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A study on the effects of species, plant density, population size and species mixture on the morphological, physiological and thermal performance of six woody shrubs growing on rooftops in Sheffield, UK

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Abstract

Urbanisation destabilises natural environments and causes the loss of ecosystem services. Green roofs are engineered structures that allow vegetation growth on rooftops and contribute to the recovery of ecosystem services, including temperature abatement for building energy savings. The present study evaluated the morphological, physiological and thermal performance of six woody shrubs growing in 300-mm substrate in containers placed on two campus building rooftops at the University of Sheffield, UK. Temperature sensors placed on bare substrate and above and beneath shrub canopies measured temperatures between January 2016 and August 2018 to assess the cooling and insulating ability of each species in the summer and winter, respectively, compared to bare substrate. Plant morphological and physiological parameters were measured in the summer to observe the effects of species, plant density, population size and species mixture on plant fitness and survival. The study also observed the same effects on the temperature profiles of the different species to evaluate shrub thermal performance. Results showed that shrubs effectively reduced extreme temperatures, with higher plant density having a greater cooling and insulating effect in the summer and winter, respectively, with maximum cooling over 25 °C in the summer and maximum insulation up to 3.5 °C in the winter compared to bare substrate. The attenuating effect on temperatures by the shrubs was most evident in the summer and in extreme warm weather, with higher plant density delaying the reaching of maximum temperatures more compared to lower plant density. There was a species-specific difference in shrub thermal performance, due to a combination of morphological canopy characteristics (leaf area index, plant height, leaf thickness) and physiological sensitivity in responding to plant density and species mixture. These findings could lead to a more widespread use of woody shrubs as green roof vegetation and to the improvement of green roof thermal performance.

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Declaration

I, the author, confirm that the Thesis is my own work. I am aware of the University's Guidance on the Use of Unfair Means (www.sheffield.ac.uk/ssid/unfair-means). This work has not been previously presented for an award at this, or any other, university.

1 Introduction and rationale of the research project

There are increasingly more studies in green roof research focusing on criteria for plant selection based on plant functional traits (Caneva et al. 2015; Lundholm, Tran and Gebert 2015; Savi et al. 2015; MacIvor et al. 2016). However, relatively less research is undertaken to encourage the use on green roofs of taller, more complex and long-lived growth forms like shrubs, or even trees, and the studies that do usually are aimed at their use on highly intensive roof gardens (e.g., Jim and Tsang 2011, Nagase and Nomura 2014, Lee and Jim 2018), because substrate depth is considerably deeper than that of extensive systems and guarantees shrub survival. Chances of promoting shrubs on green roofs becomes slimmer if local government is better disposed towards the inclusion of an extensive or semi-intensive design in its building policy so as to cut construction and maintenance costs (Cao et al. 2014; Li, Bou-Zeid and Oppenheimer 2014; Peng and Jim 2015; Simmons 2015; Cascone et al. 2018; Teotónio et al. 2018), likely precluding the inclusion of shrubs in the selection process. However, while the studies on the cooling/insulation provided by shrubs as green roof vegetation are relatively few and/or are conducted in non-temperate climates (e.g. Wong et al. 2003, Jim and Tsang 2011a, 2011b; Jim 2012; Vaz Monteiro 2017; Huang, Chen and Liu 2018; Lee and Jim 2018), a few studies have shown that drought-tolerant shrubs can have relatively high growth and survival rates on even nutrient-poor and shallow green roof substrate (Savi et al. 2015, 2016), with some evidence that shrubs can provide significantly greater cooling compared to herbaceous perennials or other low-growing plants (Love 2015; Huang, Chen and Liu 2018). Moreover, there are few studies evaluating the role of vegetation in rooftop insulation in the winter, often solely in relation to snow cover effect (e.g. Lundholm et al. 2014, Eksi et al. 2017), with contradicting results (e.g. Sailor 2008) and with no studies to date having tested shrubs specifically in the winter context. There is also no evidence of how shrub canopy structure, population density and spatial arrangement on a green roof can affect roof temperatures differently in summer and winter.

Therefore, there is a need to further explore the survival, growth and fitness of shrubs on rooftops, their direct impact on rooftop temperature and their potential to provide cooling and insulation services to buildings. The aim of the present study was to investigate the different shrub species' survival, fitness and physiological and morpho-anatomical responses to the rooftop environment and the effects of spatial arrangement, species combination and canopy structure on surface temperatures, to assess the potential of woody shrubs to buffer extreme rooftop temperatures. The better understanding of plant-rooftop interactions and the extent of the thermal benefits provided by tall woody shrubs could lead to the more widespread application of intensive vegetated roof systems and to improvements in green roof design that translate into higher energy savings for buildings.

