canopy ($p < 0.001$). There was a weak significant difference in standardised runoff volume between the *Erysimum* and Mixed layout ($p = 0.07$), with *Erysimum* retaining the lowest volume of water in its canopy (1.10 standardised runoff).

Winter: The *Erysimum* winter monoculture had the highest average standardised runoff volume at 2.40 compared to both deciduous and Mixed planting, retaining the least in its canopy despite being the only plant layout to retain leaves in winter ($p < 0.001$). In contrast, deciduous *Oenothera* retained the largest volume of water in its canopy ($p <0.001$).

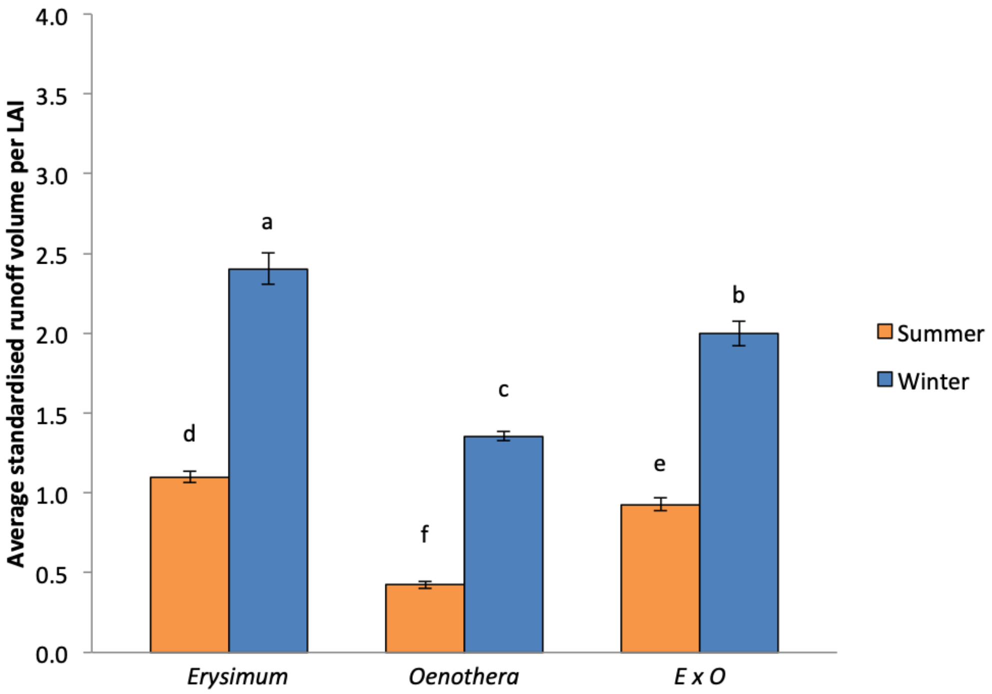


Figure 4.6: Seasonal comparison of retention of rainfall within the canopy per outdoor model garden LAI. Mean standardised runoff volumes after 15 minutes of rainfall and associated standard error of the means (n = 12). Layouts sharing a letter were not significantly different from one another.

Impact of plant biomass on retention of rainfall within plant canopies

There was a strong significant impact of both leaf area index and dried plant biomass on volumes of runoff produced. The increase in average leaf area index per garden was found to produce significantly lower standardised runoff volumes ($p < 0.001$) (data not shown), with greater leaf area index resulting in more rainwater captured and retained by the plant canopy. *Oenothera* had the largest average leaf area index of all the plant layouts in both seasons tested, and also produced the lowest standardised runoff volumes.

Overall, increased dried aboveground biomass resulted in lower runoff volumes ($p < 0.001$) (data not shown). However, this was not the case for *Oenothera* in the winter, which had the lowest average mass of the winter garden layouts at 1.32 kg, but also the lowest standardised runoff volumes. When compared to *Erysimum* at 1.74 kg and the Mixed planting at 2.10 kg, which both retained more leaves but produced greater runoff volumes, this indicates that the hairy stems of *Oenothera*, although lighter in mass, likely play a greater role in retention of rainfall within the canopy than the leaves of the evergreen *Erysimum*.

4.4.2 Experiment 4 - Rainfall application on miniature model gardens in the glasshouse - Effect of planting combinations and time of year and impact of plants' evapotranspiration and retention of rainfall within the canopy and substrate

Substrate moisture content

In both winter and summer, average substrate moisture when substrates of all layouts were watered to saturation was over 0.45 $m^3\ m^{-3}$. In the winter saturated experiments, the planted layouts had more moisture than the bare substrate, with an average of 0.53 $m^3\ m^{-3}$ for the latter, and planted layouts ranging between 0.55-0.59 $m^3\ m^{-3}$. In the summer saturated experiments bare substrate moisture content was again lower than planted layouts, but all layouts on average had a substrate moisture range between 0.58-0.65 $m^3\ m^{-3}$.

In unsaturated conditions, 2 days after watering in summer and 6 days in winter, all layouts had a significantly decreased substrate moisture content compared to their saturated readings ($p < 0.001$), although the substrate moisture decline was aided by glasshouse heating in winter conditions to enable experimentation to resume. It proved difficult to reduce substrate moisture from fully saturated model gardens because the plants had reduced transpiration rates (data not shown) and the temperature (in the range of 2.3-28.3°C without heating) was not consistently warm enough to enable significant evaporation from the substrate, which would have aided in drying the substrate. Winter experiments had an average substrate moisture range of between 0.29-0.39 $m^3\ m^{-3}$, with the lowest readings from the *Verbena* monoculture with an average of 0.29 $m^3\ m^{-3}$, which was significantly lower than all other layouts ($p = 0.001$ and $p = 0.002$ for *Erysimum* and *Pseudodictamnus* respectively, all other layouts and *Verbena* $p < 0.001$).

The summer unsaturated substrate moisture readings on average ranged between 0.22-0.42 $m^3\ m^{-3}$, but excluding bare substrate this range reduces to 0.22-0.35 $m^3\ m^{-3}$. All substrate moisture contents were significantly lower for planted layouts compared to bare substrate ($p = 0.009$ for *Erysimum*, for all other layouts $p < 0.001$). Of the planted layouts the *Pseudodictamnus x Verbena* mixture had the lowest average substrate moisture (0.22 m^3 m^{-3}) and the *Erysimum* monoculture had the highest (0.35 m^3 m^{-3}).

Impact of retention of rainfall within miniature model gardens plant canopies per garden

After 10 minutes of rainfall per model garden there was no significant seasonal difference between runoff volumes in summer compared to winter by the same layouts ($p = 0.485$) (Figure 4.7).

Summer: Both the *Pseudodictamnus* monoculture and the *Pseudodictamnus x Verbena* mixture produced significantly lower standardised runoff volumes than the control bare substrate layouts ($p = 0.002$), with standardised volumes of 6.7 and 6.6 respectively, compared to bare substrate at 11.1. The *Verbena* monoculture produced a higher runoff volume than its mixed counterpart of *Pseudodictamnus x Verbena*, and had the largest range of results (and associated standard error) from 2.8 to 14.6. All other layouts were not significantly different from one another, regardless of whether they were planted monocultures, mixtures, or bare substrate.

Winter: Winter retention of rainfall within the canopy resulted in no significant difference between runoff volumes of any layouts, and no difference between evergreen and deciduous layouts. Bare substrate produced the highest standardised runoff volume at 11.6, and all planted layout average runoff ranged from 9.7-10.5. However, deciduous planting retained more leaves than expected for plants at that time of year.

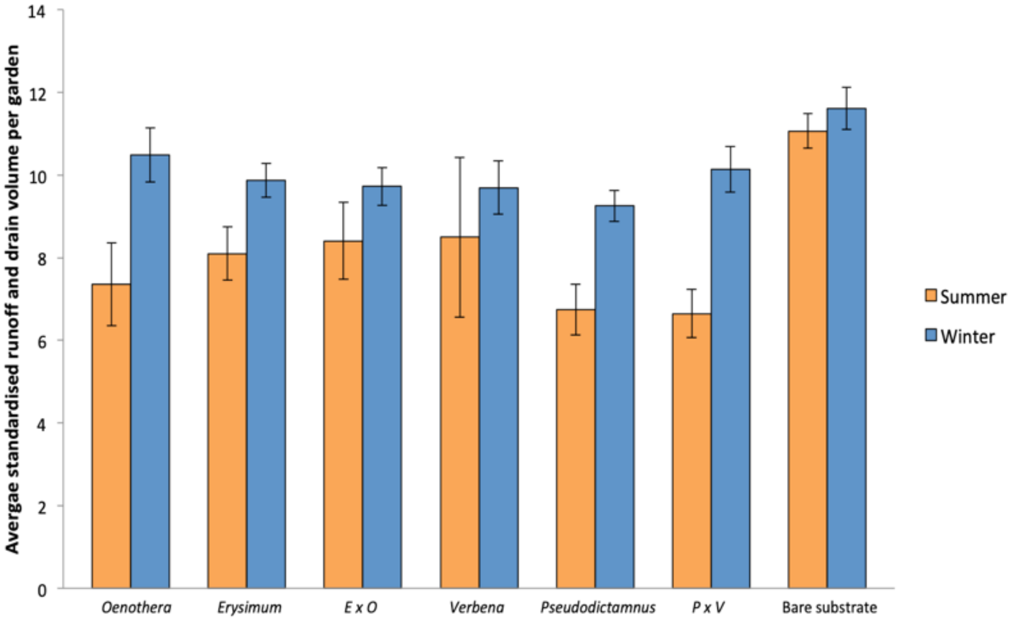


Figure 4.7: Seasonal comparison of retention of rainfall within the canopy per miniature model garden. Mean standardised runoff volumes after 10 minutes of rainfall and associated standard error of the means (n = 5 per layout). An asterisk denotes statistically significant differences between the summer and winter layout.

Impact of retention of rainfall within miniature model gardens plant canopies per LAI

There was a significant increase in leaf area index from winter rainfall application to summer for all plant layouts ($p < 0.001$), except for evergreen *Erysimum* ($p = 0.224$) and deciduous *Verbena* ($p = 0.105$). The latter had a sparse number of leaves in both testing seasons, although retained more leaves in winter than anticipated. The *Pseudodictamnus* monoculture had the largest summer leaf area index at 3.64 and *Verbena* had the lowest at 1.23; in winter *Verbena* and *Pseudodictamnus* monocultures had similar largest leaf area indexes at 1.88 and 1.82 respectively, and *Oenothera* had the lowest at 1.08. Surprisingly the two evergreen monocultures had both the largest and smallest leaf area index changes between seasons, with the biggest change from *Pseudodictamnus* at 1.83, and the smallest change from *Erysimum* at 0.27.

Retention of rainfall within the canopy per leaf area index found that both *Oenothera* and the *Pseudodictamnus x Verbena* mixed layout produced significantly lower standardised runoff volumes in summer compared to winter (p = 0.002 and p = 0.005 respectively) (Figure 4.8). With the exception of *Verbena*, all other layouts produce higher runoff volumes in winter compared to summer per leaf area index, although the volume differences were not significantly greater.

Summer: *Verbena* produced a significantly larger standardised runoff than all other planted layouts per leaf area index (for *Oenothera* p = 0.008, *Erysimum* and *Erysimum x Oenothera* p = 0.011, *Pseudodictamnus* and *Pseudodictamnus x Verbena* p < 0.001), losing an average of 7.02 more in standardised runoff volume compared to the *Pseudodictamnus x Verbena* mixture. The *Erysimum x Oenothera* mixture produced very similar volumes to its monoculture counterparts (p = 1.000), and the *Pseudodictamnus x Verbena* mixture was also similar to the *Pseudodictamnus* monoculture (p = 1.000), both producing the lowest runoff volumes in the summer experiment with 1.87 and 2.20 respectively.

Winter: In contrast to the whole garden results, when investigated per leaf area index the runoff volumes of some layouts were found to be significantly different. The *Oenothera* monoculture produced the largest standardised runoff volume per leaf area index in winter at 9.79, which was significantly higher than both the *Verbena* and *Pseudodictamnus* monocultures (p = 0.03 and p = 0.02 respectively). However, all other volumes produced were not significantly different from one another.

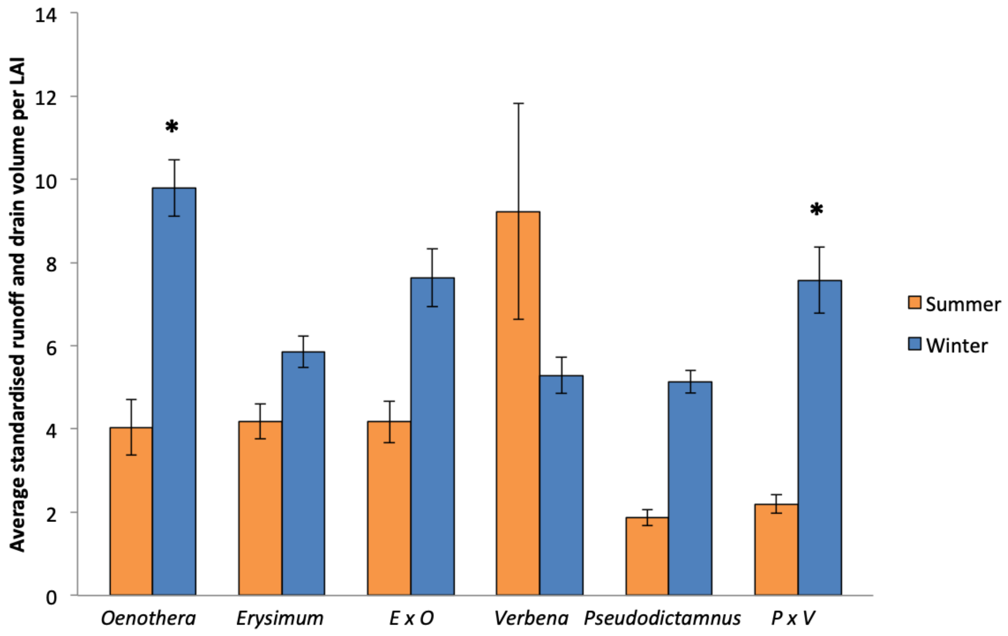


Figure 4.8: Seasonal comparison of retention of rainfall within the canopy per miniature model garden LAI. Mean standardised runoff volumes after 10 minutes of rainfall and associated standard error of the means (n = 5 per layout). An asterisk denotes statistically significant differences between the summer and winter layout.

Impact of plants' evapotranspiration on the capacity of miniature model gardens to store rainfall in the substrate per garden

In unsaturated conditions all model gardens produced significantly less standardised runoff volumes in summer compared to their winter counterparts, except for *Verbena* and bare substrate ($p = 1.000$). Although *Verbena* was not statistically different between seasons, all planted layouts followed the same trend of producing more runoff in winter unsaturated conditions, whereas bare substrate produced marginally larger volumes in the summer experiment (Figure 4.9).

Summer: All planted layouts produced significantly lower standardised runoff volumes compared to bare substrate in the summer ($p < 0.001$), however the planted layouts were not significantly different from one another. The lowest runoff was produced by the *Pseudodictamnus x Verbena* mixture, which on average across five gardens had a standardised volume of 0.002. Their average substrate moisture content was 0.22 $m^3 m^{-3}$, which was the lowest of all the layouts, which was sufficiently low substrate moisture to enable unsaturated experimentation, but not so low as to expect almost no runoff at all.

Winter: Runoff volumes were higher in the winter experimentation, and only the *Pseudodictamnus x Verbena* and the *Verbena* monoculture produced significantly less runoff than bare substrate (p = 0.008 and p < 0.001 respectively). *Verbena* produced the lowest standardised runoff volume at 1.73, significantly less than all planted layouts except for the *Pseudodictamnus x Verbena* mixture (*Pseudodictamnus* and *Erysimum* p = 0.004, *Erysimum x Oenothera* p = 0.01, *Oenothera* p < 0.001).

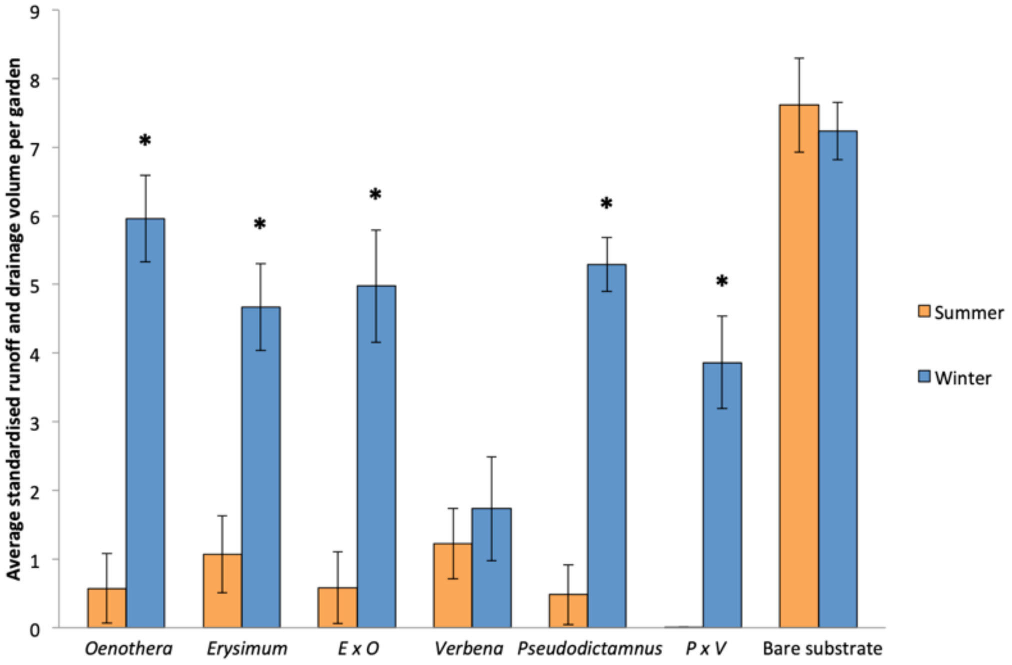


Figure 4.9: Seasonal runoff per miniature model garden for unsaturated substrate. Mean standardised runoff volumes after 45 minutes of rainfall and associated standard error of the means (n = 5 per layout). An asterisk denotes statistically significant differences between the summer and winter layout.

Impact of plants' evapotranspiration on the capacity of miniature model gardens to store rainfall in the substrate per LAI

When comparing runoff produced in unsaturated conditions per standardised unit of leaf area index *Verbena* changes compared to per garden, with a higher runoff per leaf area index in the summer instead of the winter. Both the *Verbena* and the *Erysimum* layouts were also not significantly different between seasons (p = 1.000 and p = 0.162 respectively); all other layouts had a significantly lower runoff in summer compared to winter (Figure 4.10).

Summer: No layouts produced significantly different standardised runoff volumes per leaf area index in the summer experiment, which was also seen per model garden as well (p > 0.422 for all layout combinations). The lowest volume was also the *Pseudodictamnus x Verbena* mixture, and highest volume at 1.85 was the *Verbena* monoculture.

Winter: *Oenothera* had a significantly higher standardised runoff volume per leaf area index compared to all other layouts at 5.74 (*Pseudodictamnus* p = 0.034, *Pseudodictamnus x Verbena* p = 0.045, *Erysimum* p = 0.016, *Verbena* p < 0.001). The only exception was the *Erysimum x Oenothera* mixture (p = 0.481), which produced the next highest runoff volume at 3.96.

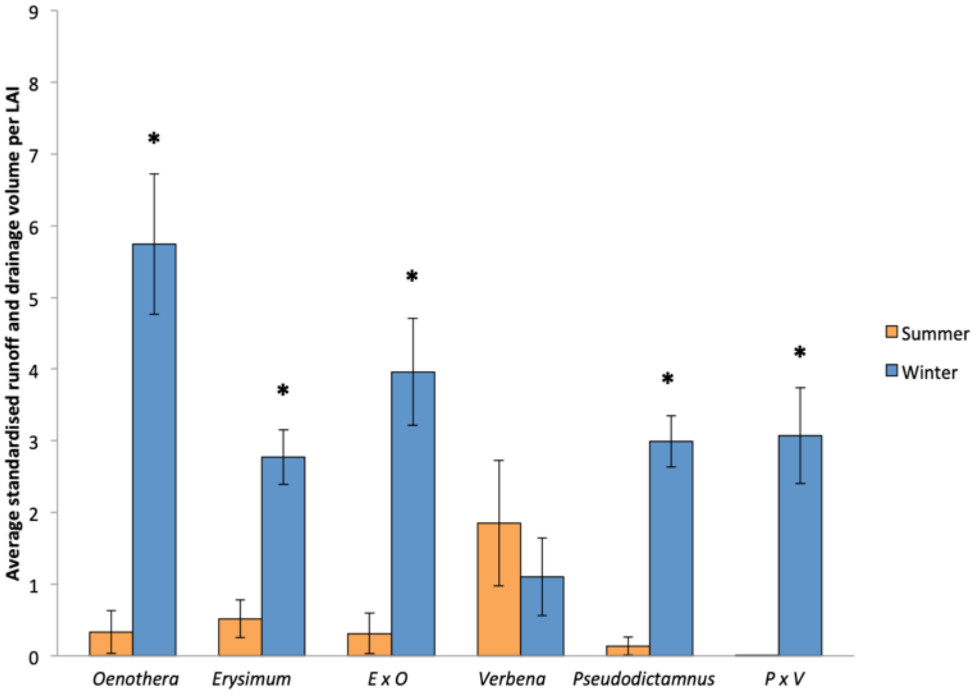


Figure 4.10: Seasonal runoff per miniature model garden LAI for unsaturated substrate. Mean standardised runoff volumes after 45 minutes of rainfall and associated standard error of the means (n = 5 per layout). An asterisk denotes statistically significant differences between the summer and winter layout.

Linear regressions for both saturated and unsaturated layouts showed a significant link between substrate moisture content pre-rainfall application and standardised runoff volumes produced for both seasons combined (p < 0.001). As can be seen in Figure 4.11 the saturated experiment has a weak negative association ($R^2 = 0.103$) whereas the unsaturated gardens have a strong positive association ($R^2 = 0.669$). The low summer runoff volumes generated by *Pseudodictamnus, Pseudodictamnus x Verbena, Oenothera*, and *Erysimum x Oenothera* do however skew these results, which can be seen as some of the points lying along the x-axis. Overall, these results indicate that the higher the substrate moisture content in the unsaturated layouts, the greater the runoff generated, but for saturated layouts this was not the case and indicates that some plant layouts are able to retain water efficiently in their canopy and therefore reduce runoff volumes generated.

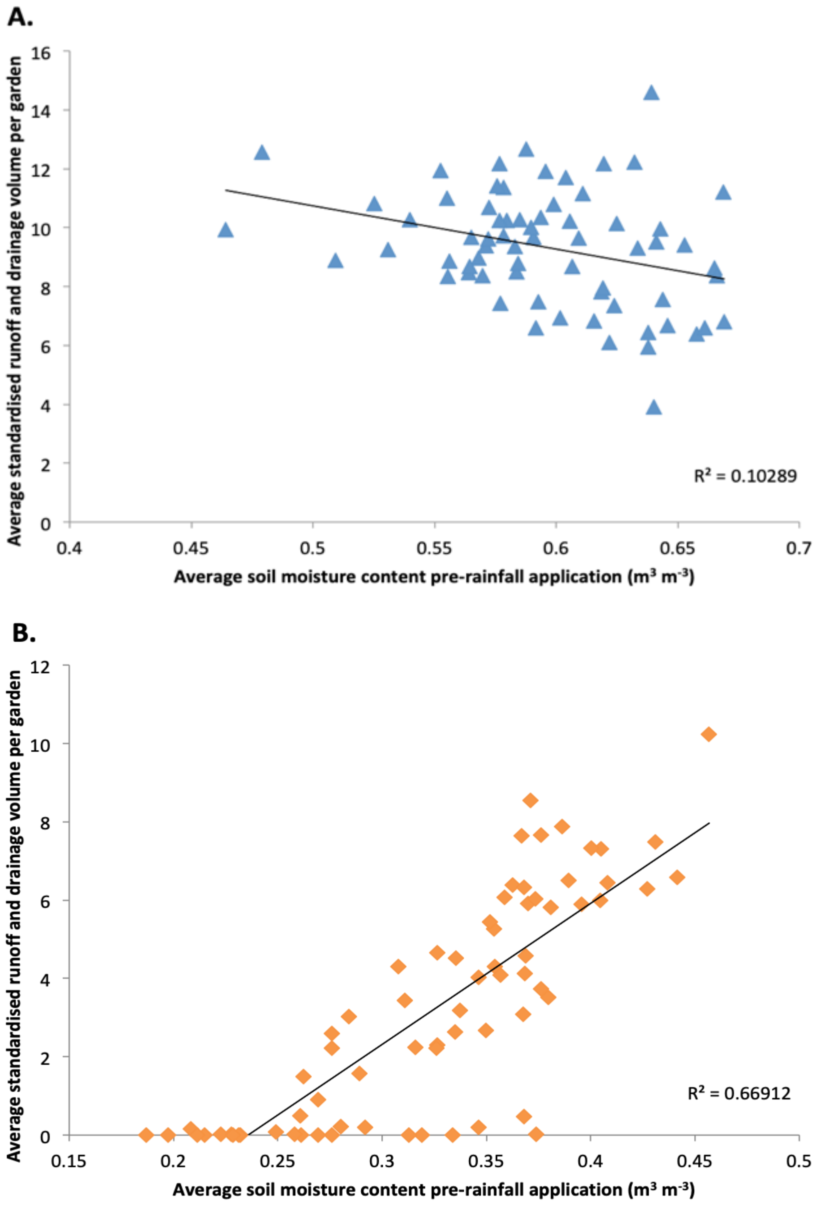


Figure 4.11: Linear regressions showing the relationship between average substrate moisture content per miniature model garden and standardised runoff volumes for saturated substrate (A) and unsaturated substrate (B).

Impact of dry plant aboveground biomass and roots mass on standardised runoff

At the end of the seasonal experiments, dried aboveground biomass was significantly larger per layout in the summer compared to winter for all layouts ($p < 0.001$) except for *Erysimum* ($p = 0.128$). The largest dry biomass increase was the *Pseudodictamnus x Verbena* layout, which increased by an average of

85% from 8.77 g in the winter to 58.40 g in the summer, which was also the largest average biomass overall.

In the summer the *Pseudodictamnus* and the *Pseudodictamnus x Verbena* layouts had the greatest aboveground biomass compared to all layouts (p < 0.001, *Pseudodictamnus* and *Oenothera* p = 0.041). There was a wider range of dry aboveground biomass in summer compared to winter, with the lowest weight from *Erysimum* at 25.53 g and the largest the *Pseudodictamnus x Verbena*. In the winter there was no significant difference in dry aboveground biomass between layouts, with all layouts averaging between 8.46-14.82 g. The *Oenothera* monoculture was found to have the lowest winter aboveground biomass and *Erysimum* to have the highest.

When comparing standardised runoff volumes and leaf area index there was found to be no significance on the retention of rainfall within the canopy (p = 0.546). However, there was a significant impact found for the unsaturated experiments (p < 0.001) and could be an explanatory variable as increased leaf area is associated with increased evapotranspiration rates.

Dry root biomass at the end of the summer experiments was significantly larger than the winter experiment for all layouts (p < 0.001). The *Pseudodictamnus* monoculture layout had the biggest increase between seasons at 81.78% and the *Erysimum* monoculture had the lowest increase at 51.96%. In the summer the root biomass fell into two distinct groupings, with the *Pseudodictamnus, Verbena*, and *Pseudodictamnus x Verbena* significantly larger than the *Erysimum, Oenothera*, and *Erysimum x Oenothera* layouts (p < 0.001). The *Pseudodictamnus x Verbena* had the largest average dried root biomass at 14.42 g and the *Erysimum* had the lowest at 4.87 g. In the winter the *Pseudodictamnus* root mass was not significantly different from the *Erysimum, Oenothera* and *Erysimum x Oenothera* (p = 1.000), which were all between 1.94-2.34 g. However, the *Verbena* and the *Pseudodictamnus x Verbena* mixture were significantly larger than the other layouts at 4.26 g and 3.97 g respectively.

Impact of winter retention of rainfall within miniature model gardens plant canopies after the removal of deciduous leaves

During winter experimentation the deciduous plants appeared to retain more leaves than typical for that time of year, and as such the decision was made to manually remove all leaves from the deciduous plants, leaving only stems, after initial testing was complete. New retention of rainfall within the canopy experimentation was conducted with the leaf area index for deciduous plants at zero, representing complete winter leaf abscission. Evergreen plants remained unaltered.

Comparing standardised runoff volumes per garden there was found to be no significant difference between runoff produced from the *Verbena, Oenothera*, and bare substrate layouts (p = 1.000) (Figure 4.12). Both of the mixed layouts were not different from either of their associated monoculture layouts. Comparing evergreen and deciduous monoculture layouts, the reduced leaf area of *Oenothera* and *Verbena* produced a significantly greater runoff than both the *Pseudodictamnus* and *Erysimum* monocultures (*Oenothera* and *Pseudodictamnus* p = 0.014, *Oenothera* and *Erysimum* p = 0.024, *Verbena* and *Pseudodictamnus* p = 0.007, *Verbena* and *Erysimum* p = 0.013).

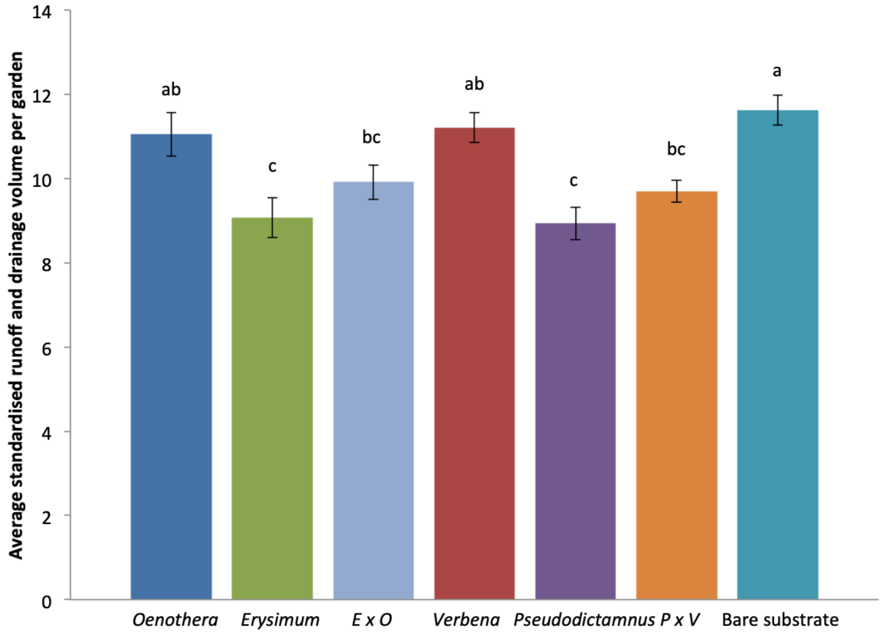


Figure 4.12: Winter retention of rainfall within the canopy per miniature model garden. Mean standardised runoff volumes after 10 minutes of rainfall and associated standard error of the means (n = 5 per layout). Leaves of deciduous plants were manually removed to reduce LAI and represent complete winter leaf abscission. Layouts sharing a letter were not significantly different from one another.

4.4.3 Experiment 5 - Rainfall application on miniature model gardens in the glasshouse - Effect of pervious surfaces compared to the impact of plants' evapotranspiration and retention of rainfall within the canopy and substrate

Substrate moisture content

Average substrate moisture content readings were difficult to obtain for the bark and gravel layouts and as such pre-rainfall substrate moisture content was monitored for bare substrate and the two planted layouts.

In saturated conditions all layouts were watered to field capacity and substrate moisture content for bare substrate, *Pseudodictamnus*, and *Pseudodictamnus x Verbena* were all above 0.37 m^3 m^{-3}. There were differences in substrate moisture content between the layouts, with planted layouts retaining more water than bare substrate, but they were within the well-watered/saturated range. In unsaturated conditions the *Pseudodictamnus x Verbena* layout was significantly drier than the *Pseudodictamnus* and bare substrate layouts ($p < 0.001$) with an average of 0.14 m^3 m^{-3}. Both *Pseudodictamnus* and bare substrate were not significantly different ($p = 0.918$) with average substrate moisture between 0.32-0.34 m^3 m^{-3}. This could be due to a number of reasons including evapotranspiration rates, size of plants, and root density. All three layouts had significantly lower substrate moisture content between the saturated and unsaturated runs (*Pseudodictamnus* and *Pseudodictamnus x Verbena* both $p < 0.001$, bare substrate $p = 0.008$).

Impact of retention of rainfall on surfaces or within miniature model gardens plant canopies

Retention of rainfall within the canopy per garden after 10 minutes of rainfall was not significantly different between layouts regardless of whether there were plants present or not ($p = 0.793$) (Figure 4.13A). The bare substrate layout produced the highest standardised runoff with an average volume of 10.8.

Impact of plants' evapotranspiration on the capacity of miniature model gardens to store rainfall in the substrate

In unsaturated conditions gardens were not irrigated for five days prior to 45 minutes of rainfall application. There were significant differences in runoff volume produced per garden, with a clear divide between layouts with and without plants (Figure 4.13B). Both plant layouts produced significantly less water than the pervious surfaces ($p < 0.001$, except for bare substrate which was $p = 0.02$ for *Pseudodictamnus* and $p = 0.01$ for *Pseudodictamnus x Verbena*). All pervious surfaces were not significantly different from each other, with gravel producing the largest standardised runoff volume with an average of 9.95.

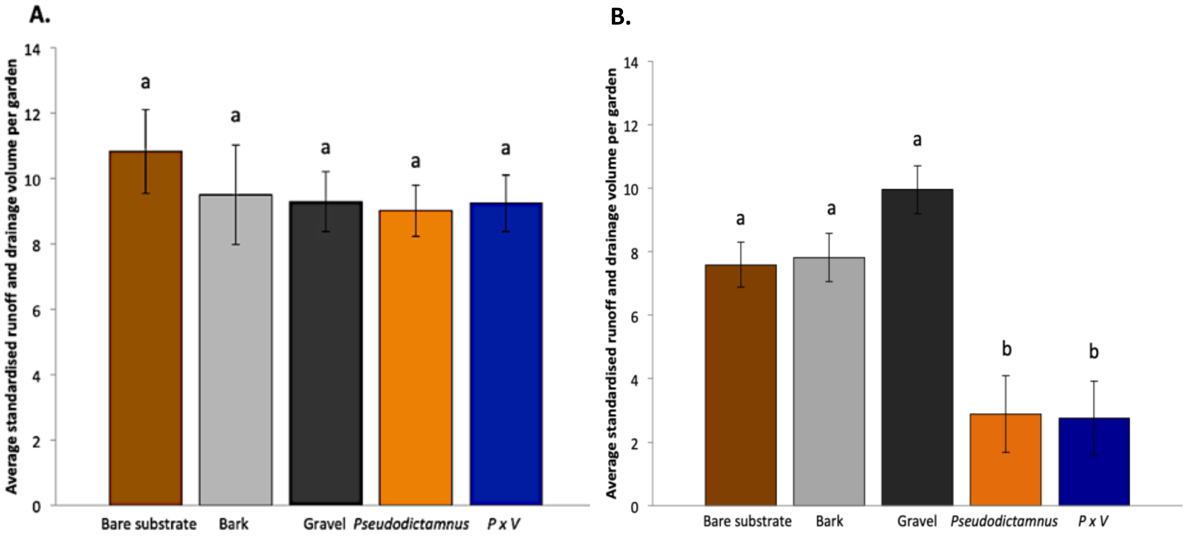


Figure 4.13: Runoff volumes for miniature model gardens comparing plants and permeable surfaces. A) Summer retention of rainfall within the canopy. Mean standardised runoff volumes per garden after 10 minutes of rainfall. B) Summer runoff for unsaturated substrate. Mean standardised runoff volumes per garden after 45 minutes of rainfall. With associated standard error of the means (n = 5 per layout). Layouts sharing a letter were not significantly different from one another.