2 Literature review

2.1 The use of shrubs on green roofs for mitigating temperature extremes and improving building thermal performance

Green roofs are engineered ecosystems atop rooftops and constitute a valuable nature-based solution for countering the urban heat island effect, through shading and insulating buildings and thereby reducing their energy consumption for cooling in the summer and heating in the winter. Plants represent an important regulating component of green roof thermal performance. Choosing functional green roof vegetation through specific 'cooling' plant traits not only has the potential to improve the provisioning of thermal benefits and plant survival, but can also promote the wider implementation of green roofs through more user-friendly selection criteria and ultimately lead to better green roof design.

The specific plant mechanisms behind evaporative cooling are complex and are still not completely understood, especially at the whole plant level and in relation to rooftop conditions. The rooftop represents a harsh environment for vegetation growth, thereby many studies have focused on plant selection criteria based on the ability of plants to survive on extensive green roof systems (i.e. < 20 cm substrate depth, little or no irrigation or maintenance) due to their more widespread use, rather than on the ability of plants to provide cooling benefits. However, the range of plants that can survive on these systems is restricted to a limited number of hardy, often succulent, drought tolerant and low-growing species (e.g. *Sedum*, *Sempervivum*, *Delosperma*, *Carex*, *Thymus*). As tall woody plants like shrubs may be more vulnerable to shallow substrate and high substrate temperatures and may require deeper substrate and irrigation, they are often discounted from testing altogether. Consequently, there is relatively less research on the survival and ecophysiological response of shrubs to rooftop environment compared to low-growing and short-lived vegetation.

Yet, tall woody plants can potentially provide higher shading, insulation and evapotranspiration compared to succulents, herbaceous perennials, grasses and other common green roof vegetation, characteristics that together reduce substrate temperatures and stormwater runoff. When combined with canopies that have high biomass, leaf density and lower absorptivity (i.e. high reflectivity), the use of tall woody plants on green roofs could greatly enhance albedo, cover and interception of solar irradiance. Shrubs in particular have a wide range of adaptations that enable them to overcome environmental stress, especially extreme temperature and drought, and have the ability to buffer temperature extremes at substrate level with their multi-stemmed canopies. Shrubs can also represent potentially more stable green roof vegetation, through greater longevity, cover and biomass, higher structural security and greater resilience to changes in rooftop conditions, all of which could improve long-term provisioning of thermal mitigation and other ecosystem services. The advantages to using deeper substrate in this respect should also not be overlooked (e.g. better water holding capacity, insulation, buffering of temperature fluctuations), as plants growing on green roofs with deeper substrate have higher survival rates, provide better cover, grow taller, transpire more and have generally better fitness. If targeted plant choice can improve green roof thermal performance and energy savings, it is crucial to not limit plant choice to only those species that survive on shallow and drought-prone substrates, but to extend it as well to the ones that can potentially optimise the delivery of thermal benefits. Plants with greater cooling capacities may require irrigation due to higher water use and may need deeper substrate to avoid temperature stress at root level and allow for bigger root systems to grow. However, it is important to take into consideration local climate in green roof vegetation and structural design, as precipitation may not be a limiting factor in temperate climates like that of the UK, and substrate type and other green roof components can be selected for greater moisture retention.

There are many studies that have used sub-shrubs, woody shrubs or even trees as part of a vegetation mixture for plant selection for both extensive and intensive green roofs. However, only about a dozen studies have tested the survival, growth, cooling performance, morpho-anatomical and/or physiological response specifically of shrubs. To date, no studies have yet investigated the effects of spatial variation, density and canopy structure of shrubs on rooftop temperature mitigation. There are also currently no studies testing shrubs or even vegetation mixes that include shrubs specifically in winter conditions. Therefore, there is a need to further explore the survival, growth and fitness of shrubs on rooftops, their direct impact on rooftop temperature and their potential to provide cooling and insulation services to buildings. The aim of the present study is to investigate the different shrub species' survival, fitness and physiological and morpho-anatomical responses to the rooftop environment and the effects of spatial arrangement, species combination and canopy structure on surface temperatures, to assess the potential of woody shrubs to buffer extreme rooftop temperatures. The better understanding of plant-rooftop interactions and the extent of the thermal benefits provided by tall woody shrubs could lead to the more widespread application of intensive vegetated roof systems and to improvements in green roof design that translate into higher energy savings for buildings.

2.2 The value of urban green infrastructure

Urban green spaces in compact and densely populated cities tend to be limited, fragmented and highly disconnected by the built environment (Tian, Jim and Wang 2014; Dobbs, Nitschke and Kendal 2017). Vegetation plays a vital role in ecosystem functioning and reconnecting cities to nature has become central to achieving sustainable urban ecosystems that can restore important ecosystem services in cities (Folke et al. 2011; Andersson et al. 2014, 2015; Costanza et al. 2014; Erb 2015; Pauleit et al. 2017; Ives et al. 2018; Barbier 2019; Elmqvist et al. 2019). Ecosystem services (ES) are the direct and indirect benefits that society and all living things receive from functioning ecosystems (Chapin 2013, Costanza et al. 2017). They represent sources of resilience that help maintain the health, functionality and biodiversity of an urban ecosystem and the benefits it can potentially provide (Gómez-Baggethun et al. 2013, Bernstein 2017, Zölch et al. 2017). Ecosystems can deliver either provisioning, cultural, regulating or supporting services. Provisioning services are quantifiable goods or products harvested from the environment (e.g. food, water, timber). An ecosystem can likewise provide non-material or cultural benefits, like amenity, recreation, sense of place and aesthetic, spiritual and educational value. Regulating services are those benefits obtained from the ecosystem processes that help regulate climate, water, air and some human diseases. Finally, supporting services are those that sustain all other ES, such as primary production, biogeochemical cycling, soil formation processes and habitat provisioning (Gómez-Baggethun et al. 2013, Scholes and Smart 2013, Chapin 2013, Bernstein 2017, Costanza et al. 2017, Pauleit et al. 2017, Barbier 2019). Regulating services such as noise and air pollution reduction, urban temperature and runoff regulation and moderation of climate extremes, as well as outdoor recreation and social cohesion, are amongst the most important ES in the urban context (Gómez-Baggethun et al. 2013). Green infrastructure can provide all of these regulatory services and thus enhance quality of life and biodiversity in urban areas (European Commission 2013, Gómez-Baggethun et al. 2013, Andersson et al. 2014).

Urban ecological or green infrastructure (GI) is defined as the network of interconnected natural (green and blue) and human-created or engineered (grey) elements incorporated within the urban fabric (Ahern 2007, Dennis 2015, Pauleit et al. 2017), especially designed to provide a wide range of long-term benefits that help regulate and mitigate the typical effects of urbanisation, e.g., stormwater runoff, flooding, the urban heat island effect, climate extremes, noise and air pollution, loss of biodiversity and habitats (European Commission 2013; Gómez-Baggethun et al. 2013; Douglas 2015; Pauleit et al. 2017; Xing, Jones and Donnison 2017). GI is an umbrella term that includes a wide variety of blue and green components operating at different ecological and spatial scales – for example, they can include anything between entire ecosystems and small patches of green space, and can be found anywhere between urban and rural areas. These components can thus range from: 1) natural and protected sites (e.g., forests, woodland, wetlands, floodplains, lakes, rivers, coastal dunes, coral reefs); 2) semi-natural areas or restored habitats outside of protected areas, such as parks and public and private gardens; 3) multi-functional buffer zones (e.g. used for both recreation and food production) that are managed sustainably, such as wildlife-friendly farms, eco-parks and allotments; 4) designed urban green spaces and other natural or artificial features, such as hedgerows, woodland strips, ponds and eco-bridges, and 5) bioengineered technologies conceived for sustainable drainage, water treatment and temperature and pollution abatement (e.g. constructed wetlands, bioswales, porous pavement, rain gardens, street trees, green walls/roofs). Bioengineered GI can use vegetation, soil and/or infiltration to collect, filter, purify and reuse rainwater, attenuate stormwater runoff and flooding and reduce the urban heat island, temperature extremes and air pollution through shading, evaporative and radiative cooling, the use of reflective and high-performing thermal materials and removal of pollutants by trees and other vegetation (Ahern 2007; European Commission 2013; Yang et al. 2013; Cettner et al. 2014; Douglas 2015; Yang, Wang and Kaloush 2015; Yazdanfar and Sharma 2015; Wright et al. 2016; Fini et al. 2017; Pauleit et al. 2017; Zölch et al. 2017; McFarland et al. 2019; Nguyen et al. 2019; Yang and Yin 2019).