4.5 Discussion

Outdoor and miniature model gardens were planted with mixed and monoculture planting to examine the role of plant traits and planting combinations on rainfall runoff. It was investigated whether mixing evergreen and deciduous plants or plants with hairy or smooth leaves could reduce rainfall runoff and increase canopy rainfall storage in summer and winter. During the winter months when deciduous plants would be dormant it was hypothesised that they would be unable to provide retention of rainfall within the canopy or transpiration services.

Impact of retention of rainfall within plant canopies

Experiment 3 - outdoor model gardens

Focusing on retention of rainfall within the canopy, experiments 3, 4 and 5 highlighted the importance of certain plant traits rather than specific planting mixtures. The *Oenothera* monoculture in experiment 3 provided the greatest retention of rainfall within the canopy of all the plant layouts regardless of season. In summer this outcome could be expected, as the *Oenothera* plants had the largest leaf area index of all the studied plants and combinations - 2.13 greater on average than the *Erysimum* monocultures. Plants with larger leaf areas are known to significantly reduce runoff compared to those with smaller canopies both via retention of rainfall within the canopy and transpiration (Beidokhti & Moore, 2021; Blanuša & Hadley, 2019; Heim *et al.,* 2023; Lundholm *et al.,* 2015). However, it was anticipated that the *Oenothera*, as a deciduous plant, would not continue to successfully retain rainfall into the winter months, at which point the evergreen *Erysimum* would provide greater canopy capture. It would therefore follow that the *Oenothera* would offer better retention of rainfall within the canopy in summer, and the least in winter, with *Erysimum* a direct counterpoint to this, and the Mixed planting, benefitting from the best of both scenarios, could maintain a steady service delivery throughout the year. This did appear to be the case, with mixed planting neither the best or worst at retaining rainfall in summer or winter, and the *Oenothera* monoculture also had the lowest rainwater runoff volume in winter, which was unexpected. The *Oenothera* underwent leaf senescence, with the greatest reduction in leaf area index between summer and winter of all layouts in experiment 3, however it still retained the largest leaf area index in winter. The *Erysimum*, in contrast, had the lowest leaf area index of all three planted layouts.

In addition to the largest leaf area index, *Oenothera* has small trichomes present on both the leaves and stems of the plants, the latter of which could play an important role in retention of rainfall within the canopy in winter. Plant branches, even without trichomes have been shown to contribute to attenuation of rainfall in winter, with rough and textured bark providing greater rainwater retention and delaying stem flow descent from the canopy to the ground (Beidokhti & Moore, 2021; Ginebra-Solanella *et al.,* 2020; Liu & Zhao, 2020). A meta-analysis of literature of urban trees undertaken by Beidokhti & Moore (2021) found that throughfall volumes were significantly higher in deciduous trees with smooth bark, compared to those with rough bark during leafless periods, although this becomes less significant when leaves are taken into account during the summer months.

It has been speculated that the function of leaf hairs is primarily to diminish absorption of radiation and therefore reduce leaf temperature, with rainfall capture a secondary function (Blanuša *et al.,* 2013). Kemp *et al.* (2019) found that *Stachys byzantina*, with its leaves covered in dense silver hairs, was able to reduce runoff compared to smooth-leaved plants. Presented results indicate that *Oenothera's* trichomes effectively retained rainfall, both on the leaves and stems, in experiment 3. The evergreen *Erysimum*, whilst still retaining its foliage during the winter months, has smooth leaves. Although both *Erysimum* and *Oenothera* are believed to prefer well-drained conditions and can tolerate drought (Beth Chatto's Plants & Gardens, 2022b; Royal Horticultural Society, 2023, no date, e & f), experiments in Chapter 3 found that *Oenothera* had a higher transpiration rate compared to *Erysimum*, and was able to remove water quickly from the substrate when it was available, indicating it has a higher water demand. *Erysimum's* traits suggest it has a lower water tolerance because in addition to its slower transpiration rate it has smooth leaves and a rounded canopy shape, and it could be hypothesised that the plant is shaped to avoid excess water to its roots by shedding water from its canopy and away from the base of the plant. Funnelling of water via the shape of the canopy and branch architecture has been observed in evergreen hedge plant *Thuja plicata*, thought to be the reason for increased runoff generation (Blanuša & Hadley, 2019). Although evergreen trees have been found in some scenarios to provide greater rainwater retention than deciduous ones (Xiao & McPherson, 2002), these winter results indicate that the role of traits, in this case trichomes, were more important for retention of rainfall within the canopy than whether or not the plant retained its leaves in the winter months.

Experiments 4 and 5 - miniature model gardens

Unlike the outdoor model gardens, the *Oenothera* did not provide the greatest retention of rainfall within the canopy in experiment 4's miniature model gardens. Instead, it was found that the majority of the plant layouts were not significantly different from one another, and that the *Pseudodictamnus* and *Pseudodictamnus x Verbena* had the lowest runoff volumes in winter and summer respectively. The lack of differences in retention of rainfall within the canopy between the plants (with the exception of *Pseudodictamnus* and *Verbena* which is discussed below when comparing planting combinations) is surprising, especially considering the combinations of evergreen and deciduous leaves in winter, various canopy shapes and sizes, and presence or absence of trichomes. Comparing planting (both monoculture and mixed layouts) with different pervious surfaces in experiment 5 found no benefit from the presence of planting, and the same was found when comparing seasonal retention of rainfall within the canopy compared to bare substrate in experiment 4. The results from experiments 4 and 5 suggest that planting was not always better than bare substrate with regards to reducing runoff via retention of rainfall within the canopy, something that has also been observed in green roof experiments (Lundholm *et al.,* 2015) but disagrees with the majority of existing literature, although the contribution of canopy is acknowledged to be relatively small (Heim *et al.,* 2023; Nagase & Dunnett, 2012; Stovin *et al.,* 2015).

There could be several explanations for the results observed in the miniature model gardens. Firstly, the lack of difference in rainfall canopy capture could be due to the small size of the plants used. As the impact of canopy and role of plant traits was clear in experiment 3, the distinction between these results could be the size of the plants, considering experiment 3 used more established plants with larger canopies, enabling *Oenothera* (with its beneficial traits) to provide a greater retention of rainfall (Heim *et al.,* 2023; Lundholm *et al.,* 2010; Nagase & Dunnett, 2012; Yuan *et al.,* 2017). Previous research has focused on trees or shrubs (Beidokhti & Moore, 2021; Blanuša & Hadley, 2019; Pataki *et al.,* 2011; Tiwary *et al.,* 2016), or using plants suitable for a green roof setting (Chu & Farrell, 2022; Kemp *et al.,* 2019; Lundholm *et al.,* 2010; MacIvor *et al.,* 2018; Nagase & Dunnett, 2012), that are all larger or more established than the plants used in experiments 4 and 5. As such, those plants would provide a greater canopy surface to capture rainfall, but due to the small size of the plants used for this study the canopy was not established enough to provide that service.

However, scale should also be taken into account, and although research on trees or larger plants indicates a greater impact, and experiment 4 and 5 suggests smaller plants have negligible rainwater retention benefits, when the number of plants and area planted increases these plants could become impactful due to this expansion. Designers in urban areas have created large-scale perennial planting beds and the potential ecosystem service delivery, even if smaller species were used, could be significantly greater due to the scale of the planted areas (see Olympic Park and the Barbican Centre, London, Hauser & Wirth in Somerset, and the High Line in New York for key examples).

The intensity of the applied rainfall could also have played a role in these results, with more intense rainfall/velocity of the droplets resulting in less water retained in the plant canopies (Beidokhti & Moore, 2021; Dunnett *et al.,* 2008; Liu *et al.,* 2020b) and although the rainfall applicator settings were previously found suitable for outdoor model garden experimentation using larger plants, and previous green roof and hedge experiments (Blanuša & Hadley, 2019; Kemp *et al.,* 2019), this setting may have been too forceful for smaller plant sizes. Leaf inclination angle and leaf stiffness has also been linked with raindrop retention on a micro scale (Ginebra-Solanellas *et al.,* 2020), and the young plants used in experiment 4 may not have fully developed to enable adequate canopy capture.

The role of evapotranspiration in rainfall runoff reduction

The role of transpiration rate and substrate in combination to reduce rainfall runoff was examined in experiment 4. In summer there was less runoff generated by planted layouts compared to bare substrate only, indicating a greater contribution from plant transpiration than evaporation from the substrate surface alone. Rainwater runoff was also lower for planted layouts in summer compared to winter, in particular the *Pseudodictamnus x Verbena* combination. Previous research has shown that plants with higher transpiration rates reduced substrate moisture content more rapidly than slower transpiring plants, thereby helping reduce runoff (Berretta *et al.,* 2014; Nur Hannah Ismail *et al.,* 2023; Kemp *et al.,* 2019; Poë *et al.*, 2015; Szota *et al.,* 2017), and it was expected that when deciduous plants were not actively transpiring in winter this would result in higher runoff volumes compared to summer. However, it was hypothesised that evergreen plants would have a lower runoff volume in winter compared to deciduous plants as the former would still be transpiring at a low level, but there was little difference in runoff volumes between the two groups of plants. The similarity in winter runoff volumes between different plant layouts could have been due to the small size of the plants, as was speculated to be the case with retention of rainfall within the canopy, with larger leaf area usually associated with higher transpiration rates (Chu & Farrell, 2022; Lundholm *et al.,* 2015; Xie *et al.,* 2018; Yuan *et al.,* 2017). The increased temperature in the glasshouse necessary to reduce substrate moisture for suitable experimental conditions (which had an average temperature of 20.9°C on the day data was collected for evapotranspiration runoff) could have also contributed to increased transpiration rates in deciduous plants (Gourdji *et al.,* 2013; Hatfield & Prueger, 2015; Poë *et al.*, 2015). Deciduous plants were expected to be dormant during the winter experiments but this could explain why the deciduous *Verbena* monoculture unexpectedly produced the lowest runoff volumes.

Comparing plants with pervious surfaces in experiment 5 found that the plants' evapotranspiration and retention of rainfall within the substrate significantly decreased runoff compared to model gardens with no plants present. The importance of substrate has been confirmed in other experiments, with different substrate compositions aiding rainwater retention more than others (Dusza *et al.,* 2016; Nasrollahpour *et al.,* 2022; Stovin *et al.,* 2015; VanWoert *et al.,* 2005). The negative impact of impervious surfaces has also been established, with tarmac, concrete, and artificial turf all increasing rainfall runoff and contributing to surface water accumulation (Chang *et al.,* 2021; Kelly, 2016; Liu *et al.,* 2020b; Pataki *et al.,* 2011; Perry & Nawaz, 2008; Simpson & Francis, 2021; Warhurst *et al.,* 2014; Zhang *et al.,* 2015). Pervious surfaces that enable rainwater to filter through, and are often mentioned as alternative options for gardeners to use for hard landscaping, have been the focus of a small number of studies and had reduced runoff volumes compared to impervious materials (Chang *et al.,* 2021; Ow & Chan, 2021). Plants significantly reduced runoff volumes compared to gravel, bark chippings, and bare substrate, but there was no significant difference between the three pervious surfaces tested, which all produced similar runoff volumes, despite VanWoert *et al.* (2005) finding gravel produced greater runoff than substrate in a green roof experiment due to the latter's increased water holding capacity. The size of the miniature model gardens could also potentially explain this result, and larger surface areas may see a significant difference in runoff. Comparing pervious and impervious surfaces would be the next step when determining the best materials to use to reduce rainfall runoff generated by domestic gardens.

The contribution of plant roots and aboveground biomass on runoff reduction

Leaf area index and dried aboveground biomass were both found to significantly contribute to retention of rainfall within the canopy in experiment 3's outdoor model gardens during the summer, although surprisingly this was not the case in winter. *Oenothera* had the largest leaf area index in both seasons, however it had the lowest aboveground biomass in winter, and yet still generated the lowest runoff volumes. Although the stems of *Oenothera* may be lighter than *Erysimum*, this result indicates that trichomes (present on *Oenothera*, but not *Erysimum*) likely play an important role. In contrast, leaf area index was not a significant factor for retention of rainfall within the canopy in miniature model gardens, potentially because the canopy was too small to retain large volumes of water (Heim *et al.,* 2023; Nagase & Dunnett, 2012). But a larger leaf area index was linked to higher evapotranspiration rates in this experiment, and the higher transpiration rate appeared to significantly reduce rainfall runoff (Chu & Farrell, 2022; Lundholm *et al.,* 2010; Yuan *et al.,* 2017; Xie *et al.,* 2018).

Experiment 4's miniature model gardens all had significantly larger dried roots mass in summer, which could have contributed to the reduced runoff volumes produced by all plants in summer compared to winter (Dunnett *et al.,* 2008; MacIvor & Lundholm, 2011; Nasrollahpour *et al.,* 2022). The *Verbena*, *Pseudodictamnus*, and *Pseudodictamnus x Verbena* layouts in summer had a larger dried roots mass than *Erysimum, Oenothera* and *Erysimum x Oenothera*.

Larger roots have been shown to have greater water volume uptake (Lundholm *et al.,* 2015; Stovin *et al.,* 2015), but the *Verbena* monoculture had a comparable (larger) root mass to the *Pseudodictamnus* monoculture and the *Pseudodictamnus x Verbena* mixture, yet produced a larger runoff volume during summer than both the *Pseudodictamnus* monocultures and mixed layouts. When examining dried roots mass alone it is surprising that the *Verbena* (average dried roots mass of 11.69 g) had significantly larger runoff volumes than the *Pseudodictamnus* (average dried roots mass of 11.76 g). This could indicate that more than one trait in addition to root mass, such as leaf hairs or leaf area in conjunction with root mass, or the shape of the plant (*Verbena* is tall and thin) impacts runoff reduction. An additional explanation could be the variation in the growth of the *Verbena's* in each model garden, with some growing much larger than others, which contributed to higher average runoff volumes from this species.

The impact of plant combinations

A striking difference between the two types of model garden experiments was the role that planting combinations played. Within outdoor model gardens (experiment 3) this was not as obvious, although per leaf area index the Mixed layout produced significantly lower runoff volumes than the *Erysimum* in winter and summer. However, when investigating the runoff volumes of *Pseudodictamnus* and *Verbena* as monocultures compared to the mixture in the miniature model gardens (experiment 4), the results were more obvious.

The *Pseudodictamnus* monoculture had a significantly lower runoff volume and greater volumes of rainfall retained in the canopy compared to *Verbena*, which could be due to the leaf hairs present on the *Pseudodictamnus*, and the shape of the *Verbena*, which is tall and thin with almost no canopy allowing greater volumes of rainfall to reach the substrate and subsequently produce runoff. When the two plants were combined within a miniature model garden, instead of the mixed runoff volume positioned between the two monoculture results, as was observed with the *Erysimum x Oenothera*, the volume of runoff became similar to *Pseudodictamnus* alone.

These results indicate that the impact of a monoculture that is unable to decrease runoff could be improved when combined with another plant. The benefits of mixed planting for ecosystem service delivery (such as surface temperature reduction or rainfall retention) has been established in a number of studies (Heim *et al.*, 2023; Lundholm *et al.,* 2010; MacIvor *et al.,* 2018; Nazemi Rafi & Kazemi, 2021; O'Carroll *et al.,* 2023; Yuan *et al.,* 2017), although Dunnett *et al.* (2008) also found that within a green roof setting the introduction of 'less efficient' species reduced the overall rainfall retention of the planting combination, so potentially multiple plant traits, or the plant species specifically, needs to be taken into account when planning planting designs for improved rainfall retention. Previous research has indicated that no specific planting combination can provide the greatest service delivery in all areas (Lundholm *et al.,* 2010), but runoff retention has been improved in some studies using mixed planting types, including increasing phylogenetic diversity to provide stormwater retention and cooling services using *Sedum* and perennials (MacIvor *et al*., 2018), and mixed prairie species reducing rainfall runoff compared to *Sedum* plants alone (Ksiazek-Mikenas *et al.,* 2023). Lundholm *et al.* (2010 & 2015) found that mixed planting on a green roof improved rainfall capture and reduced substrate temperatures in summer compared to some monocultures, and this was due in part to the increased leaf area of multiple plant species which enabled greater retention of rainfall in the canopy, increased evapotranspiration rates, and shading to cool the substrate. Increasing the proportion of certain traits including leaf thickness, leaf area and root density in planting combinations has also improved stormwater retention in other studies as well (Dunnett *et al.,* 2008; Heim *et al.*, 2023; O'Carroll *et al.,* 2023). The combination of different growth characteristics of *Pseudodictamnus* and *Verbena*, and the addition of *Pseudodictamnus's* leaf hairs and larger leaf area, could be attributed to the reason for the reduced runoff when the two species were in mixed layouts. Although the mixed *Pseudodictamnus x Verbena* layout did not provide significantly greater runoff reduction than the *Pseudodictamnus* monoculture, it was similar, and did reduce runoff compared to the *Verbena* monoculture and other plant species combinations (*Oenothera and Erysimum*), indicating mixed planting can be beneficial for rainfall retention in certain combinations.

4.6 Limitations

- The size of the outdoor model gardens in experiment 3 meant that only retention of rainfall within the canopy data was possible to collect, and alteration to the methodology was required (and implemented in experiments 4 and 5). The size of the plants and quantity of growing substrate required was too large to enable study of evapotranspiration impact because after two days of no irrigation the subsequent rainfall required to produce runoff was so great that it would have taken too long to undertake the experiment and wasteful of water as well (see section 2.7.3, Chapter 2, for details).
- The smaller size of the plants in experiment 4 compared to experiment 3 likely contributed to some of results not being significant in experiment 4. Larger plants would have had larger root systems and canopies that would have provided greater water uptake and increased the capacity for rainfall retention in the canopy, which was observed in experiment 3. The inclusion of smaller plants was a compromise to overcome design issues with the outdoor model gardens in experiment 3 including water use and the greater substrate water holding capacity (see Chapter 2) and were more manageable to undertake data collection, however miniature model gardens also limited the size of plants used.

4.7 Key conclusions

- Whether plants were evergreen or deciduous was not the greatest determinant of rainfall runoff reduction in either of the tested seasons. Plant traits including trichomes and transpiration rate are potentially as/more important.
- Plant size appears to significantly contribute to retention of rainfall within the canopy. The increased size of *Erysimum* and *Oenothera* in experiment 3 led to *Oenothera* providing significantly greater retention of

rainfall within its canopy compared to the *Oenothera* plants in experiment 4.

- Mixed planting could improve retention of rainfall within plant canopies and reduce rainfall runoff in some planting combinations, but could also improve the performance of monocultures with a lower capacity to capture rainfall in their canopies or remove water from the substrate by transpiration.

Chapter 5

Impact of plant combinations and short-term subtotal flooding treatment on plant water loss

5.1 Introduction

Climate change in the UK is resulting in hotter, drier summers and warmer, wetter winters with an increase in infrequent, heavier rainfall events during the summer (Beidokhti & Moore, 2021; IPCC, 2021; Kendon *et al.,* 2023; Webster *et al.,* 2017), the impact of which will only be exacerbated in urban areas by the increase in impermeable surfaces (Chalmin-Pui *et al.,* 2019; Simpson & Francis, 2021; Warhurst *et al.,* 2014). Therefore, plant selection for gardeners needs to include varieties able to survive periods of inundation.

Excess water in the form of waterlogging or flooding causes oxygen deprivation to plant roots, (hypoxia or, in severe cases of depletion, anoxia) (Byrne *et al.,* 2022; Lukac *et al.,* 2011; Vartapetian & Jackson, 1997). The restricted gas exchange is stressful for many plants as it limits aerobic respiration. Switching to anaerobic respiration leads to toxic accumulation of metabolites that in turn also causes stress (Cameron & Hitchmough, 2016; Li *et al.,* 2021; Pan *et al.,* 2021; Yin *et al.,* 2009). Plants sensitive to waterlogging experience diminished stomatal conductance and photosynthetic rates (Else *et al.,* 2009; King *et al*., 2012; Olorunwa *et al*., 2023; Yin *et al.,* 2012), leaf and shoot water deficit and wilting (King *et al.,* 2012; Yin *et al.,* 2012), growth/biomass and yield reductions (Byrne *et al.,* 2022; Cannell *et al.,* 1980; Dickin & Wright, 2008; Dylewski *et al.,* 2011; Shao *et al.,* 2023), and root death (Chauhan *et al.,* 1997; Davies *et al.,* 2000; King *et al.,* 2012). Spring and summer waterlogging, when plants are in their active growth phases and increased aerobic respiration is taking place, usually results in greater damage than during winter (Cameron & Hitchmough, 2016; Ren *et al.,* 2023).

Plant varieties can tolerate waterlogging by employing a number of strategies: the formation of adventitious roots (Kozlowski & Pallardy, 2002; Li *et al.,* 2023;

Yin *et al.,* 2009; Zhao *et al.,* 2022), lenticels and aerenchyma tissues (Geng *et al.,* 2023; Kozlowski & Pallardy, 2002; Yin *et al.,* 2012), and metabolic adjustments (Kozlowski & Pallardy, 2002; Geng *et al.,* 2023; Yin *et al.,* 2009), many of which have been observed in riparian species frequently inundated by flood waters (Lukac *et al.,* 2011; Vartapetian & Jackson, 1997). Plant traits including a higher evapotranspiration rate have been associated with greater waterlogging tolerance and stormwater retention (Lundholm *et al.,* 2010; Nasrollahpour *et al.,* 2022; Yuan *et al.,* 2017), and older plants with larger roots or plants able to quickly establish their roots can tolerate waterlogging conditions better than younger plants or those with less developed root systems (Ide *et al.,* 2022; Jernigan & Wright, 2011; Scharnweber *et al.,* 2013). Plants that are able to rapidly re-grow roots after waterlogging show greater recovery post-flooding (Bramley *et al*., 2011; Davies *et al.,* 2000; Dickin & Wright, 2008). However, adaptations adopted by garden perennials in these conditions are not well known.

Rain gardens have been used to study the responses of perennials (such as *Echinacea*, *Hemerocallis, Rudbeckia*) in waterlogged soils, with survival rates and decreased root/shoot biomass indicating adaptability to inundation (Bortolini & Zanin, 2019; Laukli *et al.,* 2022a & 2022b; Nocco *et al.,* 2016; Yuan & Dunnett, 2018; Yuan *et al.,* 2017). Some perennials (e.g. prairie or forb mixes, or shrubs including *Betula* and *Salix*) have been shown in rain gardens to increase stormwater infiltration and provide canopy retention and evapotranspiration services (Laukli *et al.,* 2022b; Nasrollahpour *et al.,* 2022; Nocco *et al.,* 2016; Yuan & Dunnett, 2018), and could be comparable to some domestic gardens after inundation from heavier rainfall events. Popular gardening articles have recently included lists of plants that anecdotally tolerate summer heat wave conditions when less water is available (Beth Chatto's Plants & Gardens, 2019, 2022a & 2022b; Brown, 2022; Wallington, 2022,), however there is no mention of their survival in waterlogged conditions, which would likely follow heavy summer precipitation (Webster *et al.,* 2017). Certain popular garden perennials survive and continue to grow in short-term flooded conditions, including taxa commonly associated with well-drained substrates or prairie habitats (such as *Rudbeckia* species) (Laukli *et al.,* 2022b; Nasrollahpour *et al.,* 2022; Yuan & Dunnett, 2018). Previous flooding experiments on Mediterranean garrigue plants have also found 'drought-tolerant' species *Lavandula angustifolia* and *Stachys byzantina* are resilient to winter and summer flooding (King *et al.,* 2012), as well as ornamental *Chrysanthemum* varieties (Yin *et al.,* 2009), *Angelonia salicariifolia* and *Zinnia angustifolia* (Yang *et al.,* 2020) producing adventitious roots. Flooded garrigue plant responses and rain garden experiments may indicate these plants can tolerate more water than previously realised. However, there is variation within ornamental perennials and crop taxa to waterlogging tolerance (Bortolini & Zanin, 2019; Ide *et al.,* 2022; Laukli *et al.,* 2022b; Olorunwa *et al.,* 2023) and speculation that breeding for aesthetics or increased yield may come at the expense of stress tolerance in some plants (Lewis *et al.,* 2019).

The majority of research in this field has focused on the responses of individual plants, whether this is in pot experiments, field trails, or rain gardens, but a planting bed in a domestic garden would include multiple plants of different taxa growing together and their interactions could impact each others survival. Planting combinations in the form of companion or nurse planting have been shown to increase crop yields by attracting more pollinators (Griffiths-Lee *et al.,* 2020), decrease substrate temperature (Butler & Orians, 2011), increase plant biomass and improve plant health (Aguiar *et al.,* 2019; Butler & Orians, 2011; Matsuoka *et al.,* 2019 & 2020). Combining plants with different sensitivity to environmental stress and varied shoot and root growth resulted in stress-tolerant species supporting and facilitating the growth of non-tolerant species (Ren *et al*., 2014; Zhu *et al.,* 2022). Interspecific interactions between planting combinations also have the potential to increase ecosystem service delivery (Leotta *et al.,* 2023; Nagase & Dunnett, 2012; Nazemi Rafi & Kazemi, 2021; O'Carroll *et al.,* 2023; Yuan *et al.,* 2017) or provide multiple ecosystem services, such as rainwater retention and cooling services by using planting with diverse traits and growth habits (Heim *et al.,* 2023; Lundholm *et al.,* 2010; MacIvor *et al.,* 2018). Traits shown to have the potential to aid plant survival in waterlogging conditions include higher transpiration rates, which reduces substrate moisture levels more quickly, and larger root mass or ability to quickly establish a root system, which reduces root death and has been linked with greater tolerance to flooding (Laukli *et al.,* 2022b; Nasrollahpour *et al.,* 2022; Nocco *et al.,* 2016). The experimental plants in this thesis have been categorised as either having a lower evapotranspiration rate (*Erysimum* and *Pseudodictamnus*) or a higher evapotranspiration rate (*Oenothera* and *Verbena*) (Chapter 3), the latter group which should help with plant survival during periods of excess water. By combining research on ecosystem service delivery, companion planting, and stress tolerance, the experiments within this chapter will investigate the impact of companion planting on waterlogged plants' survival and runoff reduction.

5.2 Study Aims and Hypotheses

Popular perennial garden plants in monocultures and mixed pairings were subjected to spring overwatering, and spring and summer subtotal flooding, to determine whether plant mixtures with certain plant traits were better able to survive and thrive in short-term waterlogging conditions. All of the plant species tested anecdotally prefer well-drained conditions or lower water availability (Royal Horticultural Society, no date, e, f, i, j), and therefore it was assumed that both overwatering and short-term flooding would be sufficient to induce stress responses from the plants.

The objectives of this chapter were to:

- Determine whether any of the experimental plants were able to survive overwatering or short-term flooding. It was hypothesised that plants with a higher transpiration rate would be able to maintain their transpiration rate during waterlogging or quickly regain their higher transpiration rate after removal from the water, therefore displaying rapid recovery from flooded conditions.
- Investigate the impact that combinations of different plants with varying transpiration rates had on individual plant's waterlogging tolerance. It was hypothesised that pairings of high and low transpiring plants in combinations (e.g. *Oenothera* or *Verbena* with *Erysimum* or *Pseudodictamnus*) could result in a higher rate of transpiration as a combination during waterlogging, or post-waterlogging, compared to the

lower transpiring monocultures (e.g. *Erysimum* or *Pseudodictamnus*) and therefore quicker recovery from flood stress.

It was anticipated that species with higher evapotranspiration rates would show greater tolerance to waterlogging (in the form of overwatering or flooding) than species with lower evapotranspiration rates, but as all the experimental plant species used in this thesis prefer low moisture, they would also all display some evidence of stress in waterlogged conditions.

5.3 Materials and Methods

Experiment 6 tested *Erysimum* and *Oenothera* in spring control and overwatered conditions. Experiment 7a and 7b tested *Erysimum, Oenothera, Verbena* and *Pseudodictamnus* to short-term subtotal flooding in summer and spring respectively. All experiments tested paired combinations of monocultures and mixtures. Transpirational water loss, stomatal conductance rates, and dried aboveground biomass and root mass was assessed in all experiments.

5.3.1 Plant material

For all experiments plants were grown from cuttings and potted into 9 cm containers 2-3 months later using a peat-free growing medium (SylvaGrow Multi-purpose, Melcourt, UK), and one week prior to experimentation individual plants were combined in pairs in 3 L containers and placed in an unheated glasshouse. For experiment 6 *Erysimum* and *Oenothera* were grown from cuttings in January 2022, for experiment 7a *Erysimum* and *Oenothera* were grown in April 2022, and in experiment 7b *Erysimum, Oenothera, Pseudodictamnus* and *Verbena* were grown in February 2023.

5.3.2 Experiment setup and conditions

Experiments 6 and 7 were carried out in a ventilated glasshouse at the University of Reading Whiteknights campus. Experiment 6 was conducted from the 29th March 2022 for four weeks; experiment 7a was from the 12th-20th July 2022; experiment 7b was from 10th-18th April 2024, both for 9 days. Glasshouse temperatures were not regulated, however air vents were set to close at 15°C indoor temperature and open at 20°C. Air temperatures and relative humidity were measured every 30 minutes using a Tinytag Plus 2 Data Logger (Gemini Data Loggers, Chichester, UK) positioned in a shady location in the centre of the plant layout at the same height as the monitored plants. Experiment 6 average temperature inside the glasshouse for the four weeks of experimentation was 19.5°C (±4.34 SD) with a minimum of 13.9°C and a maximum of 39.1°C; experiment 7a average temperature inside the glasshouse for the nine days of experimentation was 29.5°C (±7.88 SD) with a minimum of 17.1°C and a maximum of 49.4°C; experiment 7b average temperature inside the glasshouse for the nine days of experimentation was 16.4°C (±6.26 SD) with a minimum of 4.9°C and a maximum of 31.7°C.

5.3.3 Data collection

Experiment 6 - Spring overwatering

Five replicates of each treatment were placed in the glasshouse three days prior to experimentation, in a random pattern. Each container was connected to automated irrigation, the water volumes for each treatment having been predetermined prior to experimentation (data not shown). Irrigation timing was scheduled four times a day at 8am, 1pm, 4pm, and 6pm to allow sufficient time between irrigating to collect plant data, although the water volumes were altered when necessary to maintain substrate moisture content of approximately 0.20-0.30 $m^3 m^{-3}$ for control plants and >0.40 $m^3 m^{-3}$ for overwatered plants. For the majority of the experiment control volumes were 292 ml per day per pot and overwatered volumes were 1168 ml per day per pot. For both treatments excess water was able to drain out of the pots and onto the glasshouse floor via the holes in the containers.

A summary of data collection frequency can be found in Table 5.1 below. Container mass and substrate moisture content was measured twice daily to give transpirational water loss within a two-hour period between scheduled automated irrigations. Stomatal conductance data collection began 24 hours after plants had been subjected to control or overwatering regimes (measurement approach can be found in section 2.2.6, Chapter 2). At the end of the experiment plants were destructively harvested for leaf area and biomass.

Variable	Data collection frequency	Number of measurements	Data collection start
Container mass	Twice a day - 9.30 and 11.30 am every day for Week 1 and 2; twice a day for two days a week for Week 3 and 4	5 pots of each layout	Day 0 (first day of the experiment)
Substrate moisture content	Twice a day - 9.30 and 11.30 am every day for Week 1 and 2; twice a day for two days a week for Week 3 and 4	5 pots of each layout, 2 readings per pot	Day 0
Stomatal conductance	Daily for Week 1 and 2; twice a week for Week 3 and 4	18 leaves per layout (3 leaves per plant, both plants in each pot, 3 pots per layout)	Day 1

Table 5.1: Experiment 6 data variables collection summary.

Experiment 7a - Summer short-term subtotal flooding

Previous research by Yuan and Dunnett (2018) tested responses of *Oenothera lindheimeri* to short-term flooding, with results indicating it could tolerate four days in these conditions with reduced biomass but potentially not longer inundation, and due to this short-term and subtotal flooding was chosen rather than more prolonged flooding with total root system submergence.

Paired combinations of *Erysimum* and *Oenothera* in monocultures and mixed layouts and bare substrate control pots were subjected to control water treatment using automated irrigation; subtotal flooding was achieved using buckets. Subtotal flooding was defined as flooding 100 mm below the top of the plant pot, which equated to 60% of the total volume of the bucket (King *et al.,* 2012). This was used instead of total submergence as it was anticipated the plant species would be unable to tolerate total flooding, and that subtotal flooding would also represent a raised water table caused by heavier rainfall events.

Eight replicates of each plant layout and treatment, and five replicates for bare substrate, were used. Plant containers were placed in the glasshouse three days prior to experimentation in a random pattern. On day 0 (first day of experimentation) containers in the waterlogged treatment were placed in buckets of water and submerged so that 60% of the pot was under water; this was achieved by having 5.7 L of water within the bucket (King *et al.,* 2012) (Figure 5.1). On day 3 pots were removed from the water buckets and allowed to drain for the remainder of the experiment, during which time no additional irrigation was applied to the waterlogged pots. Control pots were connected to automated irrigation set at between 146-255.5 ml per day per pot for the majority of the experiment.

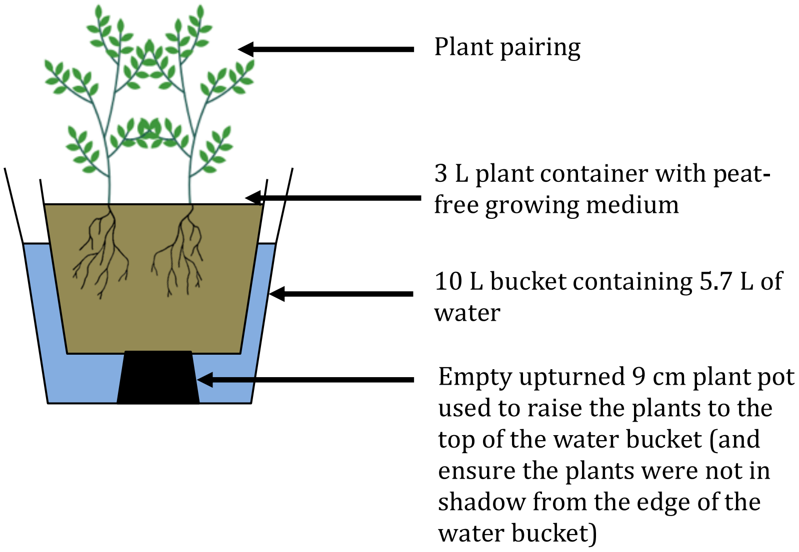


Figure 5.1: Diagram of subtotal flooding experimental setup (not to scale).