Some of the most valuable GI services in the urban context are those that regulate local temperatures and the effects of the urban heat island, or UHI (Section 1.3). Large bodies of water in cities like wetlands, lakes, ponds and rivers perform a slow buffering effect on temperature extremes due to their high thermic inertia, especially during the daytime, allowing them to absorb heat in the summer and release it in the winter (Gómez-Baggethun et al. 2013, Ward et al. 2016, Chun and Guldmann 2018). Vegetation on green roofs and walls similarly buffer extreme temperatures by reducing wind speed and providing shade and evaporative cooling in the summer and insulation during the winter (Besir and Cuce 2018, Cascone et al. 2018, Gunawardena and Steemers 2019). Roof and vertical greening can decrease heating demand of buildings by 10–30% and provide energy savings of about 215 USD per year (Besir and Cuce 2018). Urban trees are perhaps the least expensive GI method for UHI mitigation (Livesley, McPherson and Calfapietra 2016) and can reflect solar irradiance and shade streets and pavements that would otherwise absorb heat, decreasing local surface heat and air temperature (Gómez-Baggethun et al. 2013). Depending on the species, urban trees can reduce urban air temperature by 1 °C in densely populated cities solely through daily evapotranspiration (Livesley, McPherson and Calfapietra 2016). The combination of urban trees and green roofs are likely to have the highest mitigation potential among the GI systems (Santamouris et al. 2017). Increasing urban greenery by as little as 10% through the implementation of GI could significantly minimise local temperature in the summer and future temperature rise in cities (Besir and Cuce 2018), as well as increase local temperature in the winter and decrease energy consumption for heating (Chun and Guldmann 2018).

2.3 The Urban Heat Island effect and the role of vegetation in temperature mitigation

Urban development causes a type of land transformation in which construction advances the spread of impervious surfaces (e.g., concrete, asphalt, buildings, roads, parking lots) and hardened landscapes (e.g., turf, compacted soil) and the conversion of native plant communities to disjointed forms of vegetation, such as parks and open spaces (Hahs et al. 2009). The urban landscape is consequently ecologically highly fragmented (Hahs et al. 2009; Dobbs, Nitschke and Kendal 2017) and represents a special kind of 'socio-ecosystem' (Small, Munday and Durance 2017; Barot et al. 2019) in which spaces and functions are in constant physical and social evolution (Meerow, Newell and Stults 2016; Olsen et al. 2019) and nature competes with these same spaces and resources (Andersson et al. 2015). Not only do these modified surfaces shrink and fragment the pre-developed natural environments, they also alter the original energy cycle found in balanced ecosystems (Carter and Fowler 2008). The hydrological components of the energy cycle include precipitation, evaporation, transpiration, infiltration, runoff, streamflow and groundwater flow (Welty et al. 2007). In natural landscapes, this cycle is complete when precipitation is intercepted and stored by soil and vegetation and is eventually returned to the atmosphere through evapotranspiration (Lambers, Chapin and Pons 2008). Evapotranspiration is known as the combination of 1) water either transpired or retained by plant tissues, i.e. transpiration and 2) moisture in the form of water vapour that evaporates from soil, ocean and vegetation surfaces, i.e. evaporation (Ebrahimian, Wadzuk and Traver 2019). It is a process powered by solar irradiance (Cascone et al. 2019a) and constitutes an important component of the planet's energy balance. Urban development diminishes a city's capacity to intercept, evapotranspire, infiltrate and store rainwater and thereby impedes the completion of the hydrological cycle (Zölch et al. 2017).

Rising global temperatures, in combination with the heat generated when incoming solar irradiance interacts with the dark, paved surfaces of the urban landscape, have also contributed to the imbalance of the planet's energy (Estrada, Botzen and Tol 2017). In fact, urbanisation causes complex modifications to the landscape, not only in substituting nature with concrete and disrupting its water cycle, but also by causing changes to the radiative and aerodynamic characteristics of the planet's boundary layer (Trusilova et al. 2008), the part of the atmosphere in direct contact with the Earth's surface. Materials such as concrete and asphalt have higher heat capacities and thermal conductivity compared to natural ones (Estrada, Botzen and Tol 2017), therefore the transfer of heat from these impervious surfaces to the surrounding environment (i.e., sensible heat flux, or anthropogenic heat flux) has altered the temperature of cities, making them warmer compared to rural areas (Oliveros et al. 2019). The built environment encourages this transfer by absorbing much of the incident radiation during the day, storing it and then releasing it in the form of thermal radiation during the night (Garuma 2018). This causes atmospheric instability through changes in moisture, heat flux and wind regimes, in turn creating drier conditions at near-surface level that can even modify precipitation patterns (Haberlie, Ashley and Pingel 2015; Argüeso, Di Luca and Evans 2016). This phenomenon has been scientifically monitored since the early 1960s and is known as the urban heat island (UHI) effect (Oke 1973, Gallo et al. 2002). The first measured observation of this phenomenon was made by amateur meteorologist Luke Howard, who published a report in 1818 demonstrating that London was consistently almost 4 °F (2.22 °C) warmer than the surrounding rural area (Stone 2012). The seminal work by Oke (1987) showed how urbanisation can increase temperatures in large cities by a range of 2 to 10 F (approximately 1 to 5.5 °C), with extreme heat islands even reaching a 20 °F (about 11 °C) difference compared to the countryside. More recent studies identify a wider range, with the UHI effect increasing air temperature of cities by between 5 and 15 °C compared to local rural areas (Santamouris 2013).