Container mass and substrate moisture content was recorded daily on days 0, 1, 2, and 3, and again on day 8 at the end of experimentation. Due to a UK heat wave that resulted in unsafe working conditions, the university prohibited data collection on days 4-7. Stomatal conductance data collection began on day 1 of the experiment, 24 hours after plants had been subjected to control or waterlogging regimes (measurement approach can be found in section 2.2.6, Chapter 2) and collected on days 1, 2 and 3. A summary of data collection frequency can be found in Table 5.2 below. At the end of the experiment plants were destructively harvested for leaf area and biomass.

Experiment 7b - Spring short-term subtotal flooding

Paired monoculture combinations of *Oenothera, Erysimum, Verbena*, and *Pseudodictamnus*, and mixed layouts of *Erysimum* and *Oenothera*, and *Pseudodictamnus* and *Verbena*, as well as bare substrate controls were subjected to control or subtotal flooding treatments. Five replicates of each layout were used. Plant containers were placed in the glasshouse three days prior to experimentation and waterlogged on day 0 using buckets and water volumes shown in experiment 7a above (Figure 5.1). Automated irrigation as described in experiment 7a was used for control pots. On day 4 (Yuan & Dunnett, 2018) pots were removed from the water buckets and allowed to drain for the remainder of the experiments with no additional irrigation.

Container mass and substrate moisture content was measured daily for nine days, and assimilation rate and stomatal conductance data was measured daily for eight days, after which several waterlogged layouts' substrate moisture content had reduced below control plants and experimentation ceased. Stomatal conductance and net CO_2 assimilation rate data collection began on day 1 of the experiment, 24 hours after plants had been subjected to control or waterlogging regimes (measurement approach can be found in sections 2.2.6 and 2.2.7, Chapter 2). A summary of data collection frequency can be found in Table 5.2 below. At the end of the experiment plants were destructively harvested for leaf area and biomass.

Variable	Data collection frequency	Number of measurements	Data collection start
Container mass	Daily	Exp 7a - 8 pots of each planted layout, 5 bare substrate Exp 7b - 5 pots of each layout	Day 0 (first day of the experiment)
Substrate moisture content	Daily	2 readings per pot Exp 7a - 8 pots of each planted layout, 5 bare substrate Exp 7b - 5 pots of each layout	Day 0
Stomatal conductance	Daily	Exp 7a - 18 leaves per layout (3 leaves per plant, both plants in each pot, 3 pots per layout) Exp 7b - 16 leaves per layout (2 leaves per plant, both plants in each pot, 4 pots per layout)	Day 1
Net CO_2 assimilation rate	Daily	Exp 7b - 16 leaves per layout (2 leaves per plant, both plants in each pot, 4 pots per layout)	Day 1

Table 5.2: Experiment 7a and 7b data variables collection summary.

5.3.4 Data analysis

Data were analysed using R (R Core Team, 2021) and, where applicable, package lme4 (v1.1-26; Bates *et al.,* 2015). Where more than one species occurred in the same mixed layout, stomatal conductance data were separated into individual species within mixed layouts, for example *Erysimum gs* rate within the mixed layout was compared directly with *Erysimum gs* rate of plants in a monoculture.

For overwatering experiment (experiment 6), water loss was measured as mass loss per pot and per unit leaf area (per pot). Mass loss and stomatal conductance rate were analysed using linear mixed effects models. Fixed effects were overwatering treatment and species layout. Models included random intercepts for day and pot, to account for repeated measures made on the same day and on the same pot. Day was not included as a fixed effect because it did not have a significant linear or curved trend over time. Several approaches were tested to improve the normality and homoscedasticity of the model residuals, mass loss and stomatal conductance were standardised by day, and dependent variables were log-transformed. In the final model, mass loss data were log-transformed.

In summer flooding experiment 7a, water loss over time was measured as mass per pot and per unit leaf area (per pot) using data from days 3-8 (post-waterlogging days) and was analysed using mixed models. Fixed effects were flooding treatment, species layout and day, and random intercepts were included for each pot. Stomatal conductance was measured on individual plants within pots. To compare the stomatal conductance of plants in monoculture layouts with plants in mixed layouts, separate mixed models were used for each plant species, with fixed effects of layout and flooding treatment (day was not included as it was not significant), and random intercepts for pots. The final mass and substrate moisture content at the end of the experimentation (day 8) were analysed using two-way ANOVA (treatment and species layout) and post-hoc Tukey HSD tests, mixed models were not necessary as there was one measure per pot.

In spring flooding experiment 7b, water loss over time was measured as mass per pot and per unit leaf area (per pot) using data from days 5-8 (post-waterlogging days) to assess how recovery of transpiration rate varied between plant species and layouts. Analysis used mixed models as described in experiment 7a above. Models with mass per unit leaf area as a dependent variable did not meet normality assumptions and after comparing several options including log-transformation and generalised linear models, differences in leaf area were accounted for by including leaf area as a covariate. Stomatal conductance rate and net CO_2 assimilation rate were measured on days 1-4 (during-waterlogging) and days 5-8 (post-waterlogging). These data were analysed using linear mixed effects models with fixed effects for flooding treatment, species layout and day and random intercepts for each pot, as above.

For all experiments the dried root and stem biomass was analysed using a two-way ANOVA (water treatment and species layout) with post-hoc Tukey HSD tests. For experiment 6 and 7a, the dependent variables were log-transformed.

5.4 Results

5.4.1 Experiment 6 - Impact of spring overwatering on monocultures and plant mixes in pots

Daily average water loss per pot

Transpirational water loss per pot was significantly higher for overwatered *Oenothera* compared to all other overwatered layouts ($p < 0.001$) and compared to the *Oenothera* control treatment ($p = 0.002$), losing an average of 7-56 ml (23-55%) more than control pots from week 1 to 4 respectively (Figure 5.2). However, there was no significant difference between *Erysimum* control and overwatered treatments ($p = 0.832$). Both control and overwatered water loss followed very similar patterns each day for all layouts, and random fluctuation in water loss was suspected to be due to temperature change in the glasshouse rather than a trend over time due to overwatering. There was an increase in glasshouse temperature during the final two weeks of experimentation, with a daily maximum of 39.1°C recorded on day 18, which resulted in increased water loss for all treatments and layouts. Comparing monocultures and the Mixed layout found that *Oenothera* lost significantly more water per day per pot over the experiment length than the overwatered Mixed pots, losing 30.6 ml/day on average by week 4, and *Erysimum* lost significantly less water than the Mixed ($p = 0.001$).

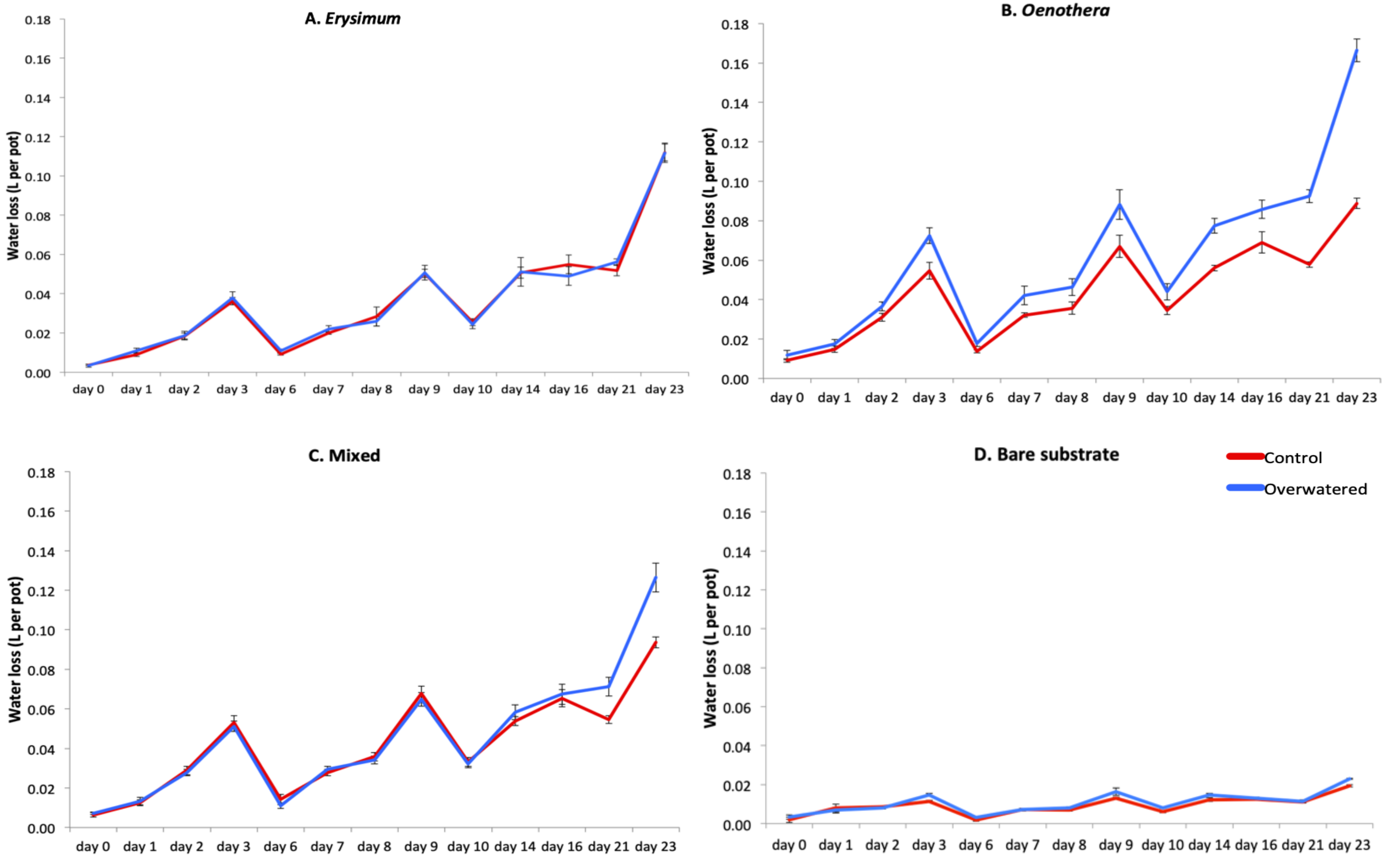


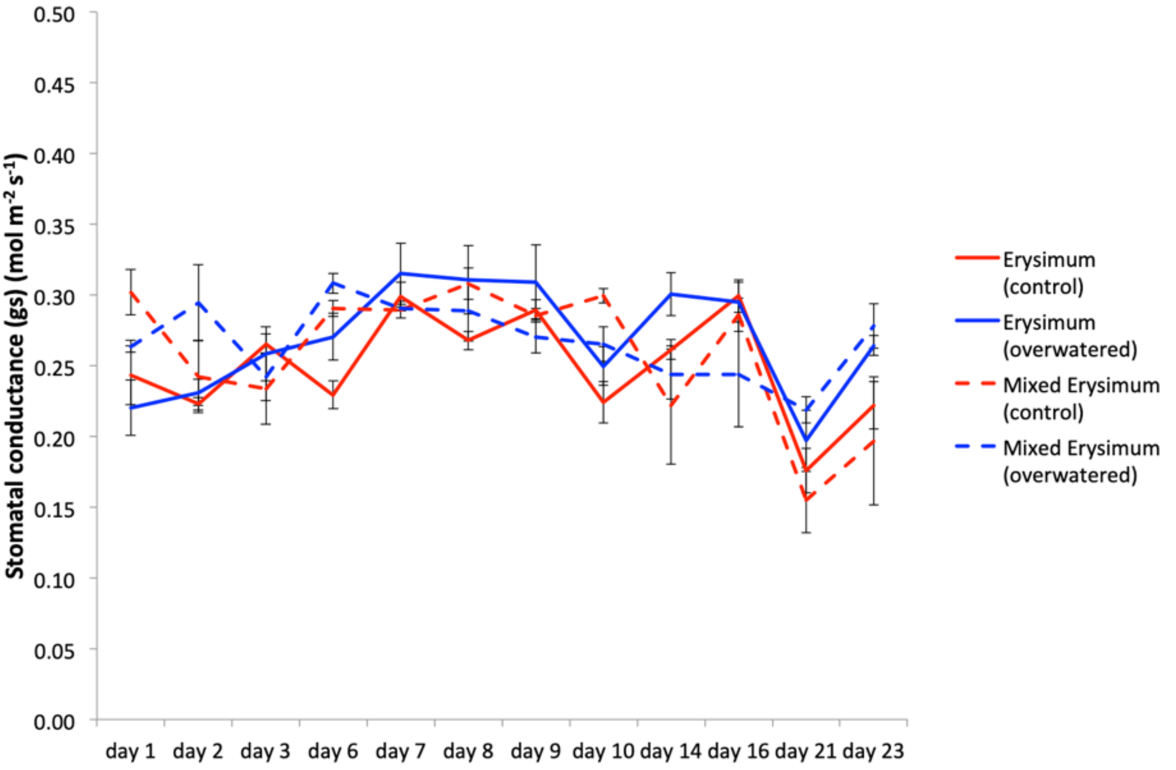
Figure 5.2: Mean daily water loss per pot within a two-hour time period and associated standard error of the means (n = 5 pots per layout and treatment). A. *Erysimum*, B. *Oenothera*, C. Mixed, D. Bare substrate.

Daily average water loss per leaf area

Standardised water loss per unit of leaf area found that, as with water loss per pot, overwatered *Oenothera* lost significantly more water than *Oenothera* control ($p = 0.040$), and *Erysimum* water loss was not significantly different between treatments ($p = 0.108$) (data not shown). However, per unit of leaf area neither monoculture was significantly different from the overwatered Mixed layout, and although overwatered *Oenothera* lost more water than overwatered *Erysimum* this was only close to significantly different ($p = 0.059$) (data not shown).

Stomatal conductance

Stomatal conductance was slightly significantly higher for overwatered *Erysimum* compared to control ($p = 0.039$), but there was no significant difference between *Oenothera* treatments ($p = 0.102$) (Figure 5.3). Comparing the monoculture stomatal conductance rates with individual *Oenothera* or *Erysimum* in the Mixed layout (Figure 5.3 dashed lines) found that neither mixed overwatered treatment was significantly different from the monoculture counterpart. However, the Mixed *Oenothera* control treatment had a significantly higher stomatal conductance rate than *Oenothera* monoculture control ($p = 0.007$), and peaked at 0.416 mol m^{-2} s^{-1} on day 8, 0.132 mol m^{-2} s^{-1} higher than the control Mixed *Oenothera*. With the exception of the Mixed *Oenothera* plants, all layouts and treatments can be seen to follow similar fluctuations, which is comparable to the daily temperature fluctuations recorded in the glasshouse during the experiment (Figure 5.4).



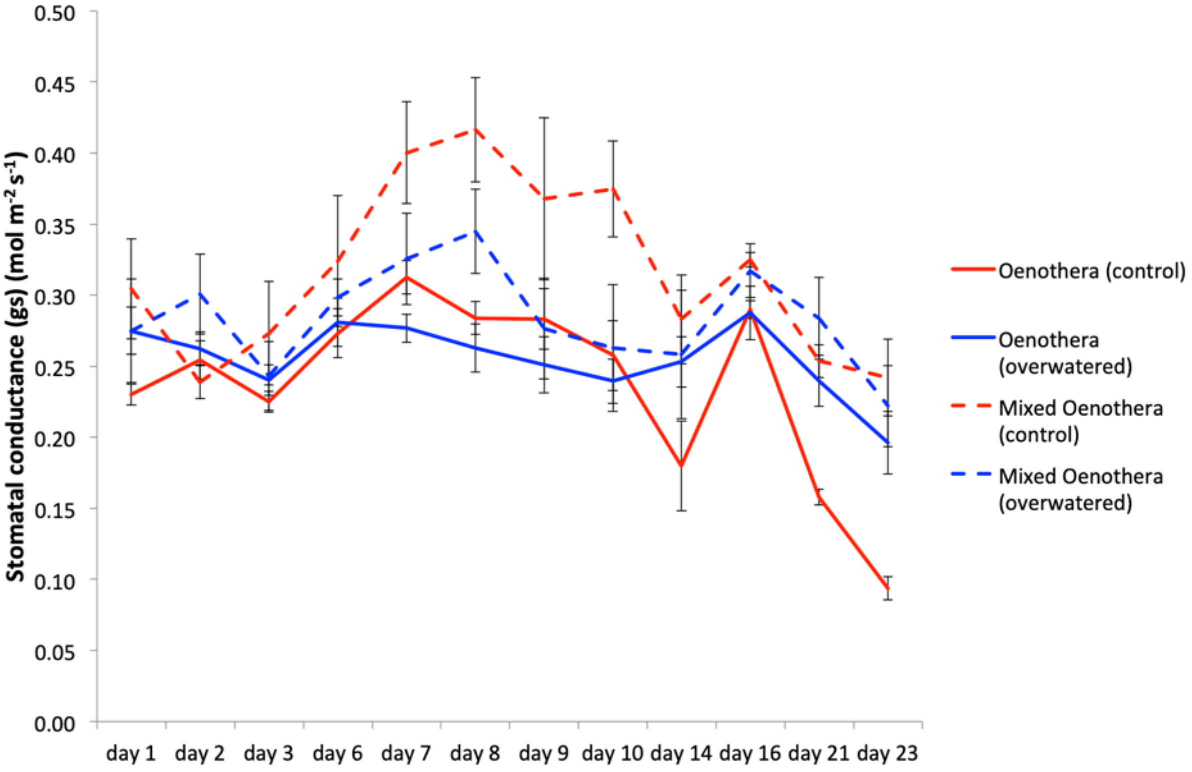


Figure 5.3: Mean daily stomatal conductance and associated standard error of the means for *Erysimum* and *Oenothera* (n = 6 plants in monocultures, n = 3 plants in mixed layout).

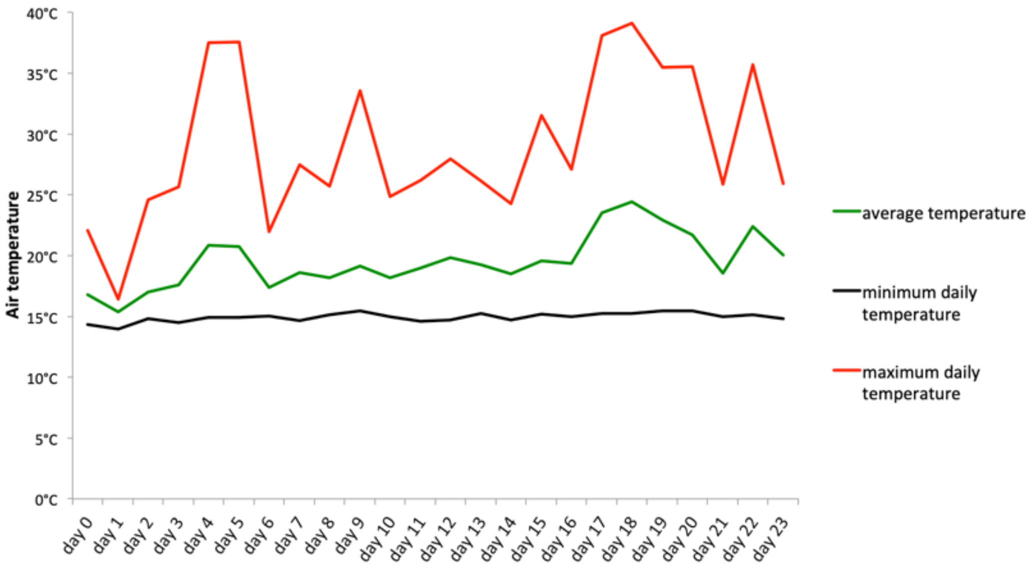


Figure 5.4: Mean air temperature, daily minimum and daily maximum for the glasshouse for the duration of experiment 6.

Dry aboveground biomass

At the end of the experiment three pots per layout were destructively harvested and there was a significant difference in dry aboveground biomass between control and overwatered layouts. Dry leaf and stem biomass for overwatered *Erysimum* and the Mixed layout was lower ($p < 0.001$) by an average of 2.67 g and 2.10 g respectively than their control counterparts per pot. Overwatered *Oenothera* had significantly higher dry shoot biomass ($p < 0.001$) than the control *Oenothera* (average increase of 3.35 g, data not shown).

Dry roots biomass

There was a significant decrease in dried roots mass of overwatered *Erysimum* compared to controls ($p < 0.001$) and significant increase for *Oenothera* ($p = 0.012$), but no significant difference between Mixed layout treatments ($p = 0.839$). The dried root mass of overwatered *Erysimum* was an average of 2.66 g smaller than control whilst the overwatered *Oenothera* was an average of 1.18 g greater than the control (Figure 5.5).

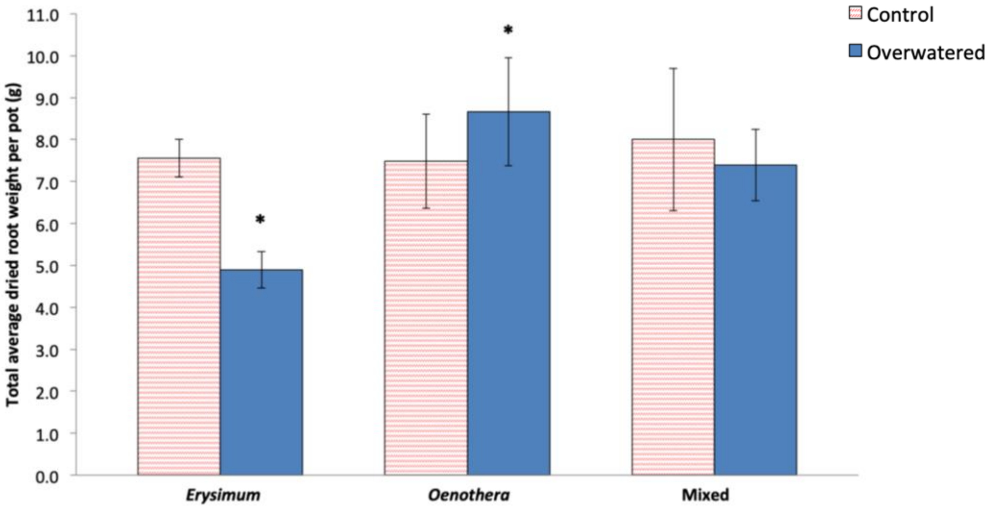


Figure 5.5: Mean dried roots mass per pot and associated standard error of the means (n = 3 pots per layout and treatment). An asterisk denotes statistically significant differences between the control and waterlogged layout pairing.

5.4.2 Experiment 7a - Impact of summer waterlogging on monocultures and plant mixes in pots

Daily average water loss per pot

Transpirational water loss was significantly greater for all waterlogged plants per pot compared to their control counterparts post-waterlogging between days 3 and 8 ($p < 0.001$) (Figure 5.6). The *Oenothera* waterlogged treatment lost significantly more water compared to all other plants and treatments ($p < 0.001$ for bare substrate and *Erysimum*, $p = 0.004$ for Mixed) with an average total decrease of 1.10 L by day 8. In contrast to this *Erysimum* waterlogged treatment water loss was significantly less than the Mixed layout ($p < 0.001$), and not significantly different from the waterlogged bare substrate, as both *Erysimum* and bare substrate likely lost water via drainage and evaporation.

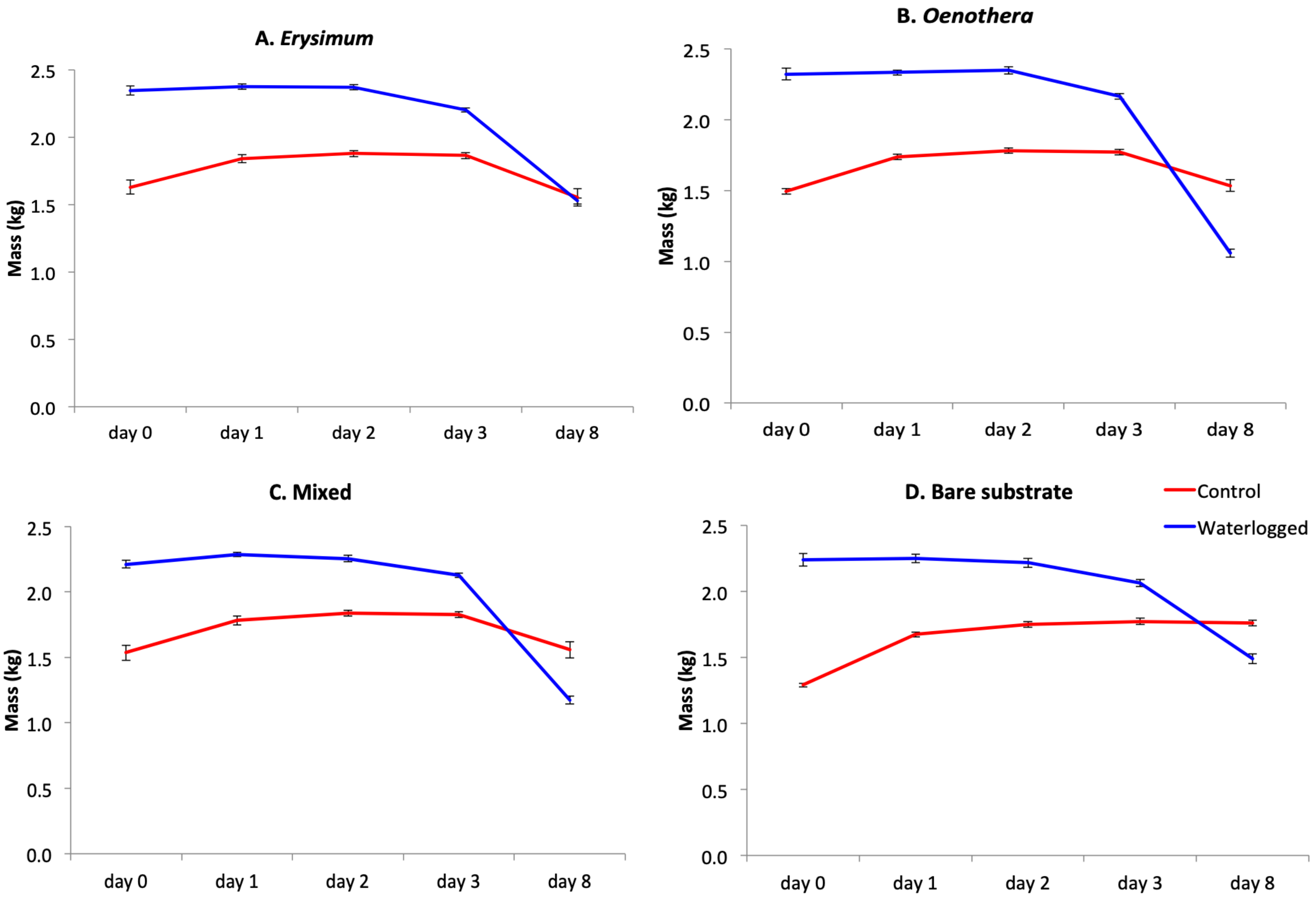


Figure 5.6: Mean daily water loss per pot and associated standard error of the means (n = 8 for all plants and n = 5 for bare substrate per layout and treatment). A. *Erysimum*, B. *Oenothera*, C. Mixed, D. Bare substrate.

Daily average water loss per leaf area

Water loss between day 3 and day 8 per standardised unit of leaf area again found that all control treatments lost significantly less water than their waterlogged counterparts ($p < 0.001$), and that the waterlogged *Oenothera* lost significantly more water than both the waterlogged *Erysimum* or Mixed layout ($p < 0.001$) (data not shown). Also as observed per pot, *Erysimum* lost significantly less water than the Mixed layout per standardised unit of leaf area ($p < 0.001$) (data not shown).

Stomatal conductance

Investigating the stomatal conductance rate found that no control treatments were significantly different from each other ($p = 1.000$; *Oenothera* vs. Mixed $p = 0.982$), however all control treatments were significantly higher than their waterlogged counterparts (*Oenothera* $p = 0.004$, *Erysimum* and Mixed $p < 0.001$) (Figure 5.7). *Oenothera* waterlogged treatment had the highest stomatal conductance rate compared to *Erysimum* waterlogged treatment ($p < 0.001$) with an average rate of 0.098 mol m^{-2} s^{-1} over three days under waterlogging. The *Erysimum* monoculture was significantly impacted by waterlogging treatment and the stomatal conductance rate decreased to a rate of 0.002 mol m^{-2} s^{-1} by day 3.

When comparing the monoculture stomatal conductance rates with the comparable individual in the Mixed treatments, the Mixed waterlogged *Oenothera* can be seen to follow a similar pattern to the *Oenothera* waterlogged monoculture ($p = 0.506$), however the waterlogged Mixed *Erysimum* conductance rate increased by day 3 with a rate of 0.038 mol m^{-2} s^{-1}, which is the first day post-waterlogging treatment, when the *Erysimum* monoculture does not, although the difference between their waterlogged rates is not statistically significant ($p = 0.348$).

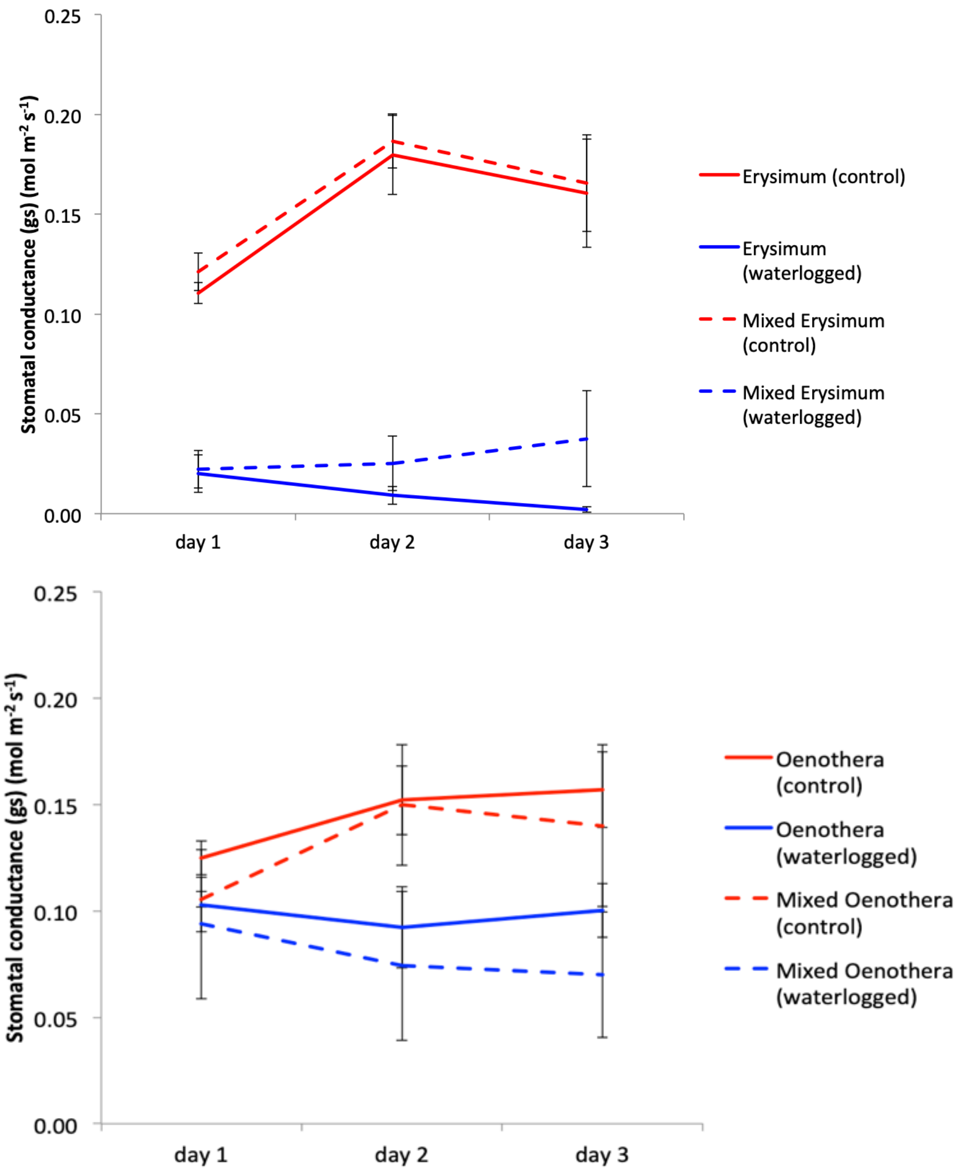


Figure 5.7: Mean daily stomatal conductance and associated standard error of the means for *Erysimum* and *Oenothera* (n = 6 plants in monocultures, n = 3 plants in mixed layout).

Final day pot mass and substrate moisture content

On the final day (day 8) of the experiment *Erysimum* control and waterlogged treatment pot mass and substrate moisture content were not significantly different from one another ($p = 1.000$ and $p = 0.925$ respectively) (Figure 5.8), however the *Oenothera* and Mixed waterlogged treatments were significantly lower than the *Erysimum* monoculture, bare substrate, and their control counterparts ($p < 0.001$).

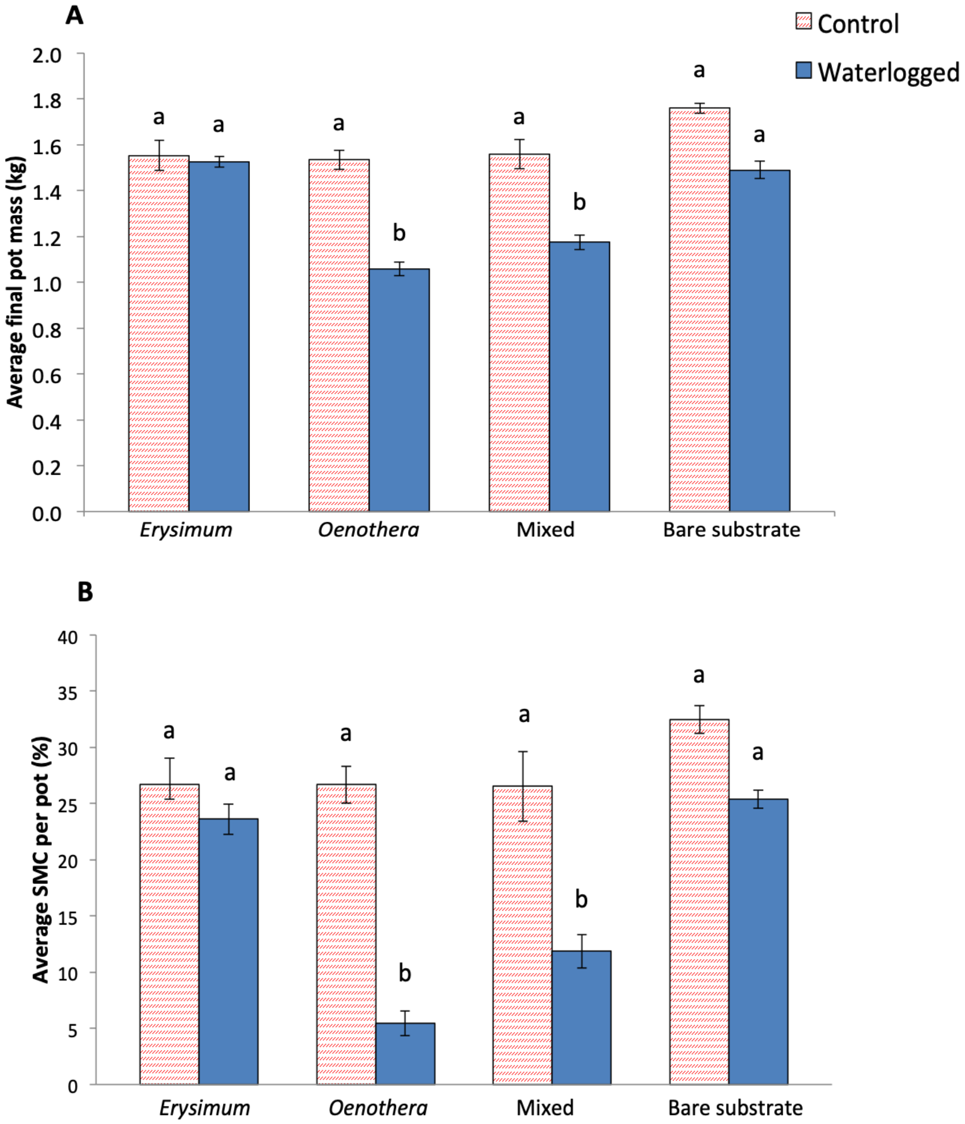


Figure 5.8: Mean final pot mass (A) and substrate moisture content (B) with associated standard error of the means (n = 8 pots per layout and n = 5 for bare substrate per layout and treatment). Treatments sharing a letter were not significantly different from one another.

Dry aboveground biomass

There was no significant difference between final dried stem and leaf biomass between any layouts and treatments (p = 0.237) (data not shown).

Dry roots biomass

Dried root mass at the end of the experiment (day 8) was significantly higher in *Erysimum* control treatment than *Oenothera* control treatment (p = 0.016), however no other plants and treatments were significantly different from one another (data not shown).

5.4.3 Experiment 7b - Impact of spring waterlogging on monocultures and plant mixes in pots

There was a large range in leaf areas per pot for both monocultures and mixed layouts. The waterlogged *Erysimum* layout had the smallest average leaf area (660.2 cm^2) but also the smallest individual leaf area at 204.3 cm^2. The control *Pseudodictamnus x Verbena* layout had the largest average and individual leaf area per pot (1662.1 cm^2 and 1853.6 cm^2 respectively). The majority of waterlogged layouts had a smaller average leaf area compared to their control layouts, except for *Verbena* and the *Erysimum x Oenothera* mix, which showed the opposite trend.

Daily average water loss per pot post-waterlogging (days 5-8)

Transpiration water loss per pot post-waterlogging found that all waterlogged monocultures experienced greater water loss over time than the control layouts ($p < 0.001$; *Pseudodictamnus* $p = 0.008$) (Figure 5.9). The *Verbena* monoculture lost significantly more water than all other waterlogged layouts between days 5 and 8 ($p < 0.001$), losing an average of 812 ml per pot between days 5 and 8, 163 ml (22%) more than *Oenothera* which had the second highest water loss. There was a significant difference in water loss between waterlogged monocultures and their mixture layout counterparts ($p < 0.001$). Both waterlogged monocultures of *Oenothera* and *Verbena* lost significantly more water than waterlogged *Erysimum x Oenothera* and *Pseudodictamnus x Verbena* respectively, whereas waterlogged *Erysimum* and *Pseudodictamnus* lost significantly less water than both of their comparable mixed layouts. Waterlogged *Pseudodictamnus* and *Erysimum* also had the lowest average water loss per pot post-waterlogging, and were not significantly different from bare substrate pots.

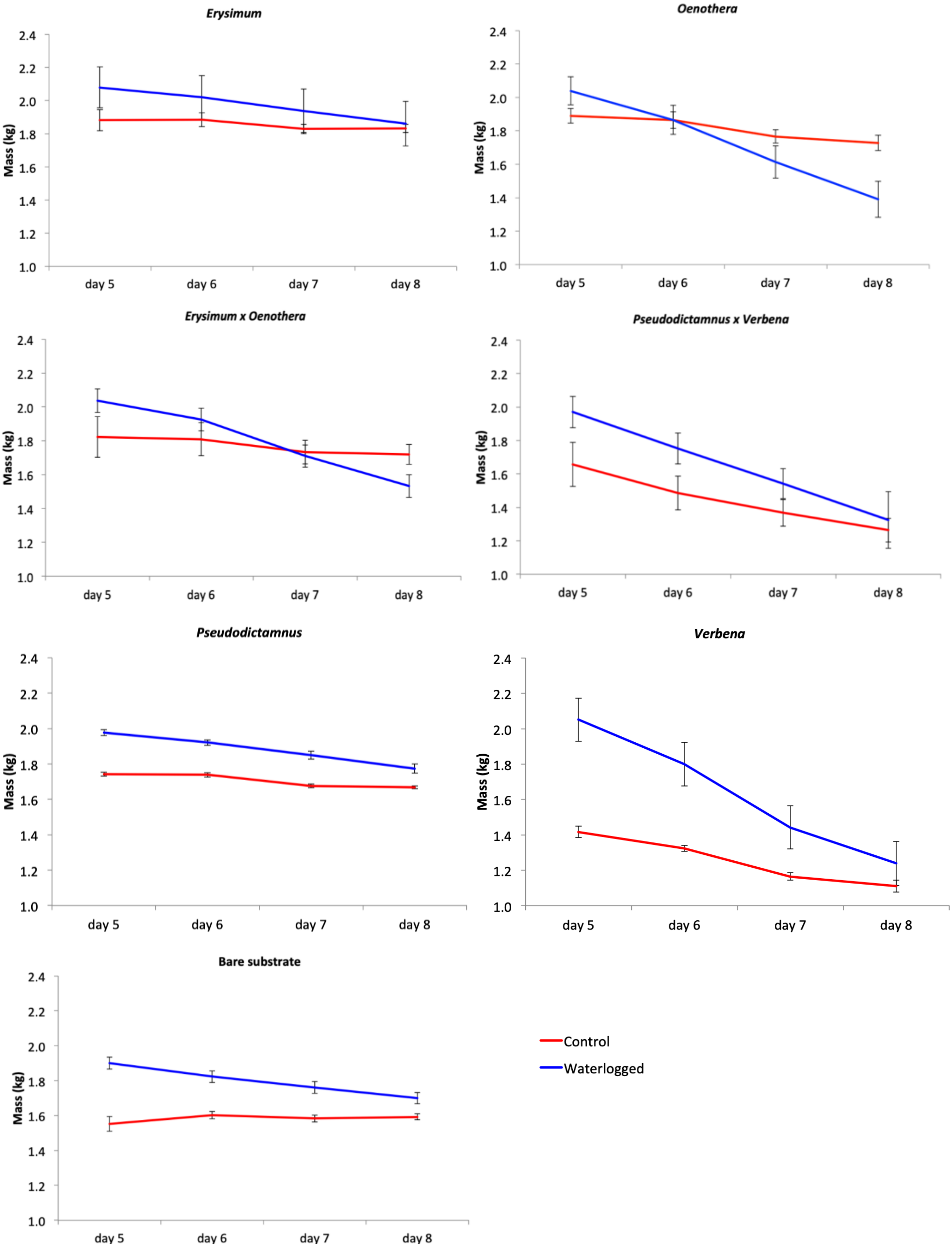


Figure 5.9: Mean daily water loss per pot and associated standard error of the means post-waterlogging treatment (n = 5 pots per layout and treatment).

Daily average water loss per leaf area post-waterlogging (days 5-8)

Water loss per standardised unit of leaf area post-waterlogging was not significantly different between control and waterlogged layouts. *Oenothera*, *Verbena*, and the mixed layouts had similar water loss rates post-waterlogging and all waterlogged layouts per leaf area had large standard errors, particularly *Pseudodictamnus* and *Erysimum* (data not shown).

Stomatal conductance

During waterlogging, days 1-4

During waterlogging stomatal conductance rates between monoculture control and waterlogged treatments were significantly different (*Pseudodictamnus* and *Erysimum* $p < 0.001$; *Oenothera* and *Verbena* $p < 0.05$) (Figure 5.10). Both waterlogged *Verbena* and *Oenothera* had higher stomatal conductance rates than their control counterparts.

Comparing waterlogged monocultures and mixed layouts there was a significant difference during this time period between only the *Oenothera* monoculture and the *Oenothera* plants in the *Erysimum x Oenothera* mixed layouts ($p = 0.023$), with the stomatal conductance of the monoculture plants significantly higher than the mixed (0.34 mol m^{-2} s^{-1} and 0.28 mol m^{-2} s^{-1} daily average respectively).

Post-waterlogging, days 5-8

Post-waterlogging stomatal conductance rates were significantly lower for both *Pseudodictamnus* and *Erysimum* waterlogged layouts compared to their controls when day was excluded ($p < 0.001$), but the rates for *Oenothera* and *Verbena* were not significantly different for post-waterlogged plants compared to control rates (Figure 5.10).

However, there was no significant difference post-waterlogging between monocultures and mixed waterlogged layouts, with both *Pseudodictamnus* and *Erysimum* plants in monocultures and mixtures maintaining similarly low stomatal conductance rates (*Erysimum* 0.04 mol m^{-2} s^{-1} vs. mixed 0.12 m^{-2} s^{-1}, and *Pseudodictamnus* 0.05 mol m^{-2} s^{-1} vs. mixed 0.08 mol m^{-2} s^{-1} averages respectively), and *Oenothera* and *Verbena* both maintaining similar higher rates than the two evergreen species (*Oenothera* 0.31 mol m^{-2} s^{-1} vs. mixed 0.32 mol m^{-2} s^{-1}, and *Verbena* 0.32 mol m^{-2} s^{-1} vs. mixed 0.35 mol m^{-2} s^{-1} averages respectively).

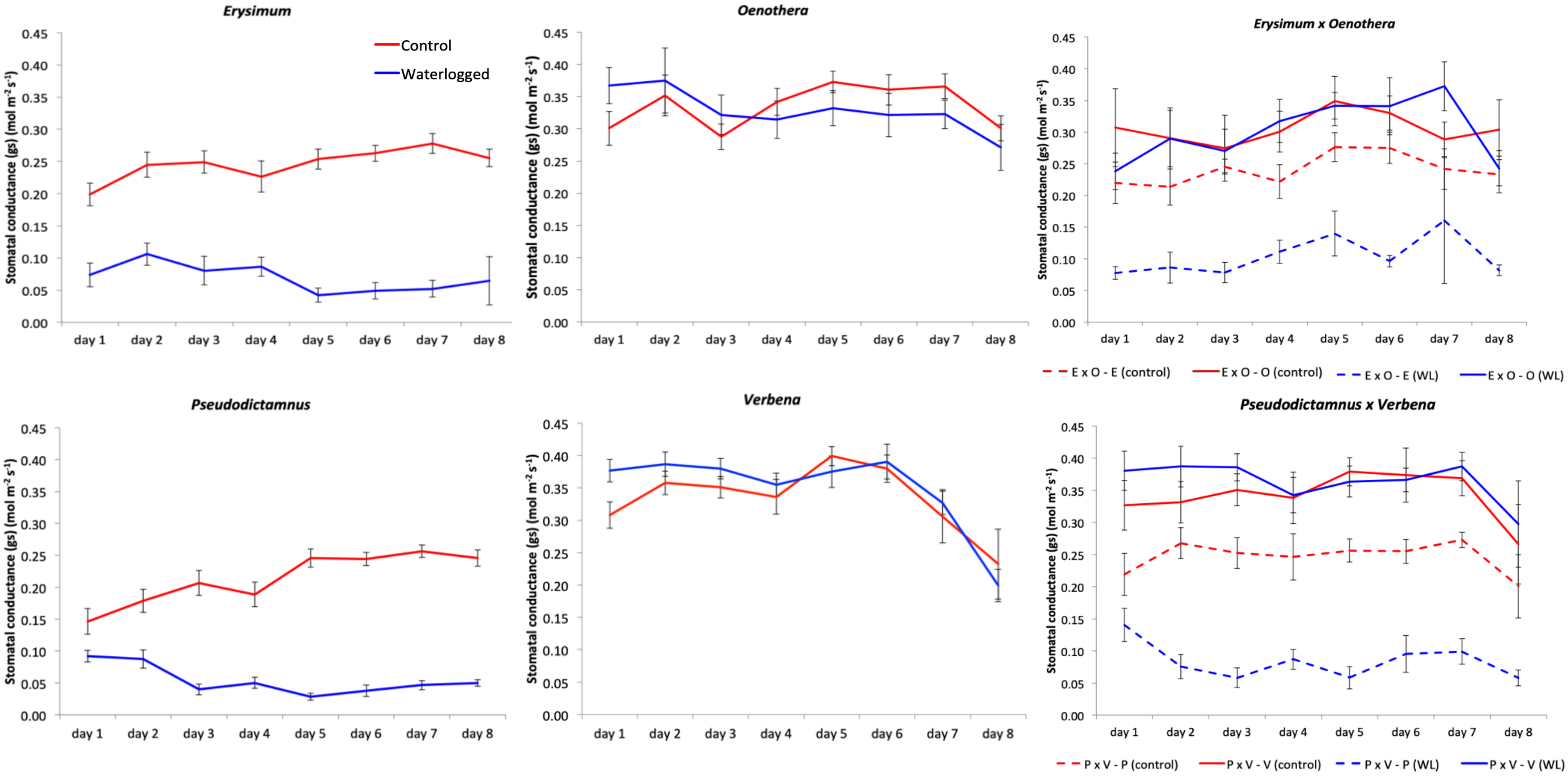


Figure 5.10: Mean daily stomatal conductance and associated standard error of the means during and post-waterlogging treatment (n = 8 plants in monocultures, n = 4 plants in mixtures (*Erysimum x Oenothera, Pseudodictamnus x Verbena*)).

At the end of the experiment (day 8) the number of visibly wilted plants was tallied, as a visual aid to transpirational water loss and stomatal conductance data. The only plants to appear visibly wilted and unable to recover in the four days post-waterlogging were some *Erysimum* and *Pseudodictamnus* (Table 5.3). Of the *Erysimum* plants, only 20% of those in monocultures responded with wilting, and this was not observed in the mixed *Erysimum* plants. The *Pseudodictamnus* monocultures and mixed plants both experienced wilting, with 40% of the *Pseudodictamnus's* in mixed pairings wilting, but 60% of plants in the monoculture wilting post-waterlogging (Table 5.3).

Plant and layout	**Number of wilted plants**	**Number of pots containing wilted plants**
Erysimum monoculture	2/10 (20%)	2/5 (40%)
Erysimum in E x O	0/5 (0%)	0/5 (0%)
Pseudodictamnus monoculture	6/10 (60%)	4/5 (80%)
Pseudodictamnus in P x V	2/5 (40%)	2/5 (40%)

Table 5.3: Number of visibly wilted plants post-waterlogging at the end of experiment 7b.

Net CO_2 assimilation rate (A)

During waterlogging, days 1-4

During waterlogging, waterlogged *Erysimum* and *Pseudodictamnus* had significantly lower assimilation rates compared to their control counterparts, although waterlogged *Erysimum's* rate was relatively steady over the four days of waterlogging but *Pseudodictamnus* significantly declined between days 2 and 3 ($p = 0.016$ and $p < 0.001$ respectively) (Figure 5.11). Both the *Oenothera* and *Verbena* rates were similar between control and waterlogged treatments, maintaining a high rate over time, with an average of 21.7 μmol m^{-2} s^{-1} for control and 21.9 μmol m^{-2} s^{-1} for waterlogged *Oenothera,* and 22. 7 μmol m^{-2} s^{-1} for control and 23.5 μmol m^{-2} s^{-1} for waterlogged *Verbena* (Figure 5.11).

There was no significant difference in A rates between waterlogged monocultures and waterlogged mixed layouts, with the exception of the waterlogged *Oenothera* monoculture and waterlogged mixed *Oenothera*, the latter of which had a lower average assimilation rate of 19.4 µmol m^{-2} s^{-1} compared to the monoculture ($p = 0.018$).

Post-waterlogging, days 5-8

Post-waterlogging assimilation rates followed a similar trend to during waterlogging. Waterlogged *Erysimum* maintained a significantly lower but consistent assimilation rate compared to *Erysimum* control ($p < 0.001$). Waterlogged *Pseudodictamnus* was lower than control *Pseudodictamnus* but had a significant increase in assimilation rate from days 5 to 7 ($p < 0.001$). Both *Oenothera* and *Verbena* rates were not significantly different between control and waterlogged treatments (Figure 5.11).

Both the mixed waterlogged *Erysimum* and *Pseudodictamnus* assimilation rates were significantly different from their waterlogged monoculture counterparts. Mixed *Erysimum* had a significantly higher assimilation rate post-waterlogging ($p = 0.016$) with an average of 10.98 µmol m^{-2} s^{-1} for the mixed compared to 5.01 µmol m^{-2} s^{-1} for the monoculture, and the mixed *Pseudodictamnus* was significantly more varied than the monoculture ($p = 0.028$) This can be seen in Figure 5.11 where the waterlogged mixed *Pseudodictamnus* assimilation rate increased between days 5 and 6 before decreasing on day 8, whereas the waterlogged monoculture slowly increased in rate between days 5 and 7 before reaching a plateau. Both *Oenothera* and *Verbena* were not significantly different between their waterlogged monoculture and mixed layouts.

Assimilation rates overall showed a similar pattern to the plant's stomatal conductance rates (Figure 5.10).

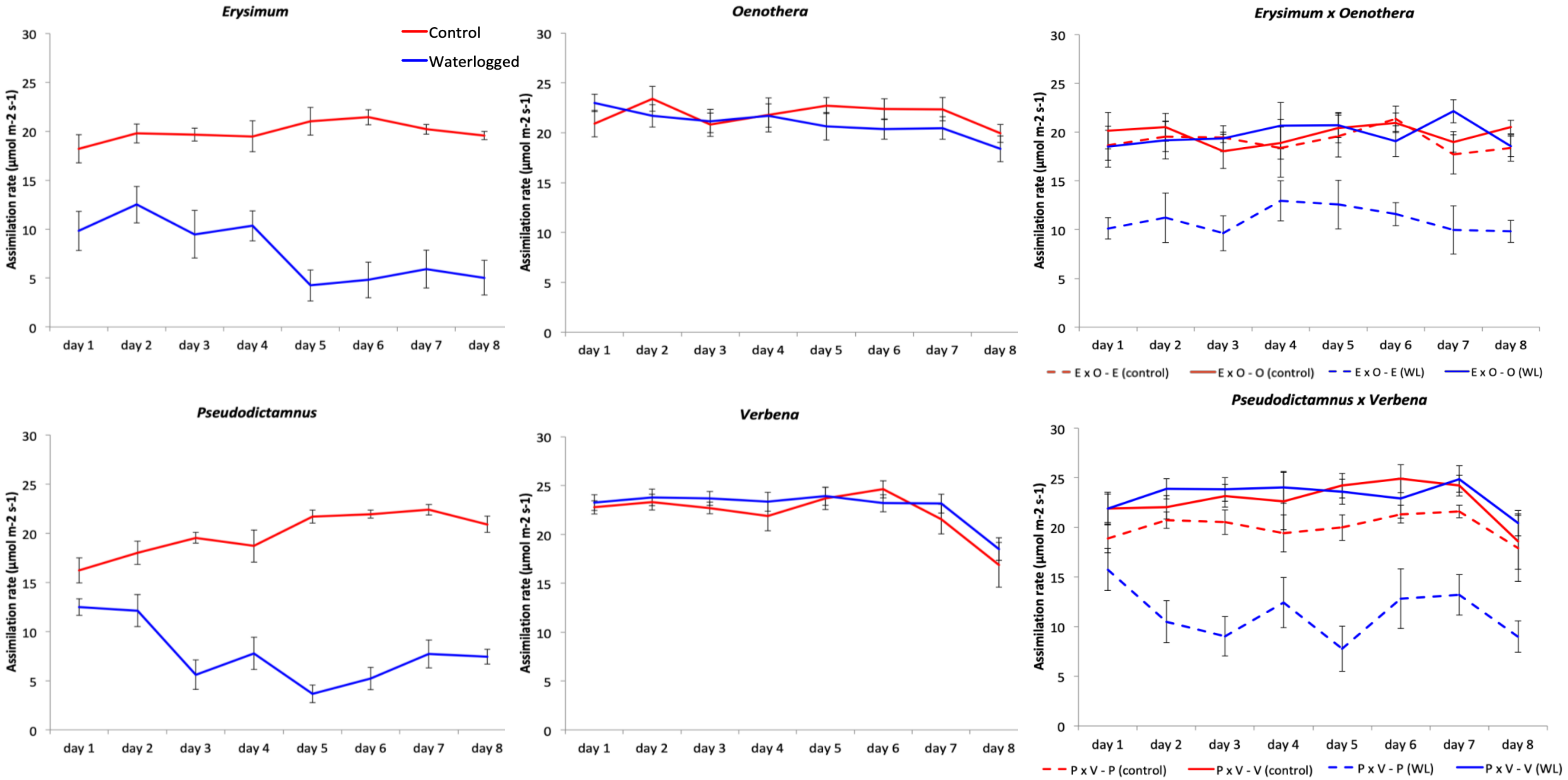


Figure 5.11: Mean daily net CO_2 assimilation rate and associated standard error of the means during and post-waterlogging treatment (n = 8 plants per monoculture, n = 4 plants per mixture).

Dry aboveground biomass

At the end of the experiment all plants were destructively harvested, and there was a significant difference in dried aboveground weight between the control and waterlogged plants (Figure 5.12). There was a significant decrease in the biomass of waterlogged *Erysimum* ($p = 0.016$), *Pseudodictamnus* and *Pseudodictamnus x Verbena* ($p < 0.001$), and a significant increase of waterlogged *Oenothera, Verbena*, and *Erysimum x Oenothera* ($p < 0.001$) compared to their control counterparts.

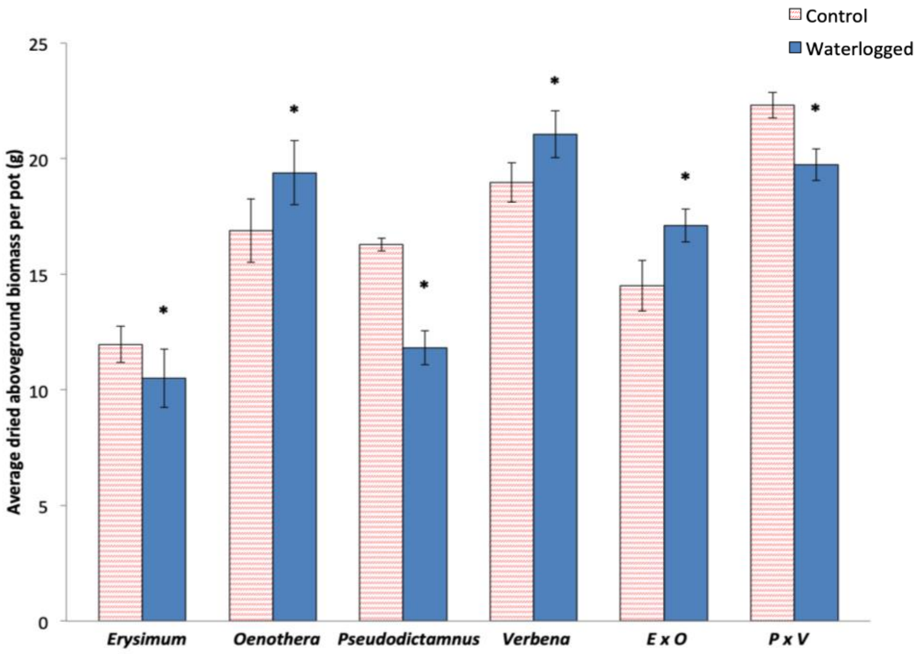


Figure 5.12: Mean total dried aboveground biomass per pot and associated standard error of the means (n = 5 pots per layout - n = 10 plants per species in monoculture and 5 plants per species in mixture). An asterisk denotes statistically significant differences between the control and waterlogged layout pairing.

Dry root biomass

At the end of the experiment there was a significant difference between the dried root mass of all plant pairings except for *Erysimum x Oenothera* ($p = 0.116$) (Figure 5.13). As with dried biomass, there was a significant decrease in dried root mass of waterlogged *Erysimum* and *Pseudodictamnus* ($p < 0.001$), and *Pseudodictamnus x Verbena* ($p = 0.03$), and a significant increase in *Oenothera* and *Verbena* ($p < 0.001$) compared to the control layouts.

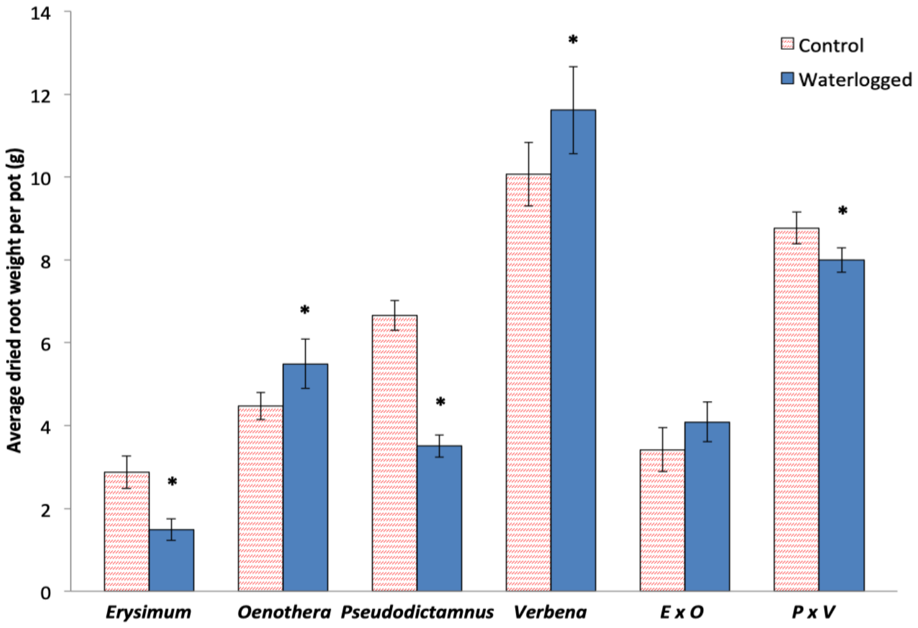


Figure 5.13: Mean total dry root mass per pot and associated standard error of the means (n = 5 pots per layout - n = 10 plants per monoculture and 5 plants per mixture). An asterisk denotes statistically significant differences between the control and waterlogged layout pairing.

5.5 Discussion

Combinations of popular garden plants known anecdotally to require well-drained substrate (Royal Horticultural Society, no date, f; Royal Horticultural Society, no date, i,) or tolerate drought (Beth Chatto's Plants & Gardens, 2019 & 2022a; Wallington, 2022) were subjected to overwatering and short-term subtotal flooding to determine the impacts of co-planting/companion planting with differing transpiration rates on plant growth and function (transpiration rates, stomatal conductance, plant biomass and roots). It was hypothesised that *Oenothera* and *Verbena*, with their higher transpiration rates, would tolerate or recover more quickly from flooding compared to *Erysimum* and *Pseudodictamnus*, and that combinations of high and low transpiring plants would also tolerate flooding more than lower-transpiring monocultures. However, because these plants prefer low moisture availability (according to the horticultural literature), it was still anticipated that stress responses (in the form of stomatal closure and reduced transpiration rates) would be observed in all species. All of the species tolerated overwatering (observed as no difference in transpiration or stomatal conductance rates between overwatered and control plants) despite the expectation of stress responses due to their preference for well-drained substrate (Royal Horticultural Society, no date, e, f, i, j). In short-term flooding *Oenothera* and *Verbena* tolerated waterlogging (using transpiration rates, stomatal conductance, assimilation rates, and plant biomass parameter as indicators), whilst *Pseudodictamnus* and *Erysimum* displayed stress symptoms (stomatal closure, lower aboveground biomass and roots mass). Combining plants of higher or lower transpiration rates led to increased waterlogging tolerance of lower-transpiring plants *Erysimum* and *Pseudodictamnus*. Waterlogging experiments suggested the studied plants fell into two categories: tolerant (*Oenothera* and *Verbena*) and intolerant (*Erysimum* and *Pseudodictamnus*), corresponding with their higher and lower transpiration rates (Chapter 3). To understand this response, initial discussion will focus on the responses of monocultures followed by how this could have impacted the responses of mixed pairings.

The impact of waterlogging on plant monocultures with lower transpiration rates

Experimental plants with lower transpiration rates were less tolerant of waterlogging compared to those with higher transpiration rates in both spring and summer short-term subtotal flooding (experiments 7a and 7b), with significant reduction in transpiration and stomatal conductance rates, and lower aboveground biomass and roots mass. Waterlogging can deprive plant roots of oxygen, resulting in hypoxia. This can be linked to symptoms including wilting and a decline in transpiration and photosynthetic rates (Bortolini & Zanin, 2019; Else *et al.,* 2009; King *et al.,* 2012; Pan *et al.,* 2021; Yin *et al.,* 2012). In sensitive plants even short-term waterlogging can reduce root hydraulic conductance within 2-6 hours and damage cells within 24 hours (Else *et al.,* 2009; Jackson, 2004). Lower-transpiring *Erysimum* and *Pseudodictamnus* (Chapter 3) had reduced stomatal conductance and net CO_2 assimilation rates when flooded compared to controls (Figures 5.10 and 5.11), which was expected from plants with waterlogging sensitivity (Cameron & Hitchmough, 2016; Else *et al.,* 2009; Olorunwa *et al.,* 2023). Previous research on crop plants linked reduced stomatal conductance and photosynthesis with reduced yield, either in grain quantity or fruit weight (Byrne *et al.,* 2022; Cannell *et al.,* 1980; Ide *et al.,* 2022; Shao *et al.,* 2023), but outcomes for garden plants cannot be measured in this way and aesthetics could be considered instead, including aboveground biomass, leaf colour and turgor (Liu *et al.,* 2021; Yang *et al.,* 2020; Yin *et al.,* 2012; Zhao *et al.,* 2022). This experiment monitored plants for four days post-waterlogging, and noted visible wilting on 20% of the waterlogged *Erysimum* monoculture plants and the majority of *Pseudodictamnus* monocultures, indicating that waterlogging these species negatively impacted their aesthetics. Stomatal conductance also remained low post-waterlogging, and although stomatal recovery after flooding was observed in other 'drought-tolerant' perennial plants *Stachys byzantina* and *Salvia officinalis* (King *et al.,* 2012), this occurred after a longer period of time than the four days post-waterlogging monitored in this experiment. This leads to the question of whether *Erysimum* and *Pseudodictamnus* could have recovered if given more time. However, there are a couple of differences between *Erysimum* and *Pseudodictamnus* and *Stachys* and *Salvia* that limit comparisons and reduce the likelihood of the former plants' recoveries. Firstly, King *et al.* (2012) categorised *Stachys* as waterlogging-tolerant, and *Salvia* as intermediate tolerance, whilst *Erysimum* and *Pseudodictamnus* would be categorised from results in this chapter as intolerant. Secondly, Chapter 3 found *Stachys* and related S*alvia* species 'Nachtvlinder' had higher transpiration rates than *Erysimum,* and this appears linked with waterlogging tolerance. *Erysimum* and *Pseudodictamnus* may therefore be unable to display stomatal post-flood recovery in part due to their lower transpiration rates.

Limited research has been conducted on ornamental plants' stress tolerance, but studies using *Brassica napus*, a related species of *Erysimum* (both Brassicaceae family), could be comparable as this species is also waterlogging sensitive (Ambros *et al.,* 2022; Ashraf & Mehmood, 1990; El-Khateeb *et al.,* 2023). Research found *B. napus* roots were unable to form aerenchyma, and had rapid stress responses in root cells including hypoxia-induced genes within 24 hours (Ambros *et al.,* 2022), reduced growth (Ambros *et al.,* 2022; Ashraf & Mehmood, 1990), and reduced yield after three days (Gutierrez Boem *et al.,* 1996). This indicates short-term waterlogging sensitivity similar to *Erysimum*, including the decreased aboveground biomass and root mass (Figures 5.12 and 5.13). Previous research using anoxia sensitive *Salvia* (King *et al.,* 2012), soybean (Bester *et al.,* 2024) and wheat (Li *et al.,* 2023) found when pre-treated with hypoxia were tolerant to subsequent anoxia. This could be investigated for plants with lower transpiration rates to determine whether their intolerance is absolute, or if pre-conditioning with mild stress beforehand would aid survival.

The impact of waterlogging on plant monocultures with higher transpiration rates

Oenothera and *Verbena* were both able to tolerate short-term subtotal flooding, continuing to transpire at comparable rates to controls. Plants with higher transpiration rates are able to rapidly reduce moisture content in saturated substrate (Berretta *et al.,* 2014; Kemp *et al.,* 2019; Stovin *et al.,* 2012), but waterlogging was anticipated to induce a decline in transpiration rates (Cameron & Hitchmough, 2016; Else *et al.,* 2009; Jackson, 2004; Wiström *et al.,* 2023). King *et al.* (2012) found higher transpiring 'drought-tolerant' *Stachys* (Beth Chatto's Plants & Gardens, 2022a) closed its stomata within a few hours of summer flooding to maintain leaf water potential. This was not observed in *Oenothera* or *Verbena,* which both maintained higher stomatal conductance rates than controls during flooding and indicates no loss of function (Figure 5.10). *Oenothera* and *Verbena* also had a similar net CO_2 assimilation rate to controls and could indicate photosynthesis efficiency (Figure 5.11). Another physiological measure, leaf chlorophyll florescence, which in previous studies was high in *Oenothera lindheimeri,* could indicate waterlogging did not induce photoinhibition or stress (Nur Hannah Ismail *et al.,* 2023; Yuan & Dunnett, 2018). Previous studies found that waterlogging leads to a decrease in root and shoot mass in susceptible plants (Bortolini & Zanin, 2019; Chauhan *et al.,* 1997; Davies *et al.,* 2000; King *et al.,* 2012; Yin *et al.,* 2012). One mechanism of waterlogging tolerance is rapid root growth after flooding to replace any roots that died (Bramley *et al.,* 2011; Davies *et al.,* 2000), but due to the short period between waterlogging and destructive harvest it is unlikely the plants grew replacement roots of this quantity in such a short time, indicating root death was unlikely. *Verbena* had a significantly larger root mass than the other plant species (in both control and waterlogged conditions), which was linked to flood tolerance in other research (Jernigan & Wright, 2011; Ide *et al.,* 2022), but *Pseudodictamnus* had a larger root mass than *Oenothera* and yet experienced reduced transpiration, stomatal conductance and physical wilting in waterlogging, therefore more factors than root mass play a part in flood tolerance.