The UHI effect is most evident when observing a city's diurnal temperature range (DTR), which is the variation between the maximum and minimum temperatures of the day. The UHI causes a contraction of this range, meaning that the difference between daytime and night-time temperatures is reduced (Wang et al. 2007). The study by Trusilova et al. (2008) found that urbanisation in Europe between 2000 and 2005 has caused a statistically significant change in precipitation and near-surface temperature, with a reduction in the DTR of urbanised regions of about 1.3 °C in the summer. The UHI effect can also be quantified by measuring the UHI intensity (UHII), which is essentially the difference in temperature between an urban site and its local rural one (Watkins et al. 2002). As the UHII is usually highest at night-time (Santamouris 2007, Wang et al. 2007), the UHI effect is more likely to affect daily minimum temperatures (recorded at night) rather than daily maximum temperatures, with the result that the average minimum daily temperature in a city will continue to increase in the future (Goddard and Tett 2019). Globally, daily minimum temperatures have in fact had a greater increase than daily maximum temperatures since the mid-20th century, with exceptionally warm nights occurring with double the frequency in much of Europe, Asia and western Pacific regions (Bell et al. 2018).

A recent study by Goddard and Tett (2019) has found that urbanisation has caused a significant increase in the daily minimum temperatures in all of the UK between 1990 and 2017. The highest increase was found, unsurprisingly, in London, with 1.70 °C, but many other UK cities have increased their daily minimum temperatures by over 1 °C. In particular, Watkins et al. (2002) had found that the urban-rural temperature difference (UHII) between the City of London and its rural surrounding area (approximately 30 miles radially from the centre) can reach 7 °C in the summer. Similar values have been found for northern cities of the UK as well. For example, the UHII for Manchester usually lies in the range of 0.5–5.0 °C but can reach 8 °C at summer maximum (Skelhorn, Lindley and Levermore 2018). The UHII for Manchester was also found to be increasing over time, a highly significant rising trend that could potentially add 2.4 °C to the city's average annual urban temperature by 2100 (Levermore et al. 2018). These values are comparable to those of other highly urbanised cities around the world, like Singapore, which can reach an intensity of approximately 7 °C in summer maximum (Aflaki et al. 2017). However, different cities will vary greatly in UHII values, due in most part to their unique topographies and climates (Watkins et al. 2002), but also to their geometry and population (Yang, Wang and Kaloush 2015). In fact, Santamouris (2007) in his review found a considerable range of UHII when he compared the maximum values reached by different cities in Europe, with Mediterranean countries generally showing higher maxima compared to Central and Northern Europe (the latter generally showed greater UHII values in winter rather than in summer).

The UHI effect is present in almost every city, independent of size, geographic location and local climate (Stewart and Oke 2012). However, certain weather conditions, such as low cloud cover, little wind and anticyclone periods, are important factors in cities reaching high UHII values (Santamouris 2007). UHII also increases with size and population density, especially in cities that are in continuous expansion (Lee, Lee and Wang 2012). Estrada, Botzen and Tol (2017) found that nearly a third of the 1,692 cities they investigated had warmed more than the world average (0.6 °C) in terms of annual mean temperature increase between 1950 and 2015, and that the top 5% most populated cities had increased by 1.72 °C in the same period. Their model also predicted that this same increase in the most populated cities will be over 2 °C by the end of this century. Their study thereby demonstrates the extent and universality of the UHI effect, but what in particular causes this phenomenon? Why are inner cities warmer than rural areas?