Oenothera and *Verbena* also did not exhibit any noticeable stress tolerance mechanisms such as formation of adventitious roots, and instead it is questionable whether short-term subtotal flooding caused stress at all. Plant tissue was not examined for aerenchyma formation, but adventitious roots were not present on either species, however there may have been microscopic changes occurring during this experiment (which were not monitored) that would have developed into adventitious roots. Observed as a response to flooding by riparian taxa (Lukac *et al.,* 2011; Vartapetian & Jackson, 1997), adventitious roots have also been noted on plants not associated with waterways including *Chrysanthemums* (Yin *et al.,* 2009), Cannas (Zhao *et al.,* 2022), *Angelonia* and *Zinnia* (Yang *et al.,* 2020) and tomatoes (Else *et al.,* 2009; Ide *et al.,* 2022), and therefore could be expected as a response by perennials as well. Previous studies have found that, depending on the species, adventitious roots can form on submerged plants after as little as 10 hours, although that was on rice plants (Lorbiecke & Sauter, 1999). Other species, including sunflowers and herbaceous vine *Solanum dulcamara*, formed visible adventitious roots within two days (Dawood *et al.,* 2014; Steffens & Rasmussen, 2016; Wample & Reid, 1978), and Cannas and tomatoes grew adventitious roots within three days of waterlogging (Ide *et al.,* 2022; Vidoz *et al.,* 2010; Zhao *et al.,* 2022). That none formed in this experiment could be because the plants were not negatively impacted by the lack of oxygen, roots were too small to be seen, or the flooding period was too short for the adaptation to occur. However, herbaceous *Angelonia* and *Zinnia* grew adventitious roots after ten days (Yang *et al.,* 2020) and *Chrysanthemums* grew adventitious roots after eighteen days (Yin *et al.,* 2009), indicating that either *Oenothera* or *Verbena* could be slow to form this adaptation, just like the *Chrysanthemums, Angelonia* or *Zinnia,* or that extending the waterlogging period might lead to this adaption in *Oenothera* or *Verbena.* Chemical changes, including production of ethylene that could signal a precursor to adaptive responses such as adventitious roots (Jackson, 2004; Li *et al.,* 2021; Pan *et al.,* 2021; Yin *et al.,* 2009), was not monitored in this experiment but it cannot be ruled out that these changes were occurring and anatomical adaptations would follow if the experiment and flooding period had been extended.

The high transpiration rates of *Oenothera* and *Verbena* might have been a key trait enabling their tolerance of waterlogging, although the lack of stomatal closure in response to a period of inundation was unanticipated. Stomatal closure in response to waterlogging is a widespread physiological reaction (Else *et al.,* 2009; King *et al.,* 2012; Olorunwa *et al*., 2023; Pan *et al.,* 2021; Yin *et al.,* 2012). Additionally, some plants known to exhibit tolerance to drought (and *Oenothera* and *Verbena* are both classed as drought tolerant in horticultural literature, Beth Chatto's Plants & Gardens, 2022a & 2022b) can also show resilience to flooding. For example, this has been observed in both garrigue plants from Mediterranean regions and prairie plants (in addition to *Oenothera*) originating from North America (King *et al.,* 2012; Laukli *et al.,* 2022b; Nasrollahpour *et al.,* 2022; Nur Hannah Ismail *et al.,* 2023; Yuan & Dunnett, 2018). Garrigue plants *Lavandula angustifolia* and *Stachys byzantina* were able to withstand seventeen days of summer flooding without increased mortality; this was credited to their higher transpiration rates (King *et al.,* 2012). Similar was also observed with *Oenothera* and *Verbena*, and discussed in Chapter 3 as part of *Oenothera's* potential drought tolerance strategy, using a high transpiration rate and potential taproot to find and rapidly absorb water when available (Nazemi Rafi *et al.,* 2019) and could explain why this species continued to transpire in short-term flooding. The ecophysiology of prairie plants has been speculated as a reason for their ability to rapidly deplete substrate moisture content in a rainfall study (Nur Hannah Ismail *et al.,* 2023). Their adaption to meadow landscapes might be contributing to them acting competitively and transpiring at higher rates to utilise available water, a potential explanation of how some prairie species thrive in stress conditions such as waterlogging.

However, related taxa of both *Oenothera* and *Verbena* have been used in previous rain garden experiments with different outcomes. *Oenothera lindheimeri* tolerated short-term cyclical flooding but this did result in significantly reduced dried root mass (Yuan & Dunnett, 2018), which was the opposite of *Oenothera* 'Whirling Butterflies' in experiment 7b. Landscape architects recommended *Verbena hastata* in rain gardens but had low survival rates when tested in three Canadian locations (Champagne-Caron *et al.,* 2024), whereas in experiment 7b *Verbena bonariensis* had a 100% survival rate. Plant breeding can lead to potential loss of stress tolerance (Lewis *et al.,* 2019) and the different taxa used in these experiments could explain the waterlogging responses. Lewis *et al*. (2019) found cultivated *Primula* species with larger flowers showed lower drought or waterlogging tolerance than progenitor species *Primula vulgaris*, and concluded breeding sacrificed stress tolerance at the expense of aesthetics. This variation in tolerance between bred taxa was also observed in garden plant *Echinacea purpurea* 'The King'. This species preferred moderate moisture rather than the permanently waterlogged base or dry margins of rain gardens, potentially due to its fibrous root system adapted to grow in moist woodlands with higher water availability, whilst other *Echinacea* species from drier prairies develop taproots to source extra water (Bortolini & Zanin, 2019; Kindscher, 1989; Royal Horticultural Society, no date, h). Yuan and Dunnett (2018) used straight species *O. lindheimeri* rather than its cultivar 'Whirling Butterflies' used in this chapter, and previous studies noted drought tolerance was lost when breeding different *Oenothera* species (Díaz-Barradas *et al.,* 2020; Gambino & Vilela, 2011), so could explain loss of waterlogging tolerance too. Although given *O. lindheimeri* is the progenitor of 'Whirling Butterflies' it was expected the latter would lose tolerance not gain it (Lewis *et al.,* 2019). Also, unlike *Echinacea*, both *Oenothera lindheimeri* and 'Whirling Butterflies' have the same root morphology (Mahr, no date) therefore root structural differences are not an explanatory factor for differing waterlogging tolerances. Lewis *et al.* (2019) compared plants with extreme floral modification that reduced fitness, and the comparative differences between these two *Oenothera* taxa, and between all the wild progenitors and study plants in this thesis, are relatively small, therefore it is likely that competitive capacity affected fitness rather than breeding impacting stress tolerance. Other factors aside from plant breeding and root structure must explain these results instead. The duration of flooding could be a contributing factor (Dylewski *et al.,* 2011; Lewis *et al.,* 2019; Taiz & Zeiger, 2002), and the cyclical flooding by Yuan and Dunnett (2018), with periods of drainage before repeat inundation, was not conducted in experiment 7b. This could cause cumulative stress from multiple flood exposures, with repeated soil oxygen depletion resulting in anaerobic respiration that accumulates toxic metabolites and leads to cell death (Cameron & Hitchmough, 2016; Li *et al.,* 2021; Pan *et al.,* 2021; Yin *et al.,* 2009). This could explain the reduction in *O. lindheimeri* biomass (Yuan & Dunnett, 2018), whereas short-term flooding in this chapter reduces the time spent anaerobically respiring, limiting metabolite accumulation and resultant stress-induced cell damage.

Comparing monocultures and mixed planting

Both *Erysimum* and *Pseudodictamnus* showed greater growth and survival rates in combined layouts with higher transpiring *Oenothera* and *Verbena* during spring and summer short-term flooding, as well as reduced wilting. How plants interact and grow together has been extensively studied, and plants can compete with one another for resources or facilitate each other's growth (Aguiar *et al.,* 2019; Chell *et al.,* 2022; Heim *et al.,* 2023; Lundholm *et al.,* 2010; Nazemi Rafi & Kazemi, 2021). The competitor-stress tolerator-ruderal (CSR) model proposes that plants in a community fall into one of these three categories (Grime, 1974; Rivière *et al.,* 2024), with traits associated with each group. Some plants sit within several categories and competitive or ruderal plants can become stress tolerators when conditions require it (Lönnqvist *et al.,* 2023). Companion planting, including nurse plants, are usually categorised as stress tolerators (Fagundes *et al*., 2022; Navarro-Caro *et al.,* 2017; Rolhauser & Pucheta, 2016; Rolhauser *et al*., 2023). *Sedum*, as a slow-transpiring plant previously classified as a stress tolerator (Rivière *et al.,* 2024), in drought conditions facilitated the increased growth of *Agastache rupestris* by decreasing substrate temperature by 5-7°C and increasing soil water content (Butler & Orians, 2011). It also supported and improved the growth and leaf health of non-carpet growing species when paired with *Sedum album* (Matsuoka *et al.,* 2019 & 2020). Although these examples are for water deficit the concept that pairing plants of differing transpiration rates can aid facilitation is something that may apply to pairings of *Oenothera* and *Erysimum* or *Verbena* and *Pseudodictamnus* during waterlogging. Both sub-total flooding experiments indicated that *Oenothera* and *Verbena* acted as companion plants to *Erysimum* and *Pseudodictamnus* in paired combinations, because their higher evapotranspiration rates facilitated water loss from the substrate. This moisture decrease could have reduced hypoxia in *Erysimum* and *Pseudodictamnus*, and post-waterlogging rapidly returned the substrate moisture content of mixed pairings to that of control conditions.

Facilitation in stress conditions can help plant survival and also provide ecosystem services (such as runoff reduction) depending on the type of stress and the traits of the interacting plants (Heim & Lundholm, 2014; Heim *et al.,* 2023; Muratet *et al.,* 2024; Rolhauser *et al.,* 2023). Traits such as a high transpiration rate would be favourable in waterlogging conditions created by excess rainfall and surface water accumulation as it would help remove water from the substrate more quickly, and this could also then mitigate the stress experienced by other plant species. Increasing plant trait diversity (including higher evapotranspiration rates, plant height, canopy and foliage diversity) increased infiltration in rain gardens (Dudrick *et al.,* 2024), optimised evapotranspirational water removal from the substrate (O'Carroll *et al.,* 2023), and provided multiple ecosystem services (Lundholm *et al*., 2010; MacIvor *et al.,* 2018). 'Fast' plants (with higher transpiration rates, greater shoot biomass and specific leaf area) quickly utilise available resources and due to their high transpiration rates took up 200% more water in a green roof setting compared to plants with 'slow' traits and lower transpiration rates (Chu & Farrell, 2022). *Oenothera* and *Verbena* could be considered 'fast' plants because in addition to higher transpiration rates they also have the greater shoot biomass and leaf area associated with 'fast' species, and their water use in experiment 7 is indicative of plants that have rapid resource acquisition. Interestingly, some plants with greater water use in well-watered conditions could down-regulate their water uptake in deficit conditions, self-monitoring resource allocation to ensure they were able to survive (Lönnqvist *et al.,* 2023). This was observed in tree species *Prunus padus* which displayed recovery from waterlogging and tolerated drought by maintaining stomatal conductance and water potential (Wiström *et al.,* 2023), and higher transpiring *Melilotus officinalis* (syn. *Trifolium vulgare*) and *Viola tricolor* adapted to maintain growth in water deficit (Lönnqvist *et al.,* 2023). Resource monitoring plants have the potential to facilitate the growth of other plants in combinations by ensuring reduced water use in deficit and increased use in excess, improving growing conditions for less tolerant plants. In addition to this, by changing strategies depending on conditions they could also provide an ecosystem service by rapidly reducing substrate moisture and surface water accumulation.

Oenothera and *Verbena* both continued to transpire and grow whilst waterlogged and improved the growth of *Erysimum* and *Pseudodictamnus* during and post-flooding, and this could be due to 'fast' plant traits and plant facilitation. Further research using higher transpiring 'drought-tolerant' plants could determine whether resource monitoring is one of the reasons this type of plant are able to grow well in waterlogged conditions (experiment 7) and also tolerate low moisture. The potential of *Oenothera* and *Verbena* to provide a runoff reduction ecosystem service and act as companion plants could help ensure a planting bed is functional, aesthetically pleasing, and provides an environmental benefit.

5.6 Limitations

- The length of the waterlogging experiments:
    - Experiment 7a was stopped due to a heat wave and therefore reduced the scope of the data analysis. Experiment 7b was stopped after day 8 due to the rapid growth of plant species *Oenothera* and *Verbena*, particularly the latter that became pot-bound in some cases. Although conducting the experiments in pots was necessary to enable short-term flooding and also the physical ability to lift the plants, the pots did also mean that roots were restricted to a finite space. Larger pots would have accommodated greater root growth but made manual handling data collection challenging. This would have allowed for

longer recovery period post-waterlogging and therefore continued monitoring of potential for stomatal recovery in *Erysimum* and *Pseudodictamnus*.

- To capture some of the changes in waterlogging intolerance it would have been useful to score the physical appearance of the plants and note chlorosis and necrosis on scales that allow comparison between species and time periods, and potentially show smaller changes, if any, with *Verbena* and *Oenothera*.

5.7 Key conclusions

- Higher transpiring *Oenothera* and *Verbena* both appeared to thrive and grow well in short-term subtotal flooding conditions, despite neither plant being known for their flood tolerance. *Erysimum* and *Pseudodictamnus,* with their lower transpiration rates, were both significantly impacted by waterlogging, with reductions in biomass, transpiration rate, stomatal conductance, and assimilation rate.
- Mixed pairings of plants with different transpiration rates in waterlogged conditions appeared to benefit the low transpiring plant, with significant increases in transpiration and assimilation rate compared to the lower transpiring monocultures. These results indicate that higher transpiring plants such as *Oenothera* and *Verbena* can facilitate the survival of stress intolerant plants and reduce the impact of hypoxia.

Chapter 6

Investigating people's planting preferences and its link to trait-based planting information

6.1 Introduction

Domestic gardens account for approximately 30% of UK urban land area (Chalmin-Pui *et al.,* 2021a) but as privately owned spaces their environmental footprint is at the discretion of the homeowner. Many owners view gardens as an extension of their homes (Dixon, 2022), therefore plant selection based on people's aesthetic preferences is to be expected. However, increased engagement with homeowners during which positive impacts of planting for the delivery of regulating ecosystem services are highlighted (such as rainwater capture and runoff reduction) could lead to more environmentally beneficial urban green spaces (Royal Horticultural Society, 2021).

Garden and landscape design preferences are diverse; gardens are shaped by many factors including aesthetics, household income, cultural backgrounds, garden use, and physical microclimatic conditions including soil type and annual rainfall (Kendal *et al.,* 2012; Peterson *et al.,* 2012). But to encourage or influence people to use environmentally beneficial planting schemes in their gardens it is necessary to understand why people prefer particular plants or styles. An appealing garden is an important goal for some homeowners, with designs influenced by what people consider beautiful (Stobbelaar *et al.,* 2021), a personal need for structure that results in formal garden designs over naturalistic ones (van den Berg & van Winsum-Westra, 2010), and cultural expectations. For the latter, how your garden is 'expected' to look can result in similar garden styles at a neighbourhood scale (Doll *et al.,* 2023; Francis *et al.,* 2018; Minor *et al.,* 2016; Stobbelaar *et al.,* 2021).

Aesthetics are one of the most important factors driving plant selection and garden styles (English Heritage, no date; Hanson *et al.,* 2021; Hoyle *et al.,* 2017b). It has been shown to produce positive emotions (Berger *et al.,* 2022) and provide cultural ecosystem services including happiness/improved wellbeing (Chalmin-Pui *et al.,* 2019; Hidalgo, 2021; Hoyle *et al.,* 2017a) or reduced stress (van den Berg *et al.,* 2014). Plant traits including foliage and flower colour influence people's preferences (Chalmin-Pui *et al.,* 2019; Kaufman & Lohr, 2004 & 2008; Kendal *et al.,* 2012) and the visual appeal of a plant is a major facilitator enabling people to recognise a plant's ecosystem service provision (Frantzeskaki, 2019).

Climate change in the UK is predicted to result in heavier, infrequent rainfall events, which can lead to flooding (Beidokhti & Moore, 2021; IPCC, 2021; Kendon *et al.,* 2023; Met Office, no date; Webster *et al.,* 2017). Vegetation can capture rainfall in canopies and by removing water from the substrate via evapotranspiration therefore reducing runoff (Berretta *et al.,* 2014; Blanuša & Hadley, 2019; Stovin *et al.,* 2012). Plant traits that aid with this include the presence of leaf hairs which facilitate droplet retention on the canopies (Beidokhti & Moore, 2021; Blanuša & Hadley, 2019) and a higher transpiration rate (that help remove greater volumes of water from the soil more quickly than other plants or unvegetated surfaces) (Berreta *et al.,* 2014; Chu & Farrell, 2022; Kemp *et al.,* 2019; Stovin *et al.,* 2012). Hairy leaves also tend to trap air pollution particulates (PM) on their surfaces better than smooth leaves, thus helping to remove PM from the atmosphere (Blanuša *et al.,* 2020; Shao *et al.,* 2019; Weerakkody *et al.,* 2018a).

Utilising plants with traits that help them deliver certain ecosystem services could help improve the environmental benefits of gardens (Royal Horticultural Society, 2021). However, recent UK nationwide surveys discovered that although there is a good awareness of climate change, less than 20% of respondents knew that plants could help mitigate localised flooding, and only 2% felt they were able to garden in a changing climate (Royal Horticultural Society, 2021; Webster *et al.,* 2017). Raising awareness about the specific environmental benefits of plants and their ability to deliver ecosystem services could result in people selecting plants in their gardens that are able to provide benefits including reducing localised surface water accumulation (Royal Horticultural Society, 2021). However, if this is not well known or aesthetics takes precedent when selecting plants, then it is necessary to provide information on the plants benefits and influence consumers to prioritise these plants.

Impacting behavioural change relating to environmental issues has been explored in past research; the type of (educational) information used to influence the change is highlighted as important for outcomes. For example, environmental gardening (e.g. reduced chemical, water or energy input in garden maintenance, providing habitats for wildlife) is more likely to be adopted when education on environmentally positive choices is provided, or when the outcomes are aesthetically appealing (Fernández-Cañero *et al.,* 2011; Hanson *et al.,* 2021; Hostetler, 2021; Royal Horticultural Society, 2021; van den Berg & van Winsum-Westra, 2010).

Previous research indicates there are three main ways in which information can be presented to increase people's knowledge, with the intention to positively alter environmental behaviours (Frick *et al.,* 2004; Neubig *et al*., 2020; Reynolds *et al.,* 2019; Williams *et al.,* 2012). It can be presented as:

1. System knowledge, which outlines the basic principles of the environmental problem.
2. Action-related knowledge, which includes how to potentially solve the environmental problem with behavioural change.
3. Effective knowledge, which highlights the resulting positive environmental benefits of the behaviour change (Frick *et al.,* 2004; Nuebig *et al.,* 2020) (Figure 6.1).

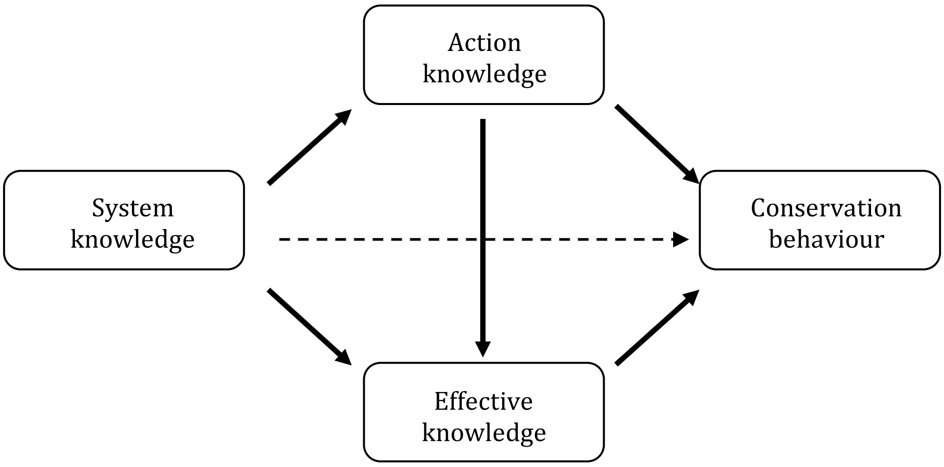


Figure 6.1: The Knowledge Structure Model, adapted from Frick *et al.* (2004). Solid arrows indicate direct influences. The dashed arrow indicates indirect effect.

Providing the Action and Effective knowledge is key to improving pro-environmental behaviours and has a direct effect on outcomes (Figure 6.1), whereas System information alone has an indirect effect but significantly influences action-related outcomes (Frick *et al.,* 2004). For example, Neubig *et al.* (2020) provided participants in their study with either information about the negative environmental impacts of food waste (system knowledge), or specific guidance on how to reduce waste (action-related knowledge). They found the latter significantly increased participants' intentions to reduce food waste compared to system knowledge alone. Previous research in other environmental fields also found similar results, including pollinator friendly plant purchases (Lange *et al.,* 2022), and willingness to accept green infrastructure (Derkzen *et al.,* 2017; Phillips *et al.,* 2023).

However, providing too much negative environmental information, or overemphasising detrimental behaviours as normal, can lead to no behavioural change in participants or negative outcomes (Birau & Faure, 2018; Cialdini, 2003; Neubig *et al.,* 2020; Stobbelaar *et al.,* 2021). Positive attitudes towards an action have been linked with a greater uptake, and a recent study found emphasising the beneficial influence planting can have on flood reduction encouraged greater positivity towards urban greening (Stobbelaar *et al*., 2021).

6.2 Study Aims and Hypotheses

Following a similar premise to the Neubig *et al.* (2020) study, the planting preferences of UK residents were tested in a survey, when participants were provided with either 'system-only' or additional 'action-related' information. Using certain plant traits linked to ecosystem service delivery - participants were asked to select preferred plant taxa (with and without the knowledge of the ecosystem services conferred). The traits (and thus certain plant taxa) were linked to ecosystem services associated with primarily better flood mitigation, although such traits could also confer benefits regarding pollution control and temperature reduction. The extent to which participants' aesthetic preferences and views on climate change influenced their choice of plants was also investigated.

The objectives of this chapter were to:

- Establish the individual participants' prior knowledge of plant benefits in the form of ecosystem services and traits, and whether demographics and prior gardening experience impact this. It was hypothesised that participants' education level and interest in gardening would equate to being more knowledgeable about both ecosystem services and plant traits. However, those who garden and enjoy gardening were not hypothesised to appreciate the benefits of a plant with a high transpiration rate, i.e. a 'thirsty' plant, due to their perceived higher water use.
- Determine the impact of different information types on flood and pollution mitigation knowledge. It was hypothesised that those who received action-related information would be more likely to consider plants delivering these benefits, and express willingness to grow them compared to the system information group.
- Investigate the impact that participants' perceptions of climate change could have on plant selection and environmental intent. It was hypothesised that those participants who have been impacted by climate change would be more willing to make environmentally conscious choices than those who are not concerned about climate change.

- Explore plant preferences and impact of planting recommendations on participants' plant preference change. It was hypothesised that those in the action-related group would be more likely to change their planting preferences after receiving planting recommendations compared to those in the system information only group. These planting preferences would link with the environmental information and trait-based recommendations, leading to a higher selection of *Pseudodictamnus*, *Oenothera*, and *Stachys* as these are noted to include leaf hairs and are 'thirsty' plants with higher transpiration rates, therefore able to mitigate rainwater runoff.
- Identify the drivers for plant preference change. It was hypothesised that the planting recommendations would significantly impact the decision to change planting preference for the action-related group, however it was hypothesised that aesthetics (or how attractive people found the plant) would still play an important role in plant selection for both groups regardless of survey information. It was expected that flowering plants *Verbena, Oenothera*, and *Erysimum*, would still be popular in both groups.

6.3 Methodology

6.3.1 Survey design

A web-based survey, created using Qualtrics XM software (Qualtrics, Provo, UT), was used to investigate people's plant preferences when provided with information related to potential ecosystem services that plants could deliver. Qualtrics software is approved by the University of Reading and suitable for most devices, enabling participants to complete the survey on their computers or phones. Participants were randomly assigned into two groups; both being asked the same questions but with different information provided in the middle of the survey (Table 6.1), to determine whether system information or action-related information about plant selection and localised flooding would result in a change of plant preference.

The survey asked both groups the same demographic questions and established their garden ownership status, interest in gardening, and hours spent gardening (Table 6.1). This is because previous studies found that age, gender, and education can all influence garden and plant style preferences (Byrne *et al.,* 2015; Hanson *et al.,* 2021; van den Berg & van Winsum-Westra, 2010). Age and gender categories were the same used in previous Royal Horticultural Society surveys to allow data comparability. The survey then asked participants for their preference when given the option of six plants (Figure 6.2 below), their knowledge on plant traits, and their knowledge on the ability of plants to improve their local environment (Table 6.1). This was necessary to establish the baseline knowledge of each participant and identify the impact that information and recommendation can have (Frick *et al.,* 2004). The middle segment of the survey introduced information, which differed depending on the group assigned (Table 6.1). The system information group received information on the impacts of climate change on urban areas, and the increased flood risk associated with impervious surfaces and removal of plants. The action-related group received a condensed version of the system information, with the intent to keep the duration of the two survey types similar, and recommendations on how to use plants with specific traits to reduce localised flooding in their gardens. Recommendations were in the form of simple planting suggestions based on trait-specific information. Framing an environmental action as easy to implement or undertake in this way has been shown to be most effective (Birau & Faure, 2018).

Information slides were kept relatively brief to reduce fatigue. Increasing information can lead to confusion, lack of trust, and scepticism that all inhibit sustainability choices (Sonntag *et al.,* 2023), which this survey aimed to avoid. In the middle of the survey (during the information sections) to ensure participants were still engaged both groups also answered questions related to their level of concern about climate change. After the system or action-related information sections both groups answered the same questions again, some of which were repetitions of the pre-information questions (Table 6.1), to determine if their plant preference had changed after received information.

The survey focused on two plant traits - presence of leaf hairs and high transpiration rate (referred to in the survey as ‘thirsty’ plants to accommodate for a non-scientific audience). Other plant traits were not covered to reduce information overload and enable a quicker and easier survey to follow. These traits were chosen as they directly related to the research undertaken in this PhD.

Reflecting our and other research findings, questions were written to include the phrases ‘can benefit’, ‘can improve’, and ‘can reduce’ to ensure no definitive statements were included, as the benefits of traits are contingent on other influencing factors including location, soil type, other green infrastructure in the area, etc. A five-point Likert scale was used to gauge people’s plant preferences and opinions on gardens, plants and the environment. No free text questions were included. The survey format, questions, and ease of use was tested via eight beta-testers prior to distribution, with feedback provided by those participants leading to question changes and adjustments to the format.

Category	Key questions
Gender	What is your gender?
Age	What is your age group?
Education	What is your highest level of education? Do you hold any qualifications (professional qualification or university degree) in biology, environmental sciences, landscaping, gardening, garden design or similar?
Interest in gardening	On average how many hours a week do you spend in a garden? This can include gardening, sitting or relaxing in your garden, etc. Do you consider yourself to be a gardener or enjoy gardening?
Plant knowledge pre-information	How much do you agree with the following reasons why you have plants? (L-5) • I like the look or scent of the plants • I believe plants improve health benefits that people get from the environment • The plants provide fruit and vegetables to eat How much do you agree with the following statements about plants in a garden setting? (L-5)

	• Plants can benefit wildlife (habitats, food sources, etc.) • Plants can reduce the risk of localised flooding • Plants can reduce air pollution • Plants can reduce noise pollution • Plants can reduce air, ground, and building temperature
Plant selection pre-information	The photos below show popular UK garden plants. Please select the plant you like the most. Using the plant you selected, how much do you agree with the following statements about the plant's appearance? (L-5) • I like the plant's growth habit (e.g. bushy) • I like the plant's colour • I like the plant's leaf shape • I like the plant's flower
Plant traits	These photos show the leaves of each plant, some of which are hairy. How much do you agree with the following statements? (L-5) • I like plants with hairy leaves • I believe plants with hairy leaves can improve the environmental benefits of gardens How much do you agree with the following statement? (L-5) • I believe 'thirstier' plants can improve the environmental benefits of gardens Certain plant characteristics can improve the impact that plants have on the environment around them. Please select all the plants from the list below that you think could help reduce surface water and localised flooding in a garden.
System information UK climate change information (IPCC, 2021; Kendon *et al.,* 2023; Met Office, no date; Webster *et al.,* 2017) was used to highlight the key problems that people and plants are facing in urban areas. Both temperature and rainfall were included as this links directly with the plant traits and subsequent ecosystem	Climate change is resulting in hotter drier summers and warmer wetter winters in the UK. Five of the hottest years on record in the UK since 1884 have all occurred since 2006 (2022, 2015, 2006, 2020 and 2011). A new high of 40°C was reached in the UK last year. Rainfall events at an intensity to cause flash flooding are predicted to be 4 times more frequent by 2070. An example of this occurred in July 2021 when a month's average rain fell in one hour in London, flooding the roads and underground network. Plants can provide environmental benefits, however people are removing vegetation from their gardens and replacing them with impermeable surfaces.

services in this survey, and are climate change outcomes that people will understand and relate to. Replacing plants with impermeable surfaces is a trend in UK gardens (Cameron, 2023) and was included to highlight the direct actions people are taking which exacerbate the impact of climate change.	Examples include paving and tarmac for driveways and patios, and artificial grass replacing lawns. This stops rainwater filtering into the soil and results in increased flood risk.
Action-related information Key system information points were included to provide the same context for each group. How plant traits, specifically leaf hairs and evapotranspiration rates, are linked to the ability of plants to provide localised flood mitigation (Berreta *et al.,* 2014; Kemp *et al.,* 2019; Stovin *et al.,* 2012) and reduction of air pollution (Blanuša *et al.,* 2020; Shao *et al.,* 2019; Weerakkody *et al.,* 2018a) was included as both information and planting recommendations.	Climate change is resulting in hotter drier summers and warmer wetter winters in the UK, causing heat waves and flash flooding. Five of the hottest years on record in the UK since 1884 have all occurred since 2006 (2022, 2015, 2006, 2020 and 2011). Rainfall events at an intensity to cause flash flooding are predicted to be 4 times more frequent by 2070. Plants can provide environmental benefits, including reducing flooding and air pollution, and improving biodiversity. However, people are removing vegetation from their gardens and replacing them with impermeable surfaces. Examples include paving and tarmac for driveways and patios, and artificial grass replacing lawns. This stops rainwater filtering into the soil and results in increased flood risk. Certain plant characteristics can help with this. Plants with naturally hairy leaves can capture pollution particles, removing them from the air, and collect rainwater droplets, preventing them from falling to the ground and contributing to flooding. Recommendation: Use plants with hairy leaves in your garden to help reduce air pollution and flooding. Plants that use more water, considered 'thirsty' plants, can remove water more quickly from the soil. This in turn helps reduce soil saturation and likelihood of flooding. Recommendation: Use 'thirsty' plants in your garden to help reduce surface water accumulation that leads to flooding.
Climate change views	Are you concerned about the impact of climate change? Have you personally experienced/noticed the effects of climate change? (for example, flooding/flash flooding).
Plant selection post-	The photos below show popular UK garden plants.

information	Based on the information you have now read, please select the plant you like the most. Has your preference for the plants changed after reading the environmental information?
Plant preference drivers	What are the reasons why your plant preference has changed? (L-5) • I find this plant more attractive • This survey's information changed my preference • This plant's characteristics can provide environmental benefits • This plant better suits my garden's conditions (e.g. my garden experiences flooding or high pollution and this plant could help mitigate this)
Plant knowledge post-information	How much do you agree with the following statements about garden plants? (L-5) • Plants can reduce the risk of localised flooding • Plants can reduce air pollution • In the future I would select certain plants for my garden based on their environmental benefits

Table 6.1: Survey categories and key questions to investigate the relationships between plant knowledge, plant selection, and climate change pre- and post-survey information. Questions with a five-point Likert scale answer are shown as L-5.

6.3.2 Planting options proposed to survey participants

Six plants were chosen for their contrasting traits, all of which have been included in the experiments from this thesis or those of this team (Blanuša *et al.* 2013; Kemp *et al.,* 2019; Vaz Monteiro *et al.,* 2017). All planting options shown to participants were accompanied by photographs displaying overall shape of the plant, and a close up of leaf shape and a flower to enable participants to clearly see as much of the plant as possible (Figure 6.2). No plants were named in this survey, and were instead referred to as Plant A, B, C, D, E, or F. Photographs were either taken by myself or obtained from the Royal Horticultural Society's website (Figure 6.2). Previous research using photographs rather than physical plants has indicated they elicit similar emotional responses as live plants, and so was used in this online study (Berger *et al.,* 2022).

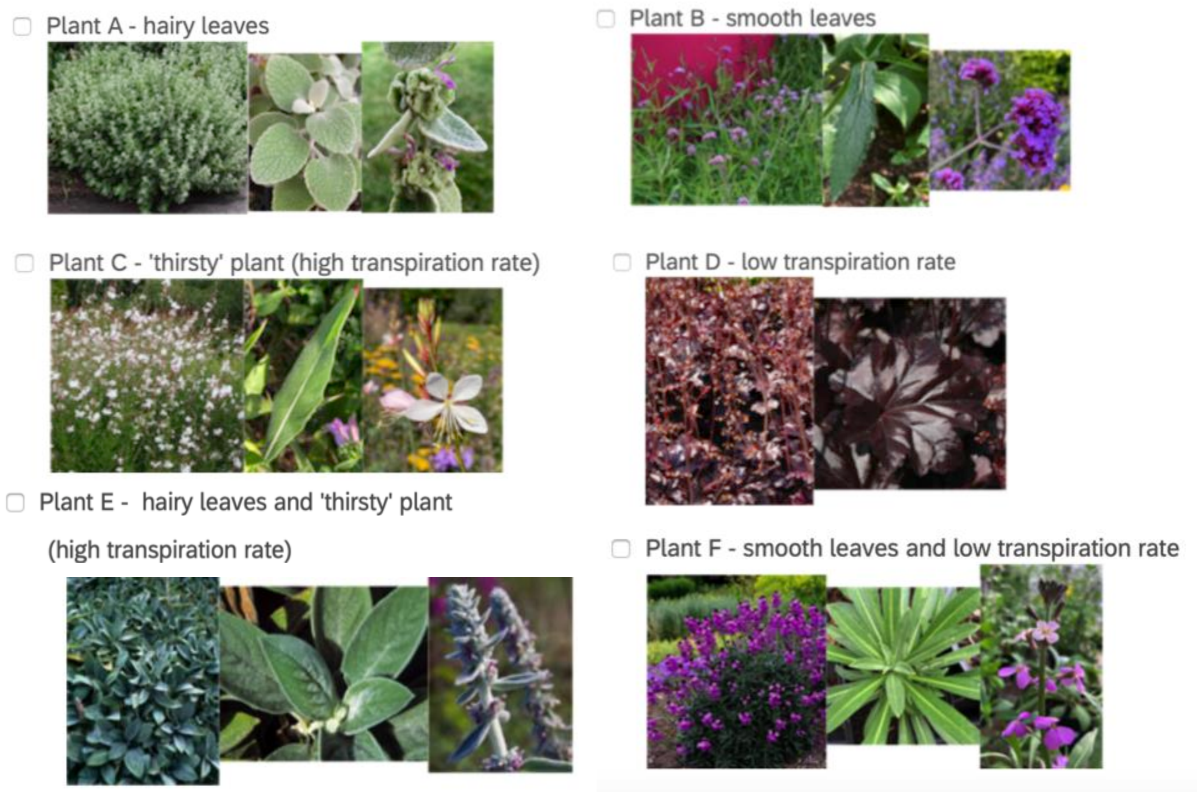


Figure 6.2: Plant species and their associated traits used in the survey. Plant A - *Pseudodictamnus mediterraneus,* Plant B - *Verbena bonariensis,* Plant C - *Oenothera lindheimeri* 'Whirling Butterflies', Plant D - *Heuchera* 'Obsidian', Plant E - *Stachys byzantina,* Plant F - *Erysimum* 'Bowles's Mauve'.