During evapotranspiration, water released by plants during transpiration absorbs sensible heat from the air as it evaporates from the surface of leaves and is released as latent heat (Lambers, Chapin and Pons 2008), thus cooling the surrounding air. This process is known as 'evaporative cooling' and represents a method for thermal or microclimate regulation (Peng et al. 2012). Consequently, when natural land is substituted with impervious surfaces the evaporative cooling, shade and moisture retention by both plants and soil diminish (Stone 2012; O'Malley et al. 2014; Wang, Berardi and Akbari 2016). Furthermore, the built environment is composed of materials that have a lower albedo (reflectivity) and a higher emissivity compared to vegetation, which can prompt a shift in the surface energy balance from latent to sensible heat flux and therefore cause the release of more energy in the form of longwave or thermal radiation into the atmosphere (Lee, Lee and Wang 2012; Stone 2012; O'Malley et al. 2014; Wang, Berardi and Akbari 2016; Ward et al. 2016). Crucial to understanding this key change is knowing what latent and sensible heat are. In short, latent heat is the thermal energy transferred in a process (i.e., the phase change between solid, liquid and gas) *without* change in the body's temperature (Faghri and Zhang 2006), while sensible heat is the thermal energy exchanged in a system that *changes the body's temperature* without there being a change in phase (Sheng 2013). In other words, cities are causing an increase in the release of energy (heat) that can be physically perceived.

Another important factor contributing to the UHI is the urban canyon effect, created when the design, layout and geometry of a densely built environment – especially narrow streets and tall, vertical buildings that have impressive heat-retaining characteristics – trap, store and release heat into near-surface atmosphere (Fan and Sailor 2005, Stone et al. 2012, Ward et al. 2016). This will often result in reduced rates of longwave radiation loss during the night (O'Malley et al. 2014) and in modified wind speeds (Wang, Berardi and Akbari 2016), with even less radiation loss due to the counter effect caused by gas and dust particles found in polluted urban air (Roloff, Korn and Gillner 2009). The UHI effect also aggravates air pollution and heat stress, in that it acts as a catalyst for chemical reactions that transform certain air pollutants (e.g. NO_2, CO, CH_4, VOCs) into harmful ground-level ozone, O_3 (IPCC 2013, Estrada, Botzen and Tol 2017), and it contributes to the acute discomfort felt by residents during heat waves, or periods of short-term but intense temperature changes caused by climate change and atmospheric anomalies (Kovats and Hajat 2008, Demirtaş 2018, Parente et al. 2018).

The number of vulnerable people exposed to heat waves increased by 125 million globally between 2000 and 2016 (WHO 2018), prompting a rise in the use of HVAC systems to alleviate heat stress. The intense use of ventilation systems, however, trigger an upsurge in energy consumption (Garuma 2018), especially in cities (Salamanca et al. 2013), and their use causes the release of "waste heat" into the surrounding environment, a type of heat also generated by other anthropogenic activities like fuel combustion in vehicles, industrial processes, conduction of heat through building walls and even through human metabolism (Sugawara and Narita 2009). Not only does this energy loss represent a shortfall in efficiency and in profits, artificial heat discharge has been shown to significantly impact surface temperature and global atmospheric circulation in developed regions of the world (Chen et al. 2014), so much so that it can contribute substantially to the UHI, with studies reporting a local rise in temperatures of between 0.4 and 3 °C caused by its release into the environment (Liao et al. 2017). Implementing urban GI can significantly reduce the UHI effect and energy consumption for air conditioning that causes this discharge of heat. By providing shade, reflectivity, evaporative cooling and moisture retention through evapotranspiration and the interception of solar radiation and stormwater, GI can thus restore the ecosystem services that are lost through urban development, in particular the cooling services that naturally mitigate temperature (Besir and Cuce 2018, Chun and Guldmann 2018).

2.4 Green roofs, building energy dynamics and trade-offs

Rooftops represent between 20 and 50% of urban surfaces (Akbari and Rose 2008) and up to 50% of impermeable urban surface areas in most developed cities (Stovin, Vesuviano and Kasmin 2012). Globally, the building sector represents the biggest and highest growing energy consumer, accounting for 40% of total energy consumption (Marínez-Molina et al. 2016). As urbanisation and energy consumption are contributing to rising global temperatures, the greening of building surfaces like rooftops has become one of the most sustainable solutions to restoring ES in urban areas and resolving issues related to the UHI (Besir and Cuce 2018). In fact, a recent study by Sharma et al. (2016) found that a widespread implementation of green roofs in Chicago could potentially reduce peak daily UHI during a summer heat wave by between 0.84 and 3.41 °C. Not least, green roofs can extend greenery and associated benefits beyond ground level, where space may be limited and cost-prohibitive, to the often unexploited and increasing number of rooftops in highly urbanised areas (Alexandri and Jones 2008; Santamouris 2014; Karachaliou et al. 2016; Herrera-Gomez et al. 2017; Xing, Jones and Donnison 2017; Besir and Cuce 2018; Teotónio et al. 2018; Cao et al. 2019). The benefits associated with green roofs are in fact numerous and include reduced stormwater runoff, improved wastewater management, thermal regulation, greater provisioning of habitat and biodiversity, removal of air pollution, reduced noise pollution, extended roof lifespan and fire-retardant effect and increased property value of the building due to higher energy savings, better aesthetics, recreation services and even food production (MacIvor et al. 2016a; Viola, Hellie and Deidda 2017; Sookhan, Margolis and MacIvor 2018; Teotónio et al. 2018; Ebrahimian, Wadzuk and Traver 2019).