For the purpose of the survey, participants were asked to select the plants they liked, but after receiving information (system or action-related) were asked to take this into account when re-selecting their plant preference. This information did not name any plants or include plant choice suggestions, only trait-based recommendations for the action group or climate change information for the system group. Plants with leaf hairs and higher transpiration rates were emphasised in the action-related information to be beneficial in a garden because they could help mitigate localised flooding (Blanuša & Hadley, 2019; Kemp *et al.,* 2019) (see Chapters 3, 4 and 5) and air pollution (Blanuša *et al.,* 2020; Shao *et al.,* 2019; Weerakkody *et al.,* 2018a), therefore the 'correct' plants for participants to select post-information in Figure 6.2 for example would be Plant A, Plant C, or Plant E.

6.3.3 Data collection

The survey was disseminated through several staff and student mailing lists at the University of Reading, my own and colleagues' social media channels (Twitter, LinkedIn, Instagram, Facebook), Whatsapp groups and personal contacts (with requests to share the link widely in addition to participating). The invitation to participate stated the survey was about people's garden plant preferences, that they had to be 18 or over to participate, and would take under 10 minutes to complete. The opening page of the survey informed the participant about consent and options for withdrawal, their anonymity, and my (and my supervisor's) contact details. The survey was submitted for ethical review and was approved on the 9th November 2023 by the School of Agriculture, Policy and Development (University of Reading) Ethics Committee.

Survey programming also enabled participants to be randomly split into the two survey groups with equal weighting, i.e. equal numbers of participants were allocated to each survey group. The survey was live for 28 days, between the 13th November and 11th December 2023.

6.3.4 Data analysis

At the end of the survey the live survey link was closed and data downloaded from Qualtrics in csv format. The data set was checked and 'cleared' of incomplete submissions. If participants spent too little time on the survey, monitored via recorded start and finish time, the aim was also to remove these, although in the case of this survey none were found. At the closing date, 94 surveys remained unfinished and were excluded from the analysis.

Data was analysed using ordinal regression models within R (R Core Team, 2021), with statistical methods outlined in Chalmin-Pui *et al.* (2021b). Kruskal-Wallis tests were used when the assumptions of ordinal regression or ANOVA were not met. Models were used to explore the significance of information type and climate change impact on plant selection, as well as inclusion of demographics and gardening related data impacts on ecosystem services and plant trait knowledge. Initial fitted models included all factors, for example when investigating the significance of factors on leaf hair knowledge:

Leaf hairs ~ Hours spent gardening + Gardener + Horticultural qualification + Age + Gender + Education

Stepwise model selection was conducted using the step() function, which uses Akaike Information Criteria (AIC) to compare candidate models and identify the simplest model that explains the variation observed. AIC penalises models with more parameters. In cases where ΔAIC was < 2 between several candidate models, the simplest model was selected. The demographic factors included in the models changed depending on the model in question (for example section 6.4 below found gender, age, and education did not impact awareness of the function of leaf hairs and were removed, but horticultural or equivalent qualification and enjoyment of gardening did. Age correlated with awareness of the concept of plant ecosystem services but gender did not). Pearson's Chi-squared tests were also carried out to determine association between variables. Where possible model assumptions were also checked using Brant models to determine best fit.

6.4 Results

A total of 519 people responded to this survey, of which 419 complete survey responses were used for analysis (208 in the system information group and 211 in the action-related information group). There was a higher proportion of respondents aged 25-34 compared to the other age groups. There were also more female participants and those with a university degree, compared to the general UK population (Office for National Statistics, 2023a, 2023b, 2023c, 2023d) (Table 6.2).

Seventy per cent of respondents considered themselves gardeners or enjoyed gardening; 41% had a qualification relating to horticulture, gardening, or the environmental sciences. Most participants (29%) gardened between 1-3 hours a week, followed by less than 1 hour a week (22.9%), 3-7 hours a week (20.8%), more than 7 hours a week (14.6%), and the least number of people never gardened (12.6%). The majority of each information group lived in a property with a garden (87% in the system group, and 85.8% in the action-related group).

	Participant number	Participant percentage	UK 2021 census data
Gender			
Female	283	67.5%	51%
Male	121	28.9%	49%
Non-binary	12	2.9%	0.06%
Other	1	0.2%	NA
Prefer not to say	2	0.5%	NA
Age			
18 -24	40	9.5%	Under 25 - 29.1%
25 - 34	99	23.6%	25 - 39 - 20.2%
35 - 44	57	13.6%	40 - 59 - 26.3%
45 - 54	82	19.6%	
55 - 64	83	19.8%	60 or older - 24.4%
65 or older	58	13.8%	
Prefer not to say	0	0%	NA
Education			
Secondary school or below (GCSE, O-level or equivalent)	20	4.8%	Level 1 - 1-4 GCSE passes or equivalent - 9.6%
Further education (A-level, GNVQ or equivalent)	40	9.6%	Level 2 - 5 or more GCSE passes or equivalent - 13.4%
Professional qualification	39	9.3%	Apprenticeships - 5.3%
Undergraduate degree	112	26.8%	Level 3 - 2 or more A levels or equivalent - 16.9%
Postgraduate degree	128	30.6%	Level 4 or above - Higher National Certificate, Higher National Diploma, Bachelor's degree, or postgraduate qualifications - 33.8%
Doctorate degree	78	18.7%	Other - 2.8%
None of the above	1	0.2%	No qualifications - 18.2%

Table 6.2: Survey participants' demographic data and comparison to UK 2021 census data (Office for National Statistics, 2023a, 2023b, 2023c, 2023d).

6.4.1 Prior knowledge of plant benefits

Awareness of the concept of plant ecosystem services

Results indicated that there were no differences between genders in their knowledge of plant ecosystem services and plant traits on all counts, and were dropped from analysis. A Pearson's Chi-squared test was carried out to assess whether hours spent gardening, a horticultural qualification, and whether someone considered themselves a gardener were related. There was significant evidence of an association between all three ($p < 0.001$) (hours spent gardening and gardener $\chi^2 = 101.44$, hours spent gardening and a horticultural qualification $\chi^2 = 11.974$, horticultural qualification and gardener $\chi^2 = 12.434$) (data not shown). Participants who considered themselves gardeners or enjoyed gardening were significantly more aware that garden plants helped wildlife, flood avoidance, noise mitigation and urban cooling, than those who did not garden (wildlife $p = 0.044$, others $p < 0.001$). A higher education level and a horticultural or equivalent qualification were associated with improved awareness of both flooding and temperature mitigation services, and the latter also improved awareness of noise mitigation ($p < 0.001$). A Fisher's exact test showed that there was a significant association between education and having a horticultural qualification ($p < 0.001$), therefore correlated and difficult to separate the influence of either. Age also significantly impacted knowledge of all ecosystem services (wildlife $p = 0.006$, flooding $p = 0.005$, pollution $p = 0.039$, noise and temperature $p < 0.001$).

Awareness of the function of leaf hairs

The majority of participants were ambivalent regarding the appearance or environmental benefits of leaf hairs, with 34.4% and 57% of participants selecting 'neither agree nor disagree' respectively (data not shown). For those that did express an opinion on the aesthetic appeal, 30.6% somewhat agreed that they liked plants with hairy leaves, whilst 19.8% strongly agreed. Only a combined 15.3% disliked them in some capacity. Demographic characteristics including gender, age, and education had no significant association with knowledge of leaf hair benefits. Both holding a horticultural or equivalent qualification and enjoyment of gardening were significant factors for participant's awareness of the environmental benefits of leaf hairs ($p = 0.04$), and the number of hours a week spent gardening also significantly associated with participant's awareness of the benefits of leaf hairs ($p = 0.015$).

Awareness of the function of transpiration rate

Participants' prior engagement with gardening was found to not significantly impact appreciation of the benefits of a higher transpiration rate in initial models. Although age and education were found in the best fit model, only the 65 and over age category was a significant factor ($p = 0.029$) (data not shown).

6.4.2 Change in ecosystem service knowledge following survey information

Awareness of flood mitigation ecosystem service delivery

To establish whether the action-related information had an impact on ecosystem service knowledge participants were asked pre- and post-information whether plants could reduce the risk of localised flooding. There was a significant difference between the system and action group, with those that received action-related information changing their answer post-information to agree with the statement more than those that received system information only ($p = 0.035$) (data not shown).

Awareness of pollution reduction ecosystem service delivery

In contrast to flooding, there was no significant difference in answer regarding pollution awareness between the two survey groups before and after survey information, indicating the type of information did not have an impact on responses ($p = 0.451$) (data not shown). However, there was a significant difference before and after information when group was not taken into account ($p < 0.001$).

6.4.3 The impact of climate change views on plant selection and environmental intent

To investigate environmental intentions, participants were asked whether they would be willing to select plants for their environmental benefits in the future, and these responses were measured against climate change impact. The majority of each group affirmed they were concerned about climate change (94.7% in the system group and 96.2% in the action group), and had experienced climate change effects (69.7% in the system group and 69.2% in the action group). Comparing these responses with the intention to select environmentally beneficial plants in the future, it was found that those who were concerned or impacted by climate change were significantly more willing to select plants for their environmental benefits ($p < 0.001$) (Figures 6.3 and 6.4). These outcomes were not altered depending on which information group the respondents were allocated to ($p = 0.168$).

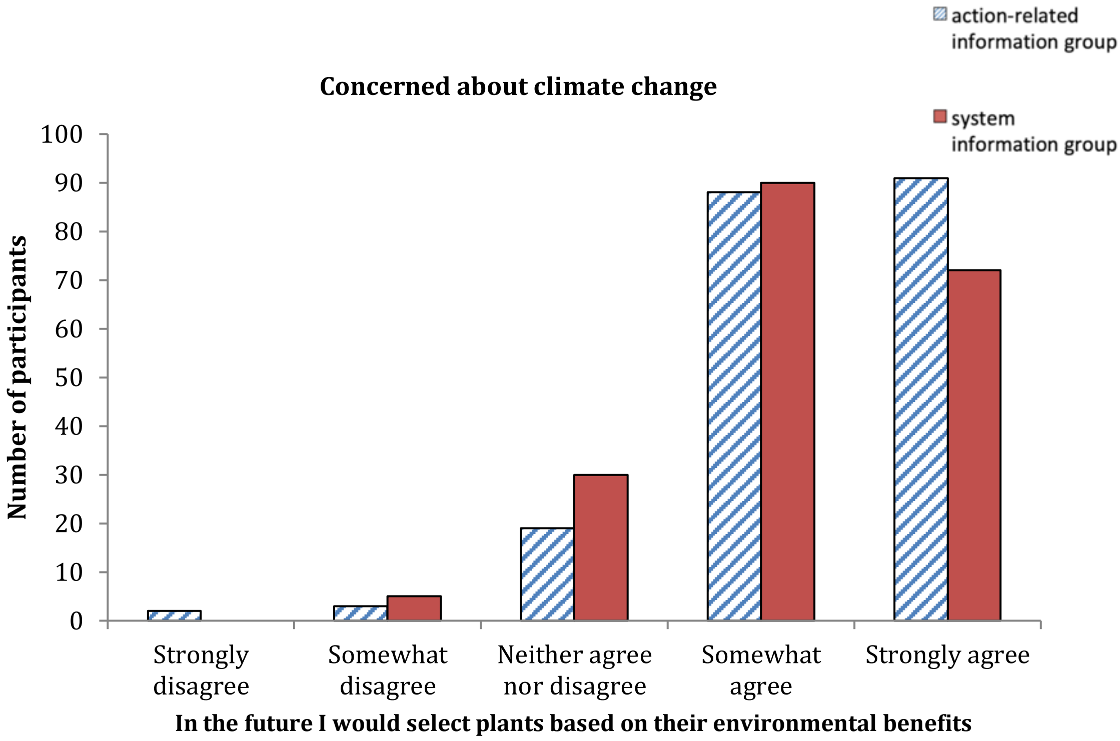


Figure 6.3: Number of participants concerned about climate change who would select plants for their environmental benefits in the future. Results divided by information groups - red bars are system information group, and blue bars are action-related information group.

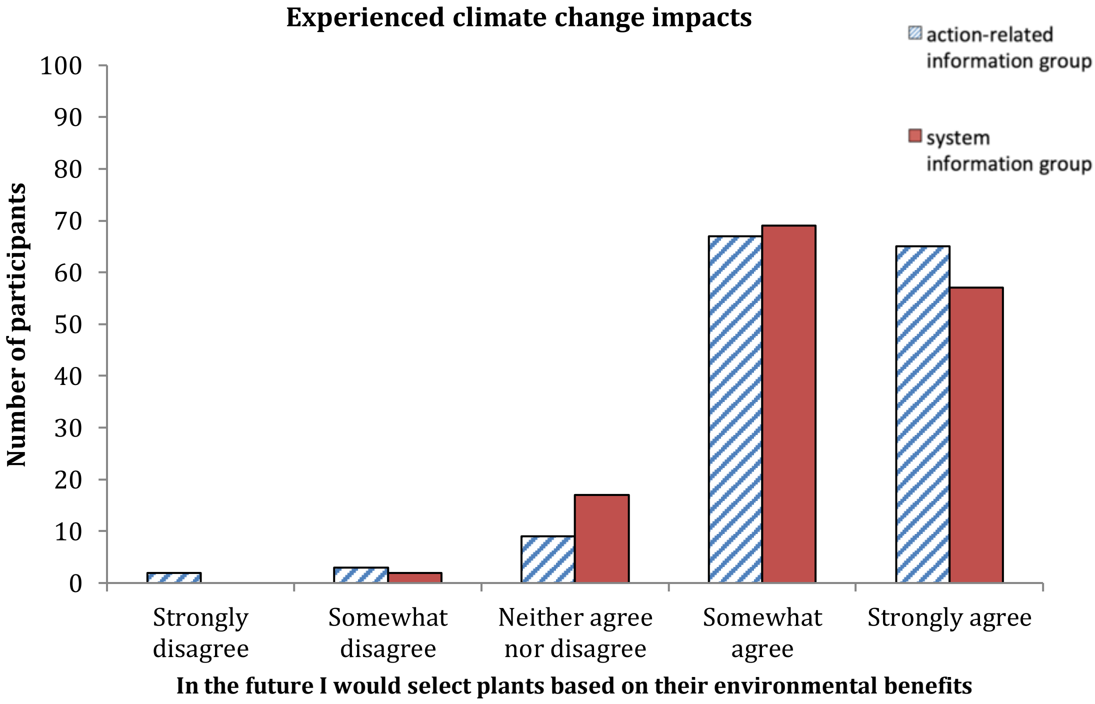


Figure 6.4: Number of participants who have experienced climate change who would select plants for their environmental benefits in the future. Results divided in information groups - red bars are system information group, and blue bars are action-related information group.

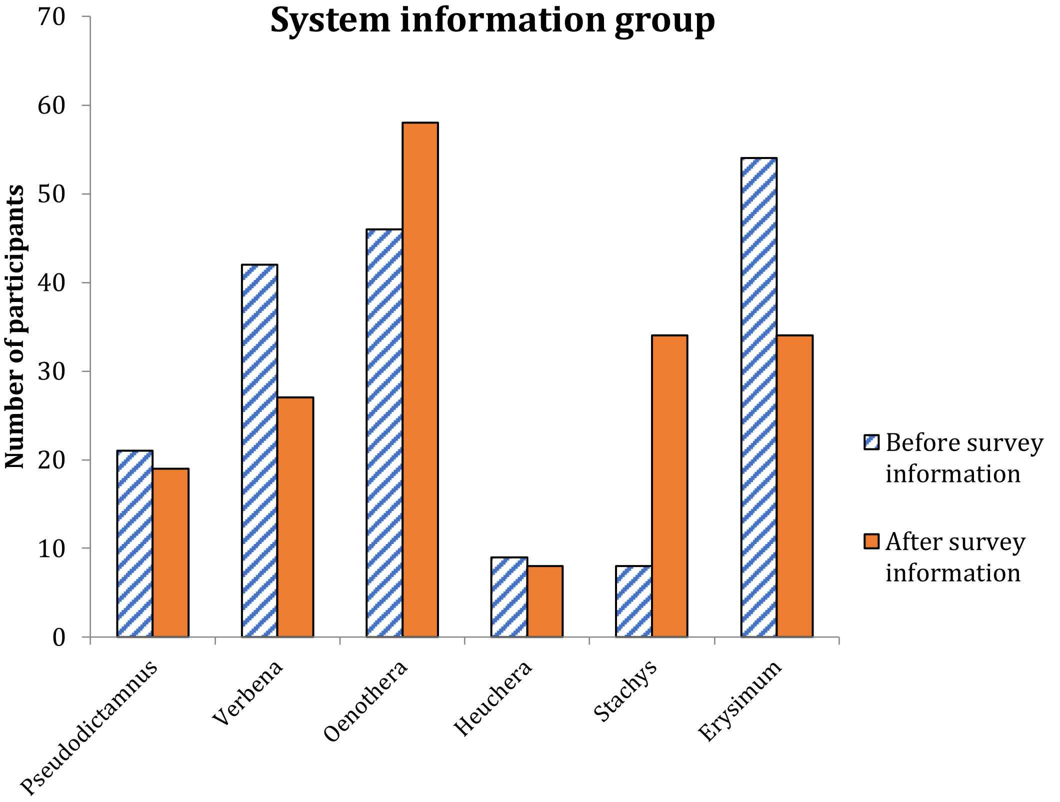
6.4.4 Plant selection

Plant preference pre-survey information

Participants were asked prior to being given additional information (pre-information phase) to select the plant they liked the most, and the majority of respondents selected *Erysimum* (Plant F), which received 131 votes, potentially due to its floral coverage, followed by *Oenothera* (Plant C) with 111 votes, and *Verbena* (Plant B) with 101 votes. In contrast the least popular plants were *Heuchera* (Plant D) with 15 votes, *Stachys* (Plant E) with 18 votes, and *Pseudodictamnus* with 45 votes.

Plant preference change post-information

After being given additional information on the ecosystem services of the different plant taxa (post-information phase) participants were asked again to select the plant they liked the most. A minority of participants selected more than one plant, and these responses were excluded from subsequent analyses. As such the data demonstrated only a direct change of preference after the additional information had been provided. This sub-group consisted of 325 participants (77% of total respondents), with 180 allocated to the system group and 145 in the action-related information group. Comparing plant selection after information, the action-related group who received planting recommendations were significantly more likely to reduce their preference of *Verbena* (Plant B) and *Erysimum* (Plant F) compared to the system group ($p = 0.02$ and $p < 0.001$ respectively) (Figure 6.5). Also comparing selection pattern change before and after information within groups, the action-related group significantly increased their selection of *Pseudodictamnus* ($p = 0.048$) while the system group decreased selection. However, both groups had similar selection patterns and *Oenothera* (Plant C) was popular before and after information, while *Heuchera* (Plant D) was unpopular. Both groups had a similar change in plant preference for *Stachys* (Plant E), with an increase in selection post-information.



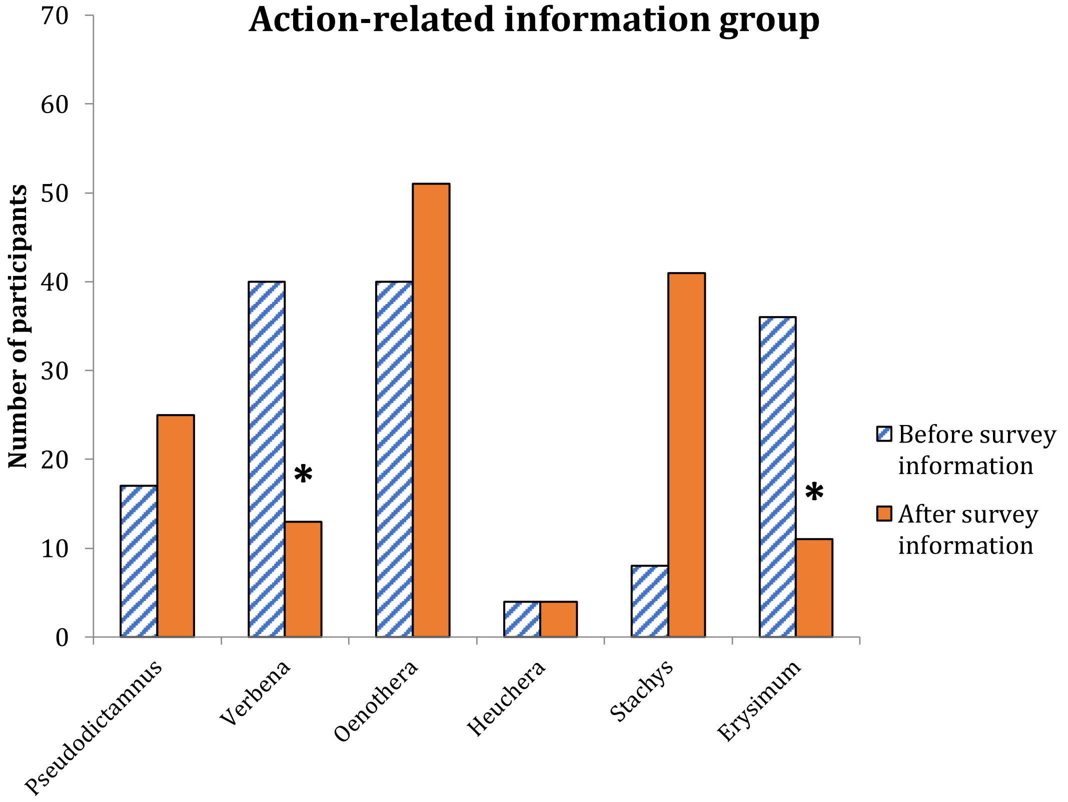


Figure 6.5: Plant selection before and after receiving survey information. The asterisks indicate a significant change in plant preference after information when comparing the system and action-related groups, and not within groups.

6.4.5 Drivers of plant preference change

The majority of participants in the action-related information group changed their plant preference after receiving planting recommendations and the majority in the system information group did not change ($p < 0.001$) (Figure 6.6). Participants were asked about the drivers for this plant preference change. The plant traits being able to provide environmental benefits was a significant factor influencing preference change in the action group compared to the system group ($p = 0.011$) (Figure 6.7). The options of plant aesthetics, the plant better suiting the participant's gardens, and the general survey information (climate change data, flood risk etc.) did not lead to significantly different selections from either group. Appreciation of a plant's aesthetics remained consistent regardless of survey group, with no significant change in opinion both pre- and post-survey information. However, the majority of both groups cited the general survey information as a driver for preference change.

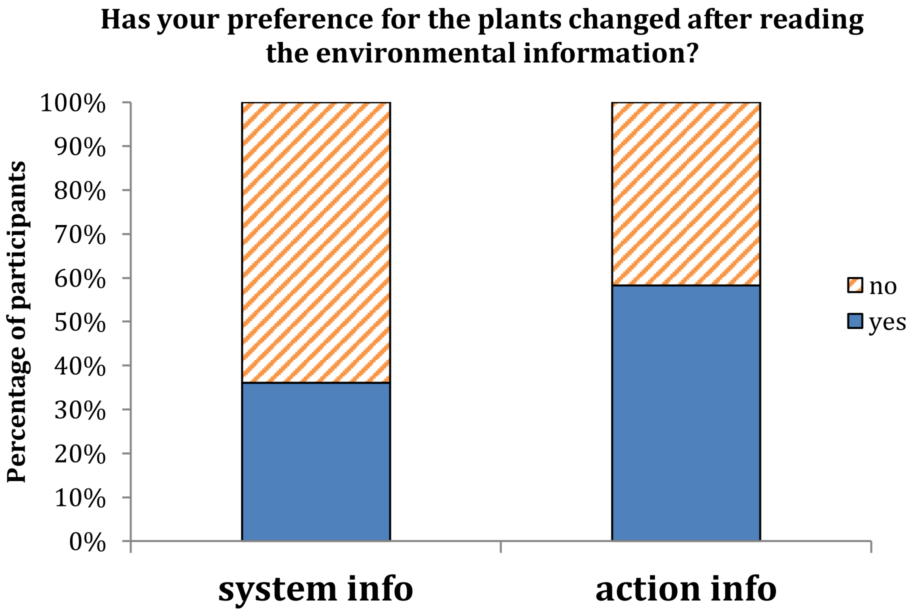


Figure 6.6: Percentage of participants that changed their plant preference after survey information.

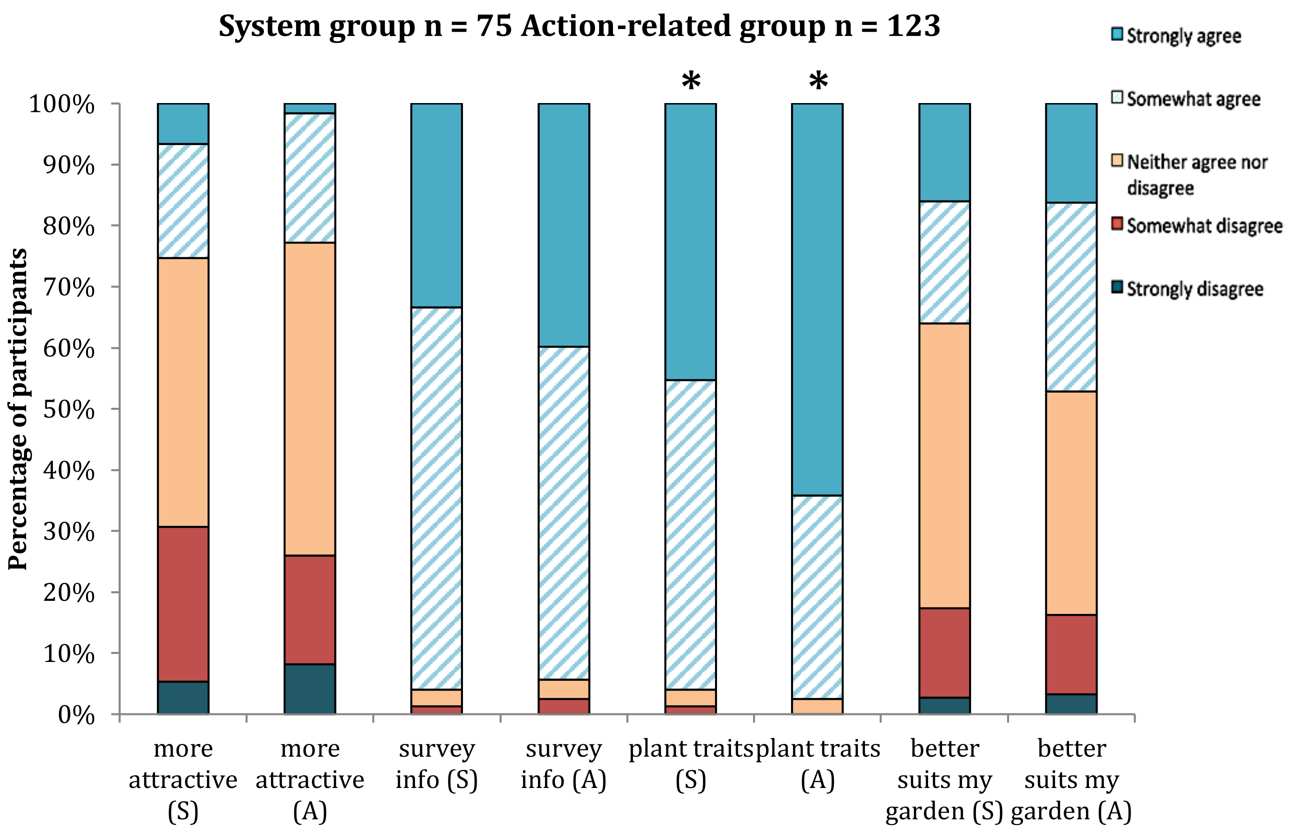


Figure 6.7: Percentage of plant preference change drivers for the system information group (labelled S) and the action-related information group (A). The asterisks indicate a significant difference between the system and action-related group.

6.5 Discussion

Pre-survey information - Prior knowledge of plant benefits

Respondents who considered themselves gardeners, or had a horticultural qualification or equivalent, were aware of all ecosystem service concepts listed in the survey. The number of hours per week spent gardening was also correlated with significantly improved awareness of the benefits of leaf hairs for capturing particulate matter pollution and aiding with localised flood mitigation. Having a horticultural qualification, considering yourself a gardener, and number of hours spent gardening fall under what could be termed an ‘interest in gardening’ and indicates that knowledge of plants, both via formal education and hands-on experience, leads to a greater comprehension of the benefits plants can provide. Previous studies have commented on a lack of awareness by the UK public of ecosystem services provided by plants (Cameron & Blanuša, 2016; Chalmin-Pui *et al.,* 2019; Derkzen *et al.,* 2017; Royal Horticultural Society, 2021), however this survey found a good level of awareness, particularly amongst those who considered themselves gardeners. Recent surge in information in the UK news outlets about the benefits of green infrastructure (Gerretsen, 2022; Horton, 2022 & 2023; Ng, 2021; The Guardian, 2021) may be contributing to a better level of awareness about the benefits of plants now compared to several years ago.

As hypothesised, an interest in gardening was not linked with an awareness of the environmental benefits of plants with higher transpiration rates, and only those aged 65 and over had any recognition of this. Climate change communications frequently centres on a reduction in water availability, particularly in the UK, and therefore a potential scarcity of water in the future (IPCC, 2021; Met Office, no date; Webster *et al.,* 2017). A key component of gardening and ensuring plant survival is to sufficiently water plants; in the current context of changing climate gardeners have however been encouraged to adapt their watering practices (and minimise watering while still enabling plant survival) as a climate change solution (Egerer *et al.,* 2019). There is evidence that plants can survive on a reduced watering regime even if they are not typically considered drought tolerant species (Blanuša *et al.,* 2009; Cameron *et al.,* 2006; Cameron *et al.,* 2008; Dodds *et al.,* 2007; Norton *et al.,* 2017; Sobeih *et al.,* 2004; Stoll *et al.,* 2000) so once plants are adapted to reduced watering the outcome could still result in healthy, flowering plants in a garden setting. In addition to water butts and harvesting rainwater, another solution to periods of water shortages is to use drought tolerant plants, which typically have lower transpiration rates (Chu & Farrell, 2022; Schrieke & Farrell, 2021; Taiz & Zeiger, 2002). Plants with higher transpiration rates are perceived to have a higher water use and therefore require more water at a time when less is available (Szota *et al*., 2017). However, research in this thesis, and that of other studies has found that a higher transpiration rate does not always result in a plants inability to tolerate reduced water. *Oenothera* and *Stachys* are cited as drought tolerant (Beth Chatto's Plants & Gardens, 2022a & 2022b; Wallington, 2022) but have also both been found to have higher transpiration rates when water is available (Kemp *et al*., 2019; McLaughlin *et al.,* unpublished), indicating plants should not be viewed within the dichotomy of low or high transpiration rates and therefore drought tolerant or drought intolerant. In addition to this, emphasis on decreased water availability is only part of the picture, with an anticipated increase in heavier rainfall events and flash flooding as a result of climate change requiring plants that will need to tolerate periods of drought and also periods of inundation (Kendon *et al.,* 2023; King *et al.,* 2012; Webster *et al.,* 2017). This survey, and other studies, indicates more work is needed to increase understanding of how to garden in a changing climate (Royal Horticultural Society, 2021).

The impact of action-related information on plant preference change

The provision of action-related information resulted in a significant change of participants' plant preferences including plant selection post-information and awareness of how plants can help alleviate the impacts of flooding. Plant selection prior to receiving survey information showed both groups favoured *Verbena*, *Oenothera* and *Erysimum*, which were all shown with visible flowers in the photographs. After the survey information the majority of the action-related group changed their plant preference, whilst the majority of the system information group did not. These results were hypothesised, and supported by existing literature that also found using action-related information could facilitate positive environmental behavioural change (Frick *et al.,* 2004; Gimenez *et al.,* 2023; Hartley *et al.,* 2015; Nuebig *et al.,* 2020). Hartley *et al.* (2015) found that using activities and information to inform school children about marine litter, which included simple recommended actions that could help reduce litter such as picking up litter or recycling, resulted in children being more concerned about the issue, had greater understanding and were engaging more in beneficial actions to remove or reduce litter. The action-related group in this survey significantly reduced their preference for *Verbena* and *Erysimum*, which were both stated to have traits that did not aid ecosystem service delivery, and increased their selection of *Stachys* and *Pseudodictamnus*, which had favourable traits. The plant traits information significantly altered the action-related group's choices compared to the system group. *Oenothera* maintained its popularity in both groups, indicating participants liked this plant for its aesthetics and ecosystem services equally.

The impact of aesthetics on plant selection

Aesthetics has been highlighted as a significant driver for plant selection in previous research (Berger *et al.,* 2022; Hanson *et al.,* 2021; Hoyle *et al.,* 2017b; Kaufman & Lohr, 2004 & 2008; Kendal *et al.,* 2012) and in this study plant selection prior to receiving survey information indicated a preference for colourful or visibly flowering plants. *Verbena, Oenothera* and *Erysimum* were all selected by participants in greater numbers than the *Heuchera, Pseudodictamnus* and *Stachys*, which all had less visible or showy flowers. Selection of the latter two only increased post-survey information, particularly in the action-related group when the plant trait signifiers could have played a role. In the action-related group both *Stachys* and *Pseudodictamnus* were selected more than *Erysimum* and *Verbena* after the survey information, and in the system group *Stachys* was selected more than *Verbena* and equal to *Erysimum* post-survey information. *Oenothera,* with its abundance of white flowers, was still more popular than all other plants in both groups after survey information. However, *Heuchera* remained unpopular in both groups pre- and post-survey information. Research demonstrates that flower colour is influential in plant selection (Chalmin-Pui *et al.,* 2019; Kendal *et al.,* 2012; Zhang *et al.,* 2023), but that foliage colour also plays an important role (Elsadek & Fujii, 2014; Hoyle *et al.,* 2017a). Both purple and grey leaves have been found to be less popular than green foliage, with green leaves not only more popular but also considered a demonstration of plant health (Berger *et al.,* 2022; Kaufman & Lohr, 2004; Kendal *et al.,* 2012). Leaf colour could potentially explain the reason behind these outcomes, as well as an aversion to what could be perceived as an unhealthy plant, which can lead to negative responses towards the plant in question (Berger *et al.,* 2022). However, grey-coloured foliage is also linked with cooling ecosystem services (Vaz Monteiro *et al.,* 2016 & 2017), therefore selecting plants based on their foliage colour would in this instance have an impact on more than just the design of a garden space.

When participants were asked after plant selection post-survey information why they selected the plants that they did, plant aesthetics (whether they found the plant attractive) was not given as a significant reason, which was surprising as it was hypothesised that plant aesthetics would influence choices. Regardless of survey group there was no significant change of opinion about the plant's appearance pre- and post-information. However, *Oenothera* was still a popular plant in both groups before and after survey information, and even if respondents did not believe they selected their plant choice based on how it looked, *Oenothera* was still consistently chosen so plant aesthetics must still subconsciously play a role. In the survey *Oenothera* was listed as having a high transpiration rate which is a trait linked to flood mitigation, so it is possible that selecting this plant enabled people to select a plant they found attractive that could also provide a service in their garden, over and above a plant that could provide a service but was potentially less visually appealing such as *Pseudodictamnus,* which increased in popularity in the action group but was selected less than *Oenothera*. Also considering the selection of visibly flowering plants before survey information was given, plant aesthetics should not be overlooked as an early driver for plant selection, especially as it has been noted in previous research that aesthetics can support people adopting environmental practices and valuing a plant's ecosystem service potential (Frantzeskaki, 2019; Hanson *et al.,* 2021; van den Berg & van Winsum-Westra, 2010).

The impact of system information and action-related information on willingness to make pro-environmental plant selections

Both groups cited the general survey information as a significant factor for changing plant preference. Only the minority in the system information group changed their plant choices, but those that did stated the survey information as the reason behind this. Although they were not provided with recommendations, the system knowledge informed participants about the environmental problems and impacts of climate change. This information was also framed in a local context, linking it to our gardens, which is something that many people have access to and can relate to, and has been found effective in previous studies

(Pidgeon, 2012; Scannel & Gifford, 2013; Spence *et al.,* 2011; Wiest *et al.,* 2015). System information can be an indirect driver for change by significantly influencing action-related outcomes (Adu-Gyamfi *et al.,* 2022; Frick *et al.,* 2004; Heo & Muralidharan, 2019; Jiang *et al.,* 2024; Liu *et al*., 2020a; Samus *et al.,* 2023), indicating that this information does still lead to people wanting to make environmental choices, even if within the context of this survey they were unable to know which plants to choose as they had not been provided with recommendations. Within a garden design context, system information in the form of environmental education changed people's landscaping preferences (van Heezik *et al.,* 2012), reducing the importance of cues to care and manicured garden styles (Hostetler, 2021), as well as an increased likelihood of adopting water saving garden designs in drought tolerant areas when information was provided (Fernández-Cañero *et al.,* 2011), demonstrating that system information alone can still have an impact on preferences and environmental behaviour. It has been found that environmental knowledge has a significant positive effect on attitude, and this in turn has a positive effect on pro-environmental behaviour (Liu *et al*., 2020a). People's attitude towards an environmental action is crucial for changing behaviours (de Leeuw *et al.,* 2015; Liu *et al.,* 2020a) and if the action is perceived as useful this has influenced whether people adopt green infrastructure (Carlet, 2015; Tsantopoulos *et al.,* 2018) and electric vehicles (Adu-Gyamfi *et al.,* 2023). What people identify as the subjective norm, which is how people perceive social expectations of behaviour (Ajzen, 1991), has been found to alter people's attitudes either positively or negatively towards an environmental behaviour (Adu-Gyamfi *et al.,* 2023; Birau & Faure, 2018; Cialdini, 2003; Schrank *et al.,* 2023). Although this survey did not investigate people's attitudes towards ecosystem services, the system information would have linked with how people feel about climate change and could have influenced attitudes towards plant selection.

The impact of action-related information on knowledge of ecosystem services

Participants in the action group changed their answers after being given survey information about flood mitigation. This was not the case for pollution reduction, as there was no significant increase in awareness between groups, but a high level of awareness overall. A greater emphasis was placed on flood mitigation within this survey, but the action-related information specified leaf hairs as an underlying mechanism for multiple ecosystem services including flooding mitigation and air particulate pollution capture (Blanuša *et al.,* 2020; Kemp *et al.,* 2019; Monteiro, 2017; Weerakkody *et al.,* 2018a), however this was not present for the system information group. Both groups had similar responses to the pollution questions, and this could link with recent survey findings by the Royal Horticultural Society that suggest a greater awareness of poor air quality compared to flood mitigation, and air pollution considered one of the greatest issues facing urban residents, particularly in London (Royal Horticultural Society, 2021). This increased awareness likely influenced this survey's results too. Another reason behind this difference in responses could be that people, in particular gardeners, are aware that 'thirsty' plants require more water and this can put increased demand on water supplies, which would be seen as negative. The level of knowledge about how a higher transpiration rate could also be beneficial is smaller among the public, as water conservation is at the forefront of UK gardening practices, and therefore people could 'learn' from this survey.

The impact of climate change on pro-environmental choices

Survey information also did not have an impact on the responses to the climate change questions. To determine the relationship between climate change and participants' environmental intent, survey questions were included to understand whether climate change concern or climate change experience had an impact on plant selection. Participants were also asked after they received the information, whether they would be willing to select plants for their environmental benefits in the future. It was found that regardless of the survey group the participants' perceptions and experiences of climate change were significant drivers for environmental plant selection. In this instance the type of information did not impact the participants' intent to make environmentally conscious planting choices, with the threat of climate change driving a willingness to make decisions that benefit the environment. This has also been found in surveys that assessed participants' attitude towards climate change, with those who have personal experience of climate change extremes or damage more likely to care about the subject and approve of mitigating adaptations (Spence *et al.*, 2011; Wong-Parodi & Berlin Rubin, 2022). Feeling environmental concern or caring about the environment results in people being more likely to undertake pro-environmental behaviours (de Leeuw *et al.,* 2015; Heo & Muralidhara, 2019; Lange *et al.,* 2022; Otto & Pensini, 2017; Samus *et al.,* 2023; Schrank *et al.,* 2023), and a connectedness to nature also results in improved attitudes and outcomes (Otto & Pensini, 2017; Samus *et al.,* 2023). The majority of Royal Horticultural Society survey participants reported they cared about environmental issues (Royal Horticultural Society, 2021) and were optimistic they could adapt their garden planting to better suit climate change conditions (Webster *et al.,* 2017). This care and willingness to adapt is something that was also seen in this survey. Participants in another survey focusing on UK planting preferences were happy to adopt (the idea of) non-native planting when it was known to be better adapted to climate change conditions (Hoyle *et al.*, 2017b), indicating again that climate change is driving people's gardening choices. In a different study however, only 30% of surveyed Australian gardeners were willing to change their planting selection in response to climate change, citing aesthetic preferences as their reason for this (Egerer *et al.,* 2019).

The potential to utilise action-related information for pro-environmental behaviours

Understanding people's willingness to make environmental choices and linking this to actionable targets could improve the environmental impact of domestic gardens. Multiple studies, including this one, indicate that people's perceptions and experiences of climate change could be key drivers to convert intent into actions. Also, that using action-related knowledge could help improve environmental behaviours, including reducing litter and food waste (Hartley *et al.,* 2015; Neubig *et al.,* 2020) and leading to more positive opinions of green infrastructure (Derkzen *et al.,* 2017). The Royal Horticultural Society's 'Plants for Pollinators' scheme also works using a similar information premise (Royal Horticultural Society, 2019) and labels plants with an easy to recognise logo which informs consumers of the benefits a plant would provide for pollinating insects. The online and printed information about the scheme delivers 'system information' (Royal Horticultural Society, 2019), and the logo conveys 'action-related' recommendations that enable people to make an environmentally informed planting choice. A 2016 survey found that 77.8% of participants were aware of the scheme and meaning behind the labelling compared to other garden centre labelling (34.3% and 31.6%), and only 13% were not aware of any pollinator scheme (Bird *et al.,* 2016). This indicates that recognisable information and actionable behaviours, and easy to follow recommendations, could be useful for facilitating beneficial change and enabling consumers to make practical choices within their own gardens. This is an example of how information on plant traits linked to functional ecosystem service delivery could also be delivered to the public, enabling easy to follow indicators of environmentally beneficial purchases. Garden design styles can be subject to copying on a larger scale in urban areas, so environmental gardening might have the potential to be replicated across neighbourhoods if it gains traction or becomes fashionable (Doll *et al.,* 2023; Francis*,* 2018), particularly if people are concerned about climate change and willing to make changes, as seen in this survey regardless of information group.

6.6 Limitations and future recommendations

Participants in this survey were predominantly female, with a university degree or higher, and considered themselves gardeners and enjoyed gardening. A bias towards female respondents in garden surveys is common (Samus *et al.,* 2023) and gender did not have a significant impact on the results of either this survey or others (Chalmin-Pui *et al.,* 2021b; de Leeuw *et al.,* 2015; Mackay & Schmitt, 2019). The participants for this survey were approached via networks that this author had access to, which would have introduced bias, including a gardening network (via Twitter and the Royal Horticultural Society), university educated cohorts (via the University of Reading and University of Sheffield), and people suspected to hold a greater knowledge of plant sciences via the School of Agriculture, Policy and Development (University of Reading). The higher proportion with a university education would likely have impacted the results, although it was noted that 41% of participants held a horticultural or equivalent qualification, which could have also been impactful to result outcomes and potentially skewed the sample to those that may respond positiviely to his survey's information. Future work could aim to have a wider reach and pool from participants that have varied levels of education and no gardening experience as access to only certain groups of people possibly restricts the scope of this research. Utilising a market research company able to sample respondents that nationally represent the UK population on all demographic fronts is recommended moving forward. The questionnaire was also only available in English, and the majority of participants were based in the UK (a very small minority were based abroad) so there is likely to be a bias towards a Global North or British viewpoint to both gardening and plant selection.

It was noted that a minority of survey respondents in the system information group changed their plant preferences after reading the survey information, even though they were not provided with planting recommendations. Although it was necessary for the plant selection questions to include the plant traits that indicate potential ecosystem services (leaf hairs and 'thirsty' plants) these could have also led some system information participants to infer a significance from their listing and change their preferences based on this assumption. Additionally, some participants in the system information group could have had prior knowledge of ecosystem services.

Acquiescence bias may play a role in survey answers, when participants answer questions as the ideal versions of themselves and how they wish to be viewed, or with responses that reflect socially desirable attitudes biased towards the social norm, therefore not answering truthfully or with their own opinions, although anonymous answers may have mitigated this slightly (de Leeuw *et al.,* 2015; Toor, 2020). This could potentially explain why aesthetic preference was not a significant driver for plant selection in the survey. Previous studies, particularly with regards to food waste or wildlife-friendly gardening behaviours, have also indicated that participants' answers in a survey (self-reporting) were not always what they intend to action in real life and there is a discrepancy between the two, referred to as the intention-behaviour gap, which can also be linked to a respondent's emotions around the topic (de Leeuw *et al.,* 2015; Graham-Rowe *et* *al.,* 2015; Samus *et al.,* 2023). Although action-related information appeared to influence a change in plant selection more work is needed to translate these findings into real life behaviours and ensure longevity of behavioural change. Some studies have found action-related information results in short-term change only, however van Heezik *et al.* (2012) found that knowledge and behaviour relating to wildlife gardening increased when homeowners were supplied with information as well as researchers visiting participants' gardens on multiple occasions and providing individual garden feedback. Therefore, behavioural change may need to be supported beyond action-related information to ensure longer-term change. This support could come additionally from other parties, including both policy and stakeholders, and industries driving garden consumerism such as garden centres and growers (Frost & Murtagh, 2024). A combination of forces including action-related information, holistically working to contribute to gardening behavioural change and environmentally positive outcomes could be the answer to supporting sustained changes (Cameron, 2023; Neubig *et al.,* 2020).

Feedback from participants

Feedback provided by some participants highlighted that when selecting plants there was no option to select none of the options, either because the participant did not like the plants or because they did not think any of them would be useful for e.g. mitigating localised flooding. Although requiring participants to select a plant was useful for the survey results, it may have forced a selection that was not genuine or organic, and therefore could impact the results. A small minority of participants mentioned electing not to finish the survey to avoid being forced to make a planting choice they did not believe in.

6.7 Key conclusions

- Action-related knowledge significantly increased the likelihood of people changing their planting preferences in favour of plants that could provide flood mitigation and air pollution reduction. The information provided in the survey, specifically the information on plant traits, was linked to this change in preference.

- Participants that were concerned about, or had experienced, the impact of climate change were significantly more willing to select plants that provided environmental benefits in the future. This effect was also not influenced by system or action-related knowledge.

Chapter 7

Discussion

This chapter will first reiterate the existing literature and research prior to experimentation, and the knowledge gaps that this thesis intended to address. The experimental findings from the four research chapters will be summarised, as well as recommendations from this work that are proposed to potentially improve the provision of runoff reduction as an ecosystem service of domestic gardens. The overall limitations and potential future improvements of this project will also be addressed.

7.1 State of knowledge before project commencement

Previous research has indicated that plants with traits including larger leaf area, leaf trichomes, and a denser canopy are able to reduce rainfall runoff and combined with higher functional evapotranspiration rates help mitigate the effects of localised flooding compared to non-vegetated surfaces or other plant species without these traits (Berretta *et al.,* 2014; Blanuša & Hadley, 2019; Chu & Farrell, 2022; Kemp *et al.,* 2019; Nagase & Dunnett, 2012; Stovin *et al.,* 2012). Factors influencing rainfall runoff reduction are summarised in Figure 7.1 below.

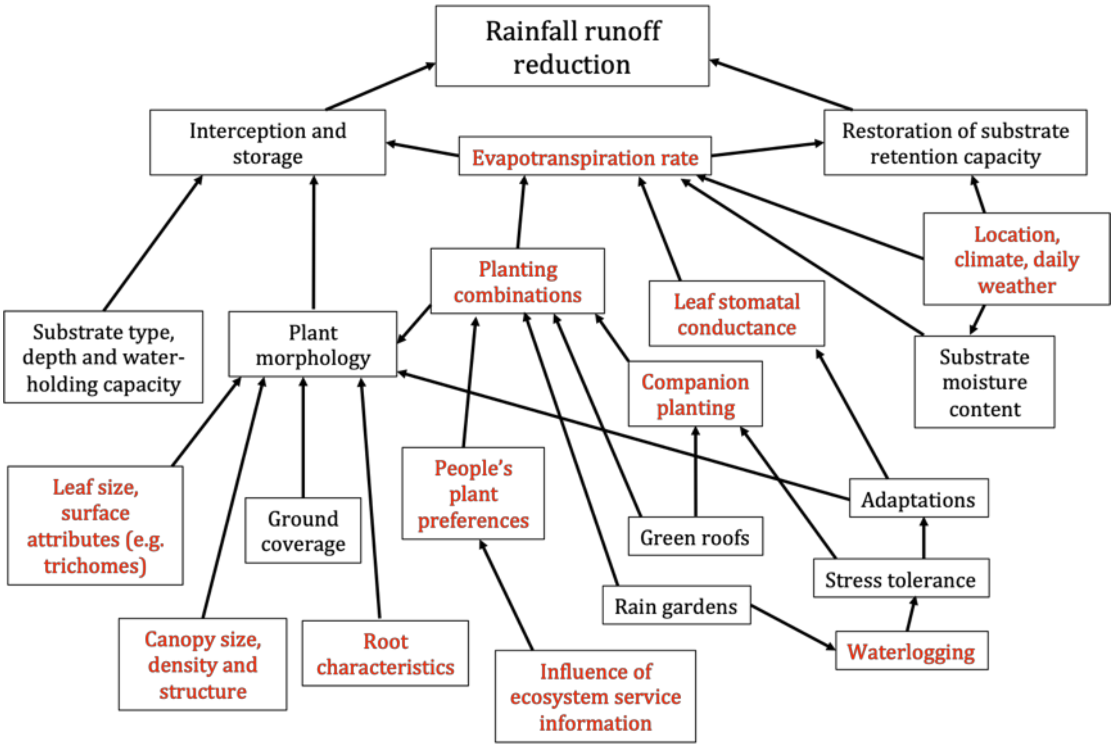


Figure 7.1: Schematic representation of factors influencing rainfall runoff reduction in domestic gardens. Variables in red were investigated in this study.

A review of the existing literature in chapter 1 indicated that the majority of these studies had been conducted in the context of green roofs. Despite this, several inferences could be made from that body of work, which would be relevant to the domestic garden context, particularly relating to the increased use of different perennial plants as alternatives to *Sedum* (Dunnett *et al.,* 2008; Farrell *et al.,* 2013; Kemp *et al.,* 2019; Ksiazek-Mikenas *et al.* 2023; Lundholm *et al.,* 2010). The review showed that these perennial plants, many of which were noted in the gardening literature to tolerate low moisture conditions, were able to provide greater rainfall retention than *Sedum* (Heim *et al.,* 2023; Kemp *et al.,* 2019; Lundholm *et al.,* 2010; MacIvor *et al.,* 2018; Schrieke & Farrell, 2021), whilst other research also showed their unexpected tolerance to short-term flooding (Dudrick *et al.,* 2024; King *et al.,* 2012; Nasrollahpour *et al.,* 2022; Yuan & Dunnett, 2018; Yuan *et al.,* 2017). Flood tolerance, and the potential ability of plants to continue transpiring and therefore continue to reduce runoff in these conditions could be particularly useful, as climate change in the UK is predicted to lead to increased heavier precipitation events and likelihood of flash flooding (IPCC, 2021; Kendon *et al.,* 2023; Webster *et al.,* 2017).

A typical domestic garden space would feature multiple plant species in designed planting beds (Rainer & West, 2015). An understanding of how the plants provide runoff reduction and also how different neighbouring plant species interact is essential for the application of this research into people's gardens. Several previous studies using a combination of plant types with different traits, including forbs, grasses and succulents, were carried out either in green roof settings (Dunnett *et al.,* 2008; Heim *et al.*, 2023; Lundholm *et al.*, 2010; O'Carroll *et al.,* 2023; Xie *et al.,* 2018) or companion planting experiments (Aguiar *et al.,* 2019; Butler & Orians, 2011; Matsuoka *et al.,* 2019 & 2020). Green roof experiments found that the combination of different leaf shapes, sizes and textures provided greater ground coverage and retention of rainfall in the canopy, whilst other plants with higher evapotranspiration rates and larger root mass were able to remove water more quickly from the substrate (Dunnett *et al.,* 2008; Heim *et al.,* 2023; Lundholm *et al.,* 2015; Nagase & Dunnett, 2012; Stovin *et al.,* 2015; Yuan *et al.,* 2017). A knowledge gap in the literature was the quantification of runoff reduction by perennial planting combinations during and after rainfall and whether this service continues to be provided in flooding conditions, and in a domestic garden setting rather than exposed to the harsh growing conditions of a green roof. The aim of this thesis was to identify the traits that could provide greater runoff reduction in mixed perennial planting beds. It was hypothesised that a combination of plant traits found in mixed planting would be able to provide greater rainfall retention due to the complimentary and combined action of multiple traits in one planting bed.

People's ornamental preferences have always been an important influence on what plants they choose for their gardens or homes (Berger *et al.,* 2022; Kendal *et al.,* 2012; Hoyle *et al.,* 2017b; Stobbelaar *et al.,* 2021; Zhang *et al.,* 2023). In a domestic garden, where homeowners have complete control of planting choices, understanding owners'/occupants' preferences is imperative. However, once understood, it is also important to know whether these choices could be influenced or changed towards more environmentally-driven ones based on additional environmental information. For example: does the newly-acquired awareness of the role of plant traits in the delivery of environmental benefits of gardens increase people's willingness to choose plants with those traits? Studies focusing on environmental behaviours such as reduction of food waste (Birau & Faure, 2018; Neubig *et al.,* 2020; Williams *et al.,* 2012) and reduction of littering (Cialdini, 2003; Cialdini *et al.,* 1990; Hartley *et al.,* 2015) found that the way environmental information was portrayed influenced outcomes. Furthermore, recommending actions that could be undertaken improved willingness of participants to engage in positive environmental behaviour (Frick *et al.,* 2004; Gimenez *et al.,* 2023; Hartley *et al.,* 2015; Nuebig *et al.,* 2020). Plant preferences are greatly influenced by the aesthetic appeal of the plants (Egerer *et al.*, 2019; Hostetler, 2021; Stobbelaar *et al.,* 2021; van den Berg & van Winsum-Westra, 2010), therefore influencing selection based on environmental benefits could prove challenging. The knowledge gap of whether planting choices could be influenced by ecosystem service information was essential to address to maximise the environmental benefits in domestic gardens. It was hypothesised that trait-based recommendations could lead to a change in planting preference, but that the look of a plant, in particular their flowers, would still influence choices.

7.2 Summary and synthesis

7.2.1 Plants with high evapotranspiration rates are able to quickly deplete substrate moisture but could be vulnerable to drought stress

The first aim of this thesis was to measure plant transpiration rates of widely used garden species with contrasting leaf and canopy characteristics and determine whether these differed in a range of UK summer temperatures. Higher transpiration rate has been linked to quicker depletion of substrate moisture content and thus an increase in its capacity to store further rainfall and to reduce surface water accumulation (Berretta *et al.,* 2014; Lundholm *et al.,* 2010; Stovin *et al.,* 2012; Thompson *et al.,* 2022). These results then informed planting combinations in chapters 4 and 5. In chapter 3, *Oenothera* and *Salvia* were found to rapidly deplete substrate moisture compared to other species in all three temperature regimes, whereas *Erysimum* had a significantly lower transpiration rate. However, in the 'medium' and 'warm' temperatures *Oenothera's* stomatal conductance rate of plants in 2 L containers decreased rapidly, with an average of 0.09 mol m^{-2} s^{-1} by day 2 in the 'warm' temperature and the plants quickly wilted, showing physical symptoms of water deficit (Matthews *et al.,* 1984; Seleiman *et al.,* 2021). The Royal Horticultural Society states that *Oenothera* can tolerate dry soils, but this did not seem to be the case, with *Oenothera* appearing intolerant to reduced moisture availability in the context of this experiment. In the field, *Oenothera* could be a water 'spender', utilising a deeper rooting system to access additional sources of water in drought conditions that enable consumption of larger volumes of water (Chapman & Augé, 1994; Nazemi Rafi *et al.,* 2019; Wiström *et al.,* 2023). This theory would correspond with existing gardening literature regarding the species' drought tolerance (Beth Chatto's Plants & Gardens, 2019 & 2022b; Díaz-Barradas *et al.,* 2020; Gambino & Vilela, 2011; Wallington, 2022). In this experiment, the plant containers restricted *Oenothera's* roots, and no additional sources of water were available, which could have resulted in *Oenothera* being unable to use its typical drought tolerance strategies. Further experimentation would be required to confirm this, and determine whether, in the field, *Oenothera* could help reduce surface water accumulation while also being able to tolerate periods of drought. If this were not the case then plants with a high transpiration rate, including *Oenothera,* would potentially require additional irrigation in periods of lower water availability.

7.2.2 Plants with leaf hairs and higher evapotranspiration rates are able to reduce rainfall runoff through better rainfall retention within the canopy and increase substrate water storage capacity, and mixed planting has the potential to decrease rainfall runoff volumes

Plants with leaf hairs, larger leaf area and higher evapotranspiration rates have been shown in previous research to increase rainfall retention and reduce runoff (Berretta *et al.,* 2014; Blanuša & Hadley, 2019; Kemp *et al.,* 2019; Nagase & Dunnett, 2012; Stovin *et al.,* 2012). Plants for experimentation were chosen to represent a range of physical traits (hairy or smooth leaves, evergreen or deciduous canopies), and the findings from chapter 3 showed that the plants could be additionally split into high or low transpiration rate groupings. In chapter 4 the plants were mixed into combinations of contrasting traits and subjected to controlled rainfall events. Mixed planting of *Pseudodictamnus* (hairy leaves, evergreen, low transpiration rate) and *Verbena* (smooth leaves, deciduous, higher transpiration rate) outperformed *Verbena* planted as a monoculture, significantly reducing runoff volumes in miniature model gardens. Mixed *Oenothera* and *Erysimum* (hairy leaves, deciduous, higher transpiration rate; and smooth leaves, evergreen, low transpiration rate, respectively) had significantly reduced runoff compared to *Erysimum* monocultures in the outdoor model gardens. However, in both experiments the *Pseudodictamnus* and *Oenothera* monocultures retained as much or more rainfall than the mixed planting. The leaf hairs of *Pseudodictamnus*, and the leaf hairs and higher transpiration rate of *Oenothera,* probably contributed to increased rainfall retention of these two species. The results indicate that mixed planting with specific traits can reduce runoff from a planting bed compared to other plants with a lower capacity to retain rainfall, but mixed planting does not outperform monocultures of plants with the beneficial traits. Existing literature also supports these results (Dunnett *et al.,* 2008; Heim *et al.*, 2023; Lundholm *et al*., 2010; O'Carroll *et al.,* 2023) but careful plant selection was necessary to ensure provision of the target ecosystem service, and random mixed planting without utilising specific traits could result in no improvement in retention or even a decrease in retention compared to certain monocultures (Dunnett *et al.,* 2008; Heim *et al.,* 2023; Nagase & Dunnett, 2012). The size of the plants and the season of rainfall application also significantly impacted the rainfall retention capacity of planting combinations.

7.2.3 Plants with high evapotranspiration rates are able to tolerate short-term subtotal flooding and act as companion plants

High evapotranspiration rates were found to be beneficial for plants surviving short-term subtotal flooding in spring and summer. In chapter 5 waterlogged *Verbena* and *Oenothera* continued to transpire at similar rates to their control counterparts both during and after flooding, whilst lower transpiring *Pseudodictamnus* and *Erysimum* almost entirely ceased transpiration during waterlogging. Combining high and low transpiring plants in mixed planting was found to aid the survival of the lower transpiring plants, and this was observed in the increased transpiration and assimilation rates of both *Pseudodictamnus* and *Erysimum,* as well as the reduced number of wilted plants post-waterlogging in mixed pairings compared to either plant as a monoculture. The higher transpiring plant appeared to act as a 'companion plant' in this scenario. Companion plants have been shown to support the survival of other plants in other stress conditions by increasing substrate moisture availability (Matsuoka *et al.,* 2019 & 2020; Muratet *et al.,* 2024) or reducing substrate temperate (Aguiar *et al.,* 2019; Butler & Orians, 2011), but this has predominantly been observed in water deficit rather than surplus water conditions. According to the horticultural literature, both *Oenothera* and *Verbena* prefer well-drained conditions and lower moisture availability, but they appeared unaffected by waterlogging in this experiment. Their high transpiration rates could potentially enable flood tolerance and could increase the planting palette used in gardens that are prone to flooding. The findings of chapter 5, alongside chapter 3, indicate a discrepancy between the horticultural literature and experimental results when comparing plant tolerance to environmental stress, with both *Oenothera* and *Verbena* more tolerant of excess substrate moisture than previously reported.

7.2.4 People are more willing to change their plant preferences after receiving environmental information and recommendations, but the impact of climate change is also a significant driver for selecting plants with environmental benefits

Chapters 4 and 5 addressed the hypotheses that plant traits, including higher evapotranspiration rates, and combinations of traits in mixed planting, could reduce runoff after rainfall or aid plant survival in short-term flooding. The influence of these findings on people's preferences for garden plants was explored in chapter 6, and it was determined that simple trait-based planting recommendations could influence people to change their preferences.

The type of information can impact environmental behaviours and has been observed by other authors (Hartley *et al.,* 2015; Hostetler, 2021; Lange *et al.,* 2022; Neubig *et al.,* 2020; Williams *et al.,* 2012). This literature and the findings of chapter 6 indicate that how environmental information is framed and disseminated (e.g. recommendations, or indication that the actions are easy to undertake), could encourage people to make planting choices which benefit the provision of ecosystem services. It was also found that people were more willing to select plants that could provide environmental benefits if they were either concerned about or impacted by climate change, and this was not influenced by the type of information they received in the experimental survey (Spence *et al*., 2011; Wong-Parodi & Berlin Rubin, 2022). It is likely that utilising a combination of environmental information and easy-to-action recommendations could lead to the greater uptake of trait-based planting choices in domestic gardens (Heo & Muralidhara, 2019; Lange *et al.,* 2022; Otto & Pensini, 2017; Samus *et al.,* 2023; Schrank *et al.,* 2023).

7.3 Recommendations

Specific plant traits including higher evapotranspiration rates and leaf hairs have been found from this project's experimental results and previous studies to provide greater runoff reduction (Blanuša & Hadley, 2019; Chu & Farrell, 2022; Kemp *et al.,* 2019; Nagase & Dunnett, 2012). In chapters 4 and 5 it was also found that combining plants with these traits had the potential in certain groupings to provide greater rainfall retention and also help the plants (monocultures and/or in mixed pairings) survive short-term subtotal flooding. Several recommendations from this research could lead to the development of a concept of more robust ornamental planting beds in private (and public) green spaces, in the face of increased flood risk (IPCC, 2021; Kendon *et al.,* 2023; Webster *et al.,* 2017). Additionally, findings relating to the use of environmental information to aid planting choices could help organisations (such as the Royal Horticultural Society in the UK, and others) to disseminate this information in the form of easy to undertake recommendations and thus help homeowners maximise the environmental benefits of their gardens.

7.3.1 Re-evaluate existing horticultural information to broaden plant environmental categorisation

The plant species selected for experimentation in this thesis were recommended for well-drained soils and could anecdotally tolerate drought (Beth Chatto's Plants & Gardens, 2019, 2022a & 2022b; Royal Horticultural Society, no date, e & h; Wallington, 2022), however the results for *Oenothera* and *Verbena* from chapters 3 and 5 did not support this. In chapter 3 *Oenothera* was found to have a higher transpiration rate and quickly deplete the substrate moisture content, and once there was limited water available the plants showed physical symptoms of water stress. Pot-bound roots and restricting access to additional water sources in our experimental context could have contributed (Chu & Farrell, 2022; Ksiazek-Mikenas *et al.,* 2021), but it might also be due to lower tolerance of selected plants' to reduced moisture availability than was previously thought. In chapter 5, neither *Oenothera* or *Verbena* were predicted to tolerate waterlogging, but both species appeared unaffected by short-term flooding, maintaining high stomatal conductance and transpiration rates that were comparable to control plants. A previous study also found *Oenothera* tolerant of short-term flooding (Yuan & Dunnett, 2018), but limited other research has been undertaken on the stress tolerance of either species or the traits linked to this.

Other authors too have found a discrepancy between horticultural literature and experimental outcomes (Cameron *et al.,* 2006; Schrieke & Farrell, 2021; Tabassum *et al.,* 2021; Watkins *et al.,* 2020). Drought-tolerant perennial plants of prairie origin such as *Rudbeckia* and *Liatris*, neither of which are known to be flood tolerant, also survived in waterlogged rain gardens (Dudrick *et al.,* 2024; Laukli *et al.,* 2022b; Nasrollahpour *et al.,* 2022; Yuan & Dunnett, 2018; Yuan *et al.,* 2017). Studies have also found flood-sensitive species can adapt to waterlogging (Bortolini & Zanin, 2019; King *et al.,* 2012; Watkins *et al.,* 2020; Yin *et al.,* 2009). If the commonality between all of these species was a single trait (such as a higher evapotranspiration rate) or combination of certain traits (high evapotranspiration rate, leaf hairs, taproots or long roots etc.) then this could be used to indicate potential flood-tolerance in other plant species. More research is required to confirm whether these broad patterns exist. It is recommended based on the outcomes of this thesis that a re-evaluation of the gardening literature is required, with additional information on plant survival and plant traits based on scientific evidence incorporated to ensure the right plant is planted in the right place. New literature would aim to challenge the way we think about cultivated plants, combining plant responses to the environment with field testing and evidence-based lived experience from institutions and practitioners, replacing many anecdotal resources with ecological knowledge. It would also aim to bring plant sciences and horticulture together and re-establish the latters important role in plant selection (Hitchmough, 2014). This would be more representative of new research, address information inconsistency, and increase the likelihood that gardens provide environmental benefits.

7.3.2 Incorporate plant traits and companion planting information when designing urban planting schemes

As mentioned above, the inclusion of plant traits within the gardening literature would increase the informed choices that gardeners could make about the planting within their gardens. The findings from this thesis could also have greater implications for plant selection, and influence design, in both domestic and public gardens.

Focusing initially on individual change, additional information added to the gardening literature could expand a gardener's planting palette and increase the potential environmental benefits provided by garden plants. Making this information available via reputable outlets could increase the dissemination of trait-based planting recommendations and contribute to changes in plant selection as indicated by chapter 6. Online sources such as the Royal Horticultural Society website and social media, media outlets including television and radio broadcasts, and print sources could all be utilised, as well as garden shows and garden centres where purchases could be directly influenced by this information (Lange *et al.,* 2022). Schemes such as the Royal Horticultural Society's 'Plant's for Pollinators' could be expanded to include plant traits, and these recommendations could help to maximise ecosystem service provision in people's gardens.

But how to target those people that do not garden or are not interested in environmental change? Other avenues are available if individuals are less willing to engage, including using a variety of information and messaging types to influence behaviours (chapter 6), as well as using the aesthetic appeal of plants as a gateway for people to recognise their ecosystem services (Frantzeskaki, 2019). Schemes to increase environmental gardening experience and knowledge, particularly for those people that do not consider themselves gardeners, has been discussed as a possible avenue to increase engagement, potentially via utilising local council or public health bodies (Frost & Murtagh, 2024; Samus *et al.,* 2023), as well as increasing the options available for gardening whilst occupying rental accommodation, which has been found to restrict undertaking gardening activities (Frost & Murtagh, 2024). As the effects of climate change are more widely felt, this is also likely to increase people's awareness and willingness to engage with environmentally beneficial behaviours (chapter 6; Spence *et al*., 2011; Wong-Parodi & Berlin Rubin, 2022).

For industry professionals, including garden designers, industry bodies such as the Society of Garden Designers could disseminate trait-based planting information to their members. Garden designers could then incorporate more planting schemes with ecosystem service information in mind, and this would also be an opportunity to bring together service provision, plant survival and companion planting to ensure robust displays that maximise benefits. Popular planting designs that incorporate scientific research have already proven influential on garden design, including the naturalistic but strategically designed schemes at Olympic Park, the Barbican Centre, and the High Line, all of which incorporate ecological findings on plant interactions to provide high impact, aesthetically pleasing spaces (Rainer & West, 2015).

Policy change has been recommended to improve public spaces and domestic gardens (Cameron, 2023; Dixon, 2022; Egerer *et al.,* 2021). It has been argued that individual willingness to make environmental improvements can only go so far, and that due to the increased threat from climate change, larger policy change is necessary (Cameron, 2023). Reducing impervious surfaces and increasing vegetation could significantly reduce surface water accumulation (Kelly, 2016; Perry & Nawaz, 2008; Simpson & Francis, 2021). However, policy change of this nature would only work successfully in conjunction with nationwide infrastructural change such as better (subsidised) public transport links and walkable urban areas to reduce dependence on cars and demand for car parking, and improved environmental schemes (green infrastructure, water runoff capture and recycling of whole urban areas rather than emphasis on water butts or SUDS within individual property boundaries, etc.), that provides a holistic approach to environmental improvement (Cameron, 2023; Egerer *et al.,* 2021). One of the main drivers for increased impervious surfaces in front gardens is the need for driveways (Chalmin-Pui *et al.,* 2021a; Perry & Nawaz, 2008; Phillips *et al.,* 2023), and to replace this with vegetation would require increased access to public transport and/or emphasis on walking and cycling as an alternative means for travel. In 2021 the UK government proposed plans for increased cycling infrastructure with the aim that half of all journeys in urban areas were walked or cycled by 2030, and implementing net zero emission buses with supporting additional infrastructure (Department for Transport, 2021). These nationwide policy changes, in addition to those for domestic gardens, must be viewed as pieces of a larger picture that need to work together to ensure success. For example, reduced car ownership could result in increased vegetation in front gardens, which could lead to a significant reduction in generated runoff; people could utilise the increased availability of public transport or cycling infrastructure to ensure that loss of car ownership does not deprive them of access to work or services.