In particular, green roofs optimise the thermal performance of buildings through higher insulation, reflectivity, shading and evapotranspiration (‘evaporative cooling’), the combination of which increases building energy savings as less energy is used for cooling and heating, thereby counteracting the UHI effect (Alexandri and Jones 2008; Scherba et al. 2011; Permpituck and Namprakai 2012; Peng and Jim 2013; Qiu et al. 2013; Li, Bou-Zeid and Oppenheimer 2014; Santamouris 2014; Simmons 2015; Berardi 2016; Costanzo, Evola and Marletta 2016; Vijayaraghavan 2016; Alvizuri et al. 2017; Francis and Jensen 2017; Herrera-Gomez et al. 2017; Cascone et al. 2018; Susca 2019). Building surface temperature strongly affects the air temperature in the surrounding area (Costanzo, Evola and Marletta 2016), including the rooftop, and the highest fluctuations in surface temperature and heat flux through the roof to the indoor environment occur during the summer and winter (Eksi et al. 2017). Green roofs help control this heat flux, reducing it by up to 90% during summer and avoiding indoor heat loss by up to 30% during winter compared to conventional bare rooftops (Teotónio et al. 2018). In fact, many studies show that green roofs reduce heat gain in the summer and provide greater insulation in the winter compared to conventional roofs

(Castleton et al. 2010, Parizotto and Lambert 2011, D'Orazio et al. 2012, Jaffal et al. 2012, Nardini et al. 2012, Zhao and Srebric 2012, Olivieri et al. 2013, Lundholm et al. 2014, Madre et al. 2014, Lundholm and Williams 2015, Van Mechelen et al. 2015, Savi et al. 2016, Pianella et al. 2017, Cascone et al. 2018, Catalano et al. 2018, Lee and Jim 2018, Susca 2019), with a few recent studies showing encouraging evidence of their ability to even mitigate temperatures of the local area beyond the building unit (Ng et al. 2012, Peng and Jim 2013, Park et al. 2018, Lee and Jim 2019, Zhang et al. 2019) and increase the photovoltaic performance of solar panels and therefore energy efficiency of buildings when used together on rooftops (Teotónio et al. 2018). Annual cost savings from using green roofs in New York has been reported to be of 0.26USD/m^2 of conditioned building area and 0.95USD/m^2 of roof area compared to conventional rooftops (Sailor, Elley and Gibson 2012).

As their name suggests, modern green roofs (also known as eco-roofs, living roofs and vegetated roofs) are a form of GI placed atop buildings and other above-ground structures that consist of different layers, typically of (from bottom to top): roof protection, insulation, a waterproof membrane, a root barrier, a drainage layer, a filter, engineered growing media or substrate and vegetation, with each layer playing a role in green roof performance (Sutton 2015). Green roofs are engineered urban ecosystems that represent particularly extreme environments for the growing vegetation, especially when on extensive green roof systems (Oberndorfer et al. 2007, Simmons 2015). Extensive systems are those in which the growing media or substrate layer is very thin (< 20 cm, usually 7–15 cm) and lightweight and the vegetation requires little or no irrigation and maintenance. Intensive systems, or roof gardens, or those that have deeper substrate (> 20 cm, generally up to 1 m), greater loads weighing on the supporting system and taller, more complex and varied vegetation that may require irrigation and maintenance. Semi-intensive systems are green roofs with intermediate characteristics between these two types (e.g. 15–30 cm, engineered lightweight growing media, limited irrigation, varied short vegetation), but the term is loosely used in literature. Depending on the height of the building on which the green roof is placed, vegetation will be exposed to high wind and solar irradiance, extreme temperature, varying air humidity and limited water and nutrient availability (Simmons 2015), especially on thin, nutrient-poor substrates in warmer climates or in climates prone to extended snow cover and freezing in the winter.