Based on the research from this thesis a combination of approaches at different levels is recommended, with each stakeholder contributing towards the environmental improvement of green spaces. Policy changes at government and local authority levels will set guidelines, industry bodies such as the Royal Horticultural Society can make recommendations and disseminate information, and individual change could be influenced by the type of information available, climate concern, the aesthetics of the plants used, and the tendency for popular garden designs to be copied, all of which could be utilised to result in planting preference and behavioural change within domestic gardens.

7.4 Issues and methodological limitations

Experimental design, particularly in controlled pot experiments compared to field trials, is likely to result in limitations that restrict direct comparisons with plants in domestic gardens (Annunziata *et al.,* 2017; Siebert & Ewert, 2014). This section discusses overall limitations of the experimental methodologies and their impacts on experimental results. Individual limitations for each experiment are discussed in the relevant chapters.

7.4.1 Controlled experimental conditions do not fully represent environmental conditions experienced in domestic gardens

As mentioned in chapter 1, heavy rainfall and flash flooding are predicted to become more frequent due to climate change; in the summer months these could also be coupled with periods of reduced rainfall and increased temperatures resulting in drought conditions (IPCC, 2021; Kendon *et al.,* 2023; Webster *et al.,* 2017). In chapters 4 and 5, plants were subjected to excess water in both rainfall and subtotal flooding experiments. Current climate change scenarios, however, predict that periods of heavy rainfall and potential flooding will increasingly occur after periods of reduced rainfall or drought, and these were not tested together in this thesis. Drought and heat could lead to a dry upper soil layer that repels rainfall and increases surface runoff when rainfall does occur (Thompson, 2022). Heat and water deficit stress occurring together physiologically damage plants (Hatfield & Prueger, 2015; Taiz & Zeiger, 2002), and subsequent flooding could increase this (Bester *et al*., 2024; Dickin & Wright, 2008; Lewis *et al.,* 2019; Shao *et al.,* 2023). Quantifying the response of test plants to both conditions in succession is therefore recommended to fully represent changing UK summertime conditions and understand plant stress responses. Whether plant species could survive water deficit followed by waterlogging, or whether companion planting could aid with stress tolerance in both conditions is to be determined. Previous research has found that water deficit and waterlogging in combination can result in more damage to plants than either stress alone (Bester *et al.,* 2024; Dickin & Wright, 2008; Shao *et al.,* 2023), and this combined effect was observed through impaired stem development and yield loss in maize and wheat (Dickin & Wright, 2008; Shao *et al.,* 2023). This is not the case for all plants, and for the tree species *Fagus sylvatica,* it was found that only summer drought significantly reduced growth rates, whilst waterlogging had little impact (Scharnweber *et al.,* 2013). How 'drought-tolerant' perennial plants respond to combined stressors is therefore not straightforward to predict. Environmental conditions tested in isolation, whilst useful to determine plant responses, are not fully representative of real-world conditions and should be tested together in future experimentation.

7.4.2 Experimentation was conducted in controlled environments with peat-free compost and primarily in pots or containers.

7.4.2.1 How would peat-free compost affect plant responses to the experimental treatments?

Peat-free compost was used as the growing medium for all experiments to ensure a standardised control substrate that also reduced environmental damage. Many nurseries now use peat-free media to grow herbaceous or perennial plants, but for investigating plant stress tolerance it might not represent growing conditions in domestic gardens. Different soil types, e.g. contrasting sand or clay soils, have different water holding capacities (Berretta *et al.,* 2014; Dusza *et al.,* 2016; Monteiro, 2017; Poë *et al.,* 2015; Stovin *et al.,* 2015). The experimental plants, according to the guidance provided by the Royal Horticultural Society, are well suited to grow in sand, loam or chalk soil, but not clay. Testing these plants in different soil types could alter plant responses, or alternatively it could be determined that these plants can tolerate more substrate types than previously cited. Discrepancies between the gardening literature and experimental results have already been identified in this thesis, and substrate type could also fall into this category. This should be explored to enable the experimental results to be more applicable to a range of UK gardens.

7.4.2.2 How could pots and miniature model gardens have affected plant responses to experimental treatments?

The use of pots and containers to grow plants, whilst necessary to conduct these experiments, may have compromised plant growth and restricted root growth (Chapman & Augé, 1994; Chu & Farrell, 2022; Ksiazek-Mikenas *et al.,* 2021) and created studies that examined irrigated pots rather than domestic gardens. Some of the plants grown from nursery stock in 2021 were found to be pot-bound, with stunted roots even in larger pots, and this was suspected to be due to the small containers the plants were grown in for an unspecified period of time prior to purchase. To overcome this, plants were subsequently grown from cuttings for experiment 2 and all experiments in 2022 and 2023. In chapter 3, *Oenothera* decreased the substrate moisture within a couple of days in 'warm' temperatures and subsequently wilted, but the literature indicated this was a drought tolerant species. *Oenothera's* roots could have been restricted by the size of the pot and the species could have shown greater tolerance to water restriction if adequate roots formed prior to experimentation, or the experiment was conducted in the field, enabling the taproot or long roots to seek out other sources of moisture. In chapter 4's miniature model gardens and chapter 5's pot experiments, faster growing *Verbena* became pot-bound, and this would have reduced plants' water absorption. Using larger pots was not possible as their greater size and weight risked injury through manual handling, however field experiments without restricted root access could have potentially changed the responses of some of the plants tested. Field experiments would have also allowed for a longer period of recovery monitoring post-waterlogging in experiment 7b, which was not possible in the iterations in this thesis due to pot-bound *Verbena* and *Oenothera*, and this could have determined whether given a longer time period the lower-transpiring *Erysimum* and *Pseudodictamnus* would have exhibited stomatal recovery. Potted plants watered to field capacity and then tested in high stress conditions may not also give the plants suitable time to acclimate as they would do in the field, which could change their responses and not fully represent how plants would behave in garden conditions.

7.4.3 Plant selection could incorporate ecological context in addition to trait information

Popular UK garden plants were selected for this thesis based on their contrasting traits for potential ecosystem service provision. These traits were also used as possible explanations for the plants' stress responses to waterlogging and drought, therefore the traits were assessed for two different aspects - aiding plant fitness and survival (stress tolerance) and service potential (ecosystem services). However ecological behaviour, in this context response to stress, is not necessarily determined at the species level but can be determined at population or ecotype level (Ahrar *et al.,* 2017; Liancourt *et al.,* 2013) and exploring evolutionary history and ecological frameworks in addition to traits could facilitate selection of a broader range of plant species.

Whilst the selected plants had similar environmental preferences (full sun, moist to well-drained substrate) to enable comparisons, these were based on horticultural literature, which has previously been discussed as not always reliable. Utilising a framework such as Ellenberg's Indicator Values (Hill *et al.,* 1999) or others (Dengler *et al.,* 2023; Scherrer & Guisan, 2019) allows the evaluation of various environmental factors (environmental indicator values including soil moisture, temperature, light, salinity etc.) that impact the performance of a plant in its realised niche and provides classification values along an environmental gradient. Combining trait research and environmental indicator values could identify where experimental plant species lie on the soil moisture gradient and whether their ability to tolerate waterlogging or drought was linked to ecological habitats. This could be investigated using species distribution models to explore environmental factors (WorldClim, 2024). For example, despite *Verbena bonariensis* being categorised as a drought tolerant plant in UK gardening horticulture, it naturally occurs in the subtropical biomes of Argentina and South America in damp grassland and along riverbanks, which could explain the waterlogging tolerance and high transpiration rate whilst also tolerating drought (GBIF, no date; Royal Botanic Gardens Kew, no date).

In addition to this, further research on understanding stress tolerance and natural conditions of populations of prairie plants could help explain the waterlogging tolerance observed in *Oenothera*. Prairies are not homogenous, and communities of plants respond to the wet, dry or mesic habitat they grow in (Hitchmough *et al.,* 2004; National Geographic, no date). *Oenothera* naturally occurs in Texas and Louisiana, which experiences high summer rainfall (Royal Botanic Gardens Kew, 2007; World Weather Information Service, 2024) and therefore could support the flood tolerance shown in Chapter 5. Climate analogue models could also prove useful for ensuring we select plants to test that are able to tolerate future climate conditions in the changing UK climate, both in warmer summers and wet winters (Copernicus, no date; Fitzpatrick & Dunn, 2019; Ramírez-Villegas *et al.,* 2011). Selecting plants with certain traits from these locations could help identify plants that survive certain stressors and provide ecosystem services in the UK.

7.4.4 Plant size and combinations could have limited experimental findings

Plants used in these experiments were relatively small and this could have limited the significance of results, in particular for the miniature model gardens. Investigating mature plants was difficult to implement with the existing experimental procedure but larger plants and leaf area have been shown in previous research to provide significantly greater canopy rainfall retention (Blanuša & Hadley, 2019; Heim *et al.,* 2023; Lundholm *et al.,* 2010; Nagase & Dunnett, 2012; Yuan *et al.,* 2017) and this is discussed in chapter 4. There is also still the question as to whether plant traits (such as leaf hairs or higher evapotranspiration rate) are more important than plant area or size, and although inferences were made about potential impact of increased scale of planting areas, the small plant sizes limited physical complexity. Replicating plant layering (ground, middle, emergent) to maximise surface area coverage and represent planting as it grows in domestic garden beds is something that could be considered in future experiments to continue this research beyond individual plants and paired taxa combinations.

7.5 Opportunities for future work

There are several areas of future research that could follow on from the findings in this thesis. This project focused only on perennial plants, and research could be expanded further to investigate different plants such as shrubs, trees, grasses or ferns, or plants that prefer different environmental growing conditions. All plants in this thesis were suitable for well-drained soils and were investigated for additional waterlogging tolerance, thereby quantifying whether they would survive and thrive in a changing UK climate. This could be explored in reverse, using plants that prefer waterlogged substrate tested for rainfall retention and drought tolerance as well, using habitat frameworks to source lists of possible species and then investigate traits and their link to ecosystem services. In addition to increasing the tested planting palette, investigations with mixed planting could be explored using a combination of different plant groups (shrubs, trees, perennials, grasses, ferns etc.). This would make it comparable to domestic garden planting and has already been found in certain combinations to increase runoff retention in some green roof studies (Heim *et al.*, 2023; Lundholm *et al.,* 2010 & 2015). Mixed shrub and herbaceous planting has also been found to increase substrate moisture availability and reduce substrate temperatures in summer (Nazemi Rafi & Kazemi, 2021). It would be useful to develop on this to broaden our understanding of planting interactions and determine if runoff reduction service provision is linked with particular plant traits such as evapotranspiration rate and leaf hairs, like this thesis found for perennial plants, or whether the size of the plants has a greater impact on retention. Increasing planting in this way would also increase the surface area coverage and create ground, middle and emergent layers, which is an important aspect of planting design.

As mentioned in the limitations section (section 7.4 above), both the environmental conditions and substrate tested may not have been representative of domestic gardens or predicted climate change conditions. *Oenothera* and *Verbena*, with their higher transpiration rates, supported *Pseudodictamnus* and *Erysimum* in waterlogged conditions, and it would be interesting to determine whether this companion planting support may also occur in reverse when testing drought. Do the lower transpiration rates of

Erysimum and *Pseudodictamnus* provide the necessary moisture availability for *Oenothera* and *Verbena* during drought, and when testing drought followed by waterlogging are the plants able to switch from their roles as stress intolerant to stress tolerators and companions? This would provide a comprehensive test of evapotranspiration rates and determine its role in service provision and stress tolerance. Substrate type also impacts how much water is retained and can affect plant survival (Poë *et al.,* 2015; Stovin *et al.,* 2015). This leaves scope for future work testing these plants and their traits in different substrates, to determine if this would produce different outcomes compared to control compost.

Rainfall retention and runoff reduction responses have been tested on several types of plants in different experimental settings including green roofs (Kemp *et al.,* 2019; Ksiazek-Mikenas *et al.* 2023; Lundholm *et al.,* 2010; O'Carroll et al., 2023), rain gardens (Bortolini & Zanin, 2019; Laukli *et al.,* 2022b; Nasrollahpour *et al.,* 2022; Yuan & Dunnett, 2018), hedgerows (Blanuša & Hadley, 2019), and model gardens (chapter 4). Flood tolerance has also been examined in perennial plants (Bortolini & Zanin, 2019; King *et al.,* 2012; Yin *et al.,* 2009 & 2012; Yuan & Dunnett, 2018), trees (Li *et al.,* 2021; Lukac *et al.,* 2011), and crops (Else *et al.,* 2009; Geng *et al.,* 2023; Ide *at al.,* 2022; Li *et al.,* 2023). Simple modelling studies could be developed with the resulting data to quantify the potential impact of these plants in combinations to reduce runoff in different UK climate scenarios. Such modelling studies could link a vast catalogue of plant trait information to different plant types and sizes, thereby combining plants together and predicting outcomes in a way that would be limited when measuring in individual model gardens. Plant densities and the number of traits could be increased with greater ease than in experimental studies, and additional layers of information could be included that have been excluded from previous studies for the sake of experimental focus, such as different soil types, pollinator interactions, and weather and climate predictions. The latter, as mentioned above, could also begin to quantify the stress impacts of drought and heat followed by flooding. These studies could also help tackle the question of scale that the experiments in this thesis were only able to speculate on, helping to develop a bigger picture of how these plant traits and perennial plants might work together across the approximate 30% of UK urban areas covered by domestic gardens (Chalmin-Pui *et al.,* 2021a), and enable us to see the potential impact of beneficial planting on a city scale.

Chapter 6 discussed the potential to utilise plant-trait recommendations to increase environmentally beneficial plant purchases for domestic gardens, and how this information could be disseminated to the public is another potential area of further study. As previously discussed, existing information schemes such as the Royal Horticultural Society's 'Plants for Pollinators' (Anderson *et al.,* 2020; Royal Horticultural Society, 2019; Salisbury *et al.,* 2017) have used insect pollinator research and popular garden plants to create easy to follow guides that help gardeners select plants with these benefits in mind. This format or similar could be tested with traits for provision of other ecosystem services, and in the case of this project's continued research, rainfall retention traits could be the focus of in person trials in a commercial setting to determine if the responses from the survey in chapter 6 are representative of people's purchasing behaviour (Lange *et al.,* 2022). Impact of education and other demographic factors would also be useful to explore using a market research company to sample nationally representative populations for all demographics to determine if, for example, those with a higher education respond more positively to trait-based information and recommendations.

7.6 Concluding remarks

This thesis intended to establish the role of perennial planting in the provision of rainfall retention ecosystem service delivery in domestic gardens, and take into account people's planting preferences as part of this research. It was shown that this is an interdisciplinary subject, combining aspects of plant physiology including study of plant traits and stress responses, planting design, ecology (including species interactions and companion planting), and psychology with the incorporation of different types of knowledge on plant selection outcomes. This work produced further evidence supporting the role of specific plant traits in improving rainfall retention, and also highlighted the range of stress tolerance that certain plants, specifically those with higher evapotranspiration rates, can have. This work also showed the impact of climate change on people's planting choices, and the effectiveness of simple planting recommendations. There was also further support for the notion that there is a discrepancy between the horticultural literature and experimental findings. Perennial plants have been found to deliver runoff reduction provision, and combinations of plants may increase this beneficial outcome, but to maximise the environmental benefits of domestic gardens there needs to be a collaboration between different fields of research to ensure plant survival, service provision, and the satisfaction of homeowners.

7.7 Practical recommendations for gardeners

- Water retention can be promoted by more complex, 3D vegetation structures. Gardeners may wish to increase the complexities of their plantings (e.g. meadows rather than close, fine-mown lawns) to help reduce runoff. This combined with other features, such as stormwater planters, rain gardens and detention ponds might be worth considering if they feel localised flooding is a threat to themselves or their neighbours.
- Combinations of plants with different traits can reduce rainfall runoff. Gardeners should consider planting mixtures of plants with different leaf textures, including leaf hairs and ridges, to capture a greater volume of rainfall droplets within the canopies compared to smooth leaved plants alone. This could, along with other features to mitigate runoff, help reduce localised flooding.
- Plants with higher evapotranspiration rates (considered 'thirsty' as they have a high water use) appear to reduce surface water accumulation or localised flooding. Gardeners could plant a selection of species with higher water use into their planting beds, particularly in zones prone to flooding, or surrounding impermeable surfaces such as driveways or patios to utilise rainfall runoff from these areas.
- Combinations of plants with different water use can potentially support each other's growth and survival in periods of short-term flooding or drought due to their different water demands. Plants with higher evapotranspiration rates and high water use ('thirsty' plants) planted

alongside species with a lower water use (lower evapotranspiration rates) can remove excess water from the substrate during periods of high rainfall and help plants with a lower tolerance to waterlogging survive these conditions. Conversely, plants with lower water use do not take up as much water during periods of drought, leaving a slightly higher volume of water available in the substrate for 'thirstier' plants, which can prevent the latter from wilting. Gardeners may want to consider planting species with different water demands into their planting beds to create companion planting that support overall survival.

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A.1 Experiment 7a - Summer short-term subtotal flooding post-heat wave results (additional data, chapter 5).

After the heat wave of July 2022 three plants per treatment and layout were maintained on control irrigation for 8 weeks to monitor the recovery and regrowth of the plants after short-term subtotal flooding followed by heat stress. This was the end of the summer season, and determined to be a long enough period of time post-waterlogging to test the responses and determine the difference between the mixed plants compared to the monocultures after heat stress. At the end of 8 weeks plants were destructively harvested for aboveground biomass and roots. Photographs of plants at week 0 and week 8 were used on the WinDIAS 3 Image Analysis System (Delta-T Devices, Cambridge, UK) to determine percentage change in leaf greenness, which equated to plant regrowth. Data were analysed using R (R Core Team, 2021) with two-way ANOVA (treatment and species layout) and post-hoc Tukey HSD tests.

Dry aboveground biomass

Waterlogged *Erysimum* dry aboveground biomass (shoots and leaves) was significantly reduced compared to control plants (average of 1.11 g less, $p = 0.038$) (Figure 1). *Oenothera* and Mixed control and waterlogged biomass were not significantly different between treatments (*Oenothera* $p = 0.60$, Mixed $p = 0.70$). *Erysimum* control plants were also found to have a significantly larger dried mass than the *Oenothera* and Mixed waterlogged plants ($p = 0.032$ and $p = 0.08$ respectively).

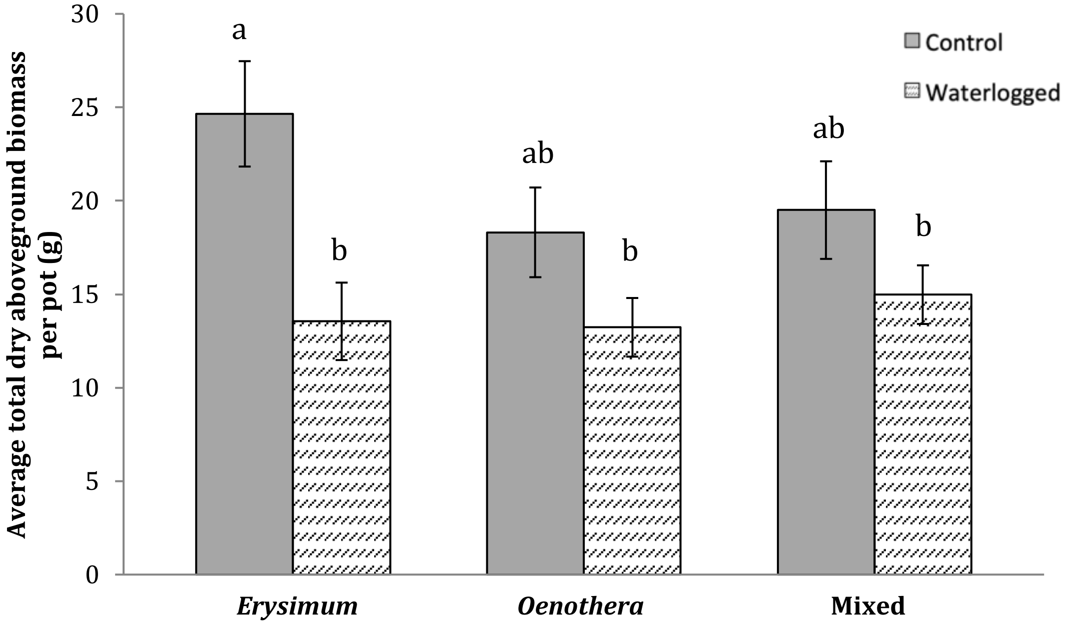

Figure 1: Mean total dried stem and leaf biomass per pot 8 weeks post-heat wave, and associated standard error of the means (n = 3 per layout). Treatments sharing a letter were not significantly different from one another.

Dry roots biomass

Waterlogged *Erysimum* dry root mass on average weighed 1.60 g per pot, significantly lower per pot compared to *Erysimum* control plants at 4.51 g (p = 0.05) (Figure 2). *Oenothera* and Mixed waterlogged plant roots, although weighing less than their control treatment counterparts, were not significantly different overall (p = 0.94 and p = 2.94 respectively). All waterlogged roots weighed less than the control roots but were not significantly different from each other (p = 1.00).

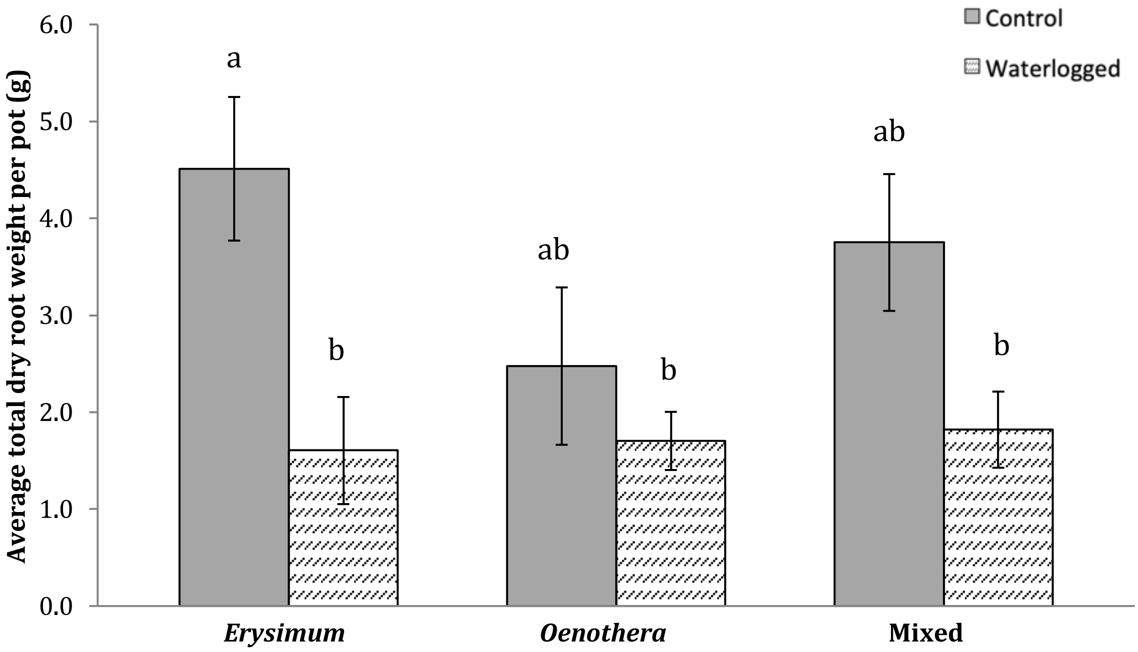

Figure 2: Mean total dried root biomass per pot 8 weeks post-heat wave, and associated standard error of the means (n = 3 per layout). Treatments sharing a letter were not significantly different from one another.

Dry green leaf weight

Dried biomass was weighed per pot (Figure 1), but the green leaves of each plant were also separated and weighed, resulting in average total dry green leaf weight per pot. Leaf greenness was equated with plant recovery post-heat wave. *Erysimum* control plants had the largest dried green leaf mass per pot at 6.17 g, and were significantly larger than all layouts ($p \leq 0.016$) except for Mixed control pots ($p = 0.380$) (Figure 3). *Erysimum* control and waterlogged plants had the significantly largest green leaf mass difference between treatments with waterlogged pots 5.12 g less than control ($p = 0.004$). Mixed waterlogged pots had significantly less dry green leaf weight than Mixed control ($p = 0.079$) but *Oenothera* control and waterlogged pots were not significantly different ($p = 0.968$). All waterlogged treatments were not significantly different from each other ($p = 1.00$).

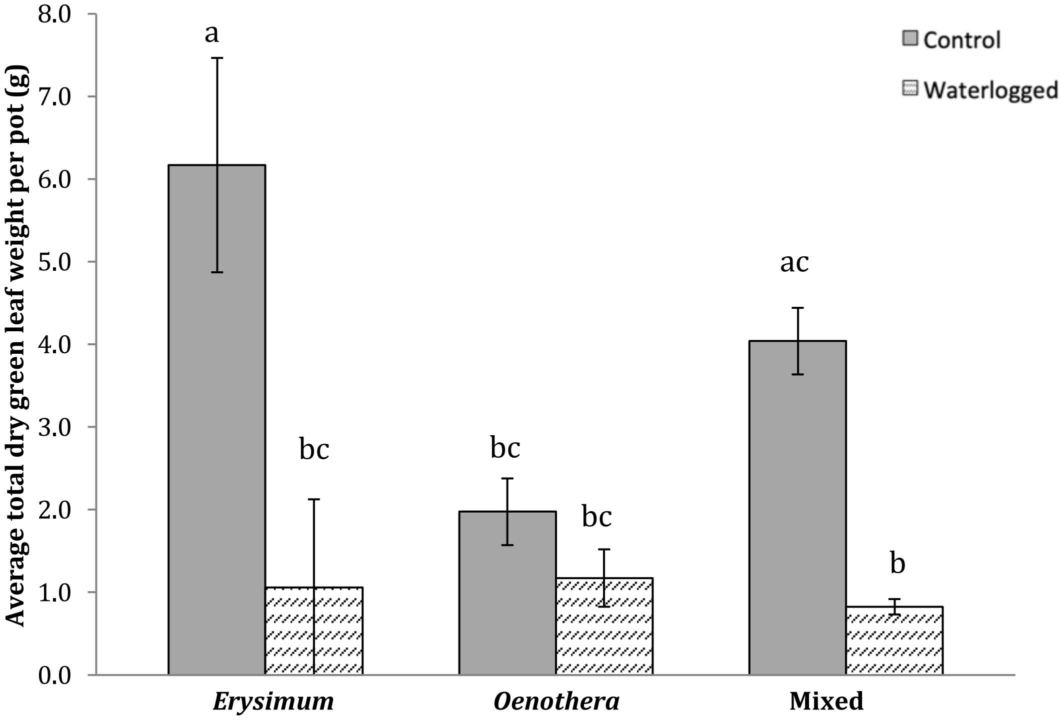

Figure 3: Mean total dried green leaf mass per pot 8 weeks post-heat wave, and associated standard error of the means (n = 3 per layout). Treatments sharing a letter were not significantly different from one another.

Green leaves (percentage change)

The percentage difference in leaf greenness between week 0 and week 8 post-heat wave was analysed to indicate plant regrowth, with dead leaves discounted and new green leaves counting towards the total percentage change. Although all plants and treatments had varying regrowth percentages, the variation between the results was large and therefore overall, not significant (p = 0.58) (Figure 4). *Erysimum* control treatment had the least change in leaf greenness, maintaining almost the same leaf greenness at week 0 and week 8 post-heat wave, and *Erysimum* waterlogged treatment had the largest percentage decrease.

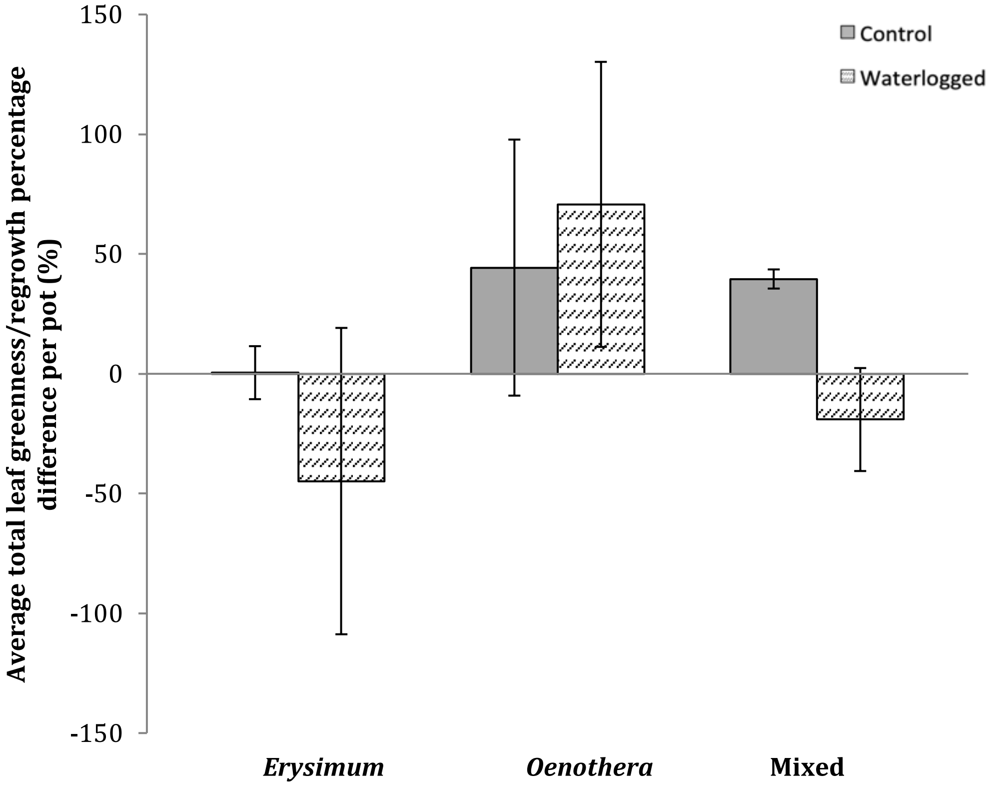

Figure 4: Mean total leaf greenness/regrowth percentage difference per pot between week 0 and week 8 post-heat wave, and associated standard error of the means (n = 3 per layout).

A.2 Survey questions used in Chapter 6

Category	Questions
Gender	What is your gender?
Age	What is your age group?
Education	What is your highest level of education?
	Do you hold any qualifications (professional qualification or university degree) in biology, environmental sciences, landscaping, gardening, garden design or similar?
Interest in gardening	Does the property where you live have a garden?
	On average how many hours a week do you spend in a garden? This can include gardening, sitting or relaxing in your garden, etc.
	Do you consider yourself to be a gardener or enjoy gardening?
	Do you have plants in a garden? (This can be at home, a workplace, or other location) *[skip next question if No is selected]*
Plant knowledge pre-information	How much do you agree with the following reasons why you have plants? (L-5) • I like the look or scent of the plants • I believe plants improve health benefits that people get from the environment • The plants provide fruit and vegetables to eat
	How much do you agree with the following statements about plants in a garden setting? (L-5) • Plants can benefit wildlife (habitats, food sources, etc.) • Plants can reduce the risk of localised flooding • Plants can reduce air pollution • Plants can reduce noise pollution • Plants can reduce air, ground, and building temperature
Plant selection pre-information	The photos below show popular UK garden plants. Please select the plant you like the most.
	Using the plant you selected, how much do you agree with the following statements about the plant's appearance? (L-5) • I like the plant's growth habit (e.g. bushy) • I like the plant's colour • I like the plant's leaf shape • I like the plant's flower
Plant traits	These photos show the leaves of each plant, some of which are hairy. How much do you agree with the following statements? (L-5)

	- I like plants with hairy leaves - I believe plants with hairy leaves can improve the environmental benefits of gardens
	How much do you agree with the following statement? (L-5) - I believe 'thirstier' plants can improve the environmental benefits of gardens
	Certain plant characteristics can improve the impact that plants have on the environment around them. Please select all the plants from the list below that you think could help reduce surface water and localised flooding in a garden.
System information and climate change views	Climate change is resulting in hotter drier summers and warmer wetter winters in the UK. Five of the hottest years on record in the UK since 1884 have all occurred since 2006 (2022, 2015, 2006, 2020 and 2011). A new high of 40°C was reached in the UK last year. Rainfall events at an intensity to cause flash flooding are predicted to be 4 times more frequent by 2070. An example of this occurred in July 2021 when a month's average rain fell in one hour in London, flooding the roads and underground network. Are you concerned about the impact of climate change? Plants can provide environmental benefits, however people are removing vegetation from their gardens and replacing them with impermeable surfaces. Examples include paving and tarmac for driveways and patios, and artificial grass replacing lawns. This stops rainwater filtering into the soil and results in increased flood risk. Have you personally experienced/noticed the effects of climate change? (for example, flooding/flash flooding).
Action-related information and climate change views	Climate change is resulting in hotter drier summers and warmer wetter winters in the UK, causing heat waves and flash flooding. Five of the hottest years on record in the UK since 1884 have all occurred since 2006 (2022, 2015, 2006, 2020 and 2011). Rainfall events at an intensity to cause flash flooding are predicted to be 4 times more frequent by 2070. Plants can provide environmental benefits, including reducing flooding and air pollution, and improving biodiversity. However, people are removing vegetation from their gardens and replacing them with impermeable surfaces.

	Examples include paving and tarmac for driveways and patios, and artificial grass replacing lawns. This stops rainwater filtering into the soil and results in increased flood risk. Are you concerned about the impact of climate change? Have you personally experienced/noticed the effects of climate change? (for example, flooding/flash flooding). Certain plant characteristics can help with this. Plants with naturally hairy leaves can capture pollution particles, removing them from the air, and collect rainwater droplets, preventing them from falling to the ground and contributing to flooding. Recommendation: Use plants with hairy leaves in your garden to help reduce air pollution and flooding. Plants that use more water, considered 'thirsty' plants, can remove water more quickly from the soil. This in turn helps reduce soil saturation and likelihood of flooding. Recommendation: Use 'thirsty' plants in your garden to help reduce surface water accumulation that leads to flooding.
Plant selection post-information	The photos below show popular UK garden plants. Based on the information you have now read, please select the plant you like the most.
	Has your preference for the plants changed after reading the environmental information? *[skip next question if No is selected]*
Plant preference drivers	What are the reasons why your plant preference has changed? (L-5) • I find this plant more attractive • This survey's information changed my preference • This plant's characteristics can provide environmental benefits • This plant better suits my garden's conditions (e.g. my garden experiences flooding or high pollution and this plant could help mitigate this)
Plant knowledge post-information	How much do you agree with the following statements about garden plants? (L-5) • Plants can reduce the risk of localised flooding • Plants can reduce air pollution • In the future I would select certain plants for my garden based on their environmental benefits