Green roof temperature abatement potential depends on a combination of climatic, optical (absorptivity of plants), thermal (thermal capacity of roofs and overall heat transfer coefficient, *U*-value), and hydrological (latent heat budget of the green roof) parameters. The climatic parameters include solar radiation, air temperature, wind speed, relative humidity, and precipitation. In particular, solar radiation determines the thermal balance and general temperature of the roof, air temperature regulates the amount of sensible heat released to the atmosphere as convective heat flux, wind speed determines the heat transfer coefficient between the roof and the atmosphere, and relative humidity and precipitation define the moisture balance in green roofs (Santamouris 2014). Green roofs reduce solar heat gain when the absorbed solar heat on the rooftop is converted to latent heat through evapotranspiration by the substrate and vegetation, resulting in a reduction in solar heat absorbed by the building itself, in lower surface temperatures, less longwave radiation emitted and reduced air temperatures (Sharma et al. 2016, Cascone et al. 2019a). The three main factors affecting heat gain/retention by a green roof are: 1) the albedo (reflectivity) of the vegetation, which decreases the heat gain by 70% when doubled; 2) the air convection rate near the canopy (wind speed and atmospheric dynamics between canopy and atmosphere), which increases evapotranspiration and latent heat dissipation and reduces heat retention by nearly half when air rate is increased from 12 to 16 m/s, and 3) the substrate water content, which reduces heat storage by nearly a fourth when moisture is doubled (Tsang and Jim 2011). Wind, for example, can significantly affect green roof performance, with some evidence that wind could reduce temperatures of the roof deck more than green roof vegetation (Jim and Peng 2012). In fact, Jin et al. (2018) recommend implementing green roofs in upwind zones for increased temperature reduction at even neighbourhood scale. On the other hand, green roofs themselves can reduce wind speed and affect atmosphere dynamics (Sharma et al. 2016). Building type and height also affect heat flux and the cooling ability of green roofs, with building cooling and perceived cooling at pedestrian level decreasing with building height, becoming negligible at building height above 60 m (Morakinyo et al. 2017).

Unsurprisingly, the cooling performance of green roofs is strongly influenced by climate and geographic location. How climate affects green roof performance, however, is uncertain, as Zhang et al. (2019) found that green roofs in hot-dry climates showed higher cooling performances compared to hot-humid and temperate climates, whereas Sailor, Elley and Gibson (2012) found that building energy performance was greatest with green roofs on midrise apartment buildings in colder U.S. climate. In agreement with Zhang et al., Ascione et al. (2013) found that the maximum annual energy reduction by green roofs can be 6–7% in northern Europe (mainly savings in heating) and 8–11% in southern Europe (mainly savings in cooling). Green roofs were found to reduce heating demand in northern Europe, for example by 8% in Stockholm (Jaffal et al. 2012), but may even result in an increase in heating demand (3–9%) when placed on insulated Mediterranean buildings (Santamouris et al. 2007). In fact, roof insulation drastically reduces the natural insulating effect of green roofs during the winter, with total energy demand decreasing from 50% with green roofs on uninsulated rooftops to 3% with green roofs on 30-cm insulated rooftops (Jaffal et al. 2012). Not only roof insulation, but also certain climate regions have shown to influence negatively the thermal performance of green roofs in winter. For example, studies on intensive green roofs in subtropical climates showed reduction in the cooling load in the summertime but greater heating load to the building in winter due to heat loss from the substrate, which drew heat upwards from the warm indoor environment to the outdoor ambient air (Jim and Tsang 2011a, Peng et al. 2019).

The type of green roof itself has a major influence on rooftop temperatures, with intensive green roof systems showing significantly higher thermal insulation, cooling performance (at both rooftop and pedestrian level), water retention capacity and noise absorption compared to extensive systems (Ng et al. 2012; Sailor, Elley and Gibson 2012; Peng and Jim 2013; Teotónio et al. 2018; Zhang et al. 2019). For example, the study by Peng et al. (2019) found that an intensive green roof (35 mm) that grew a mixed vegetation that included shrubs and trees was more effective than an extensive green roof (5 mm) covered in *Sedum lineare* in decreasing daytime and night-time surface temperatures, cooling the ambient air and reducing the summer cooling load in a subtropical region. Permpituck and Namprakai (2012) also found a 59% and 96% reduction in heat transfer and 31% and 37% energy use reduction for green roofs with 10 cm and 20 cm substrate depth, respectively. Moreover, maximum cooling can occur during the night when the UHI is strongest. For example, an intensive green roof in Manchester presented both a maximum reduction of 1.58 °C at night and a monthly median air temperature of 1.06 °C lower compared to a conventional roof when recorded at *30 cm above the vegetation layer* (Speak et al. 2013). This means that the presence of vegetation alone contributes considerably to the overall cooling effect of the green roof.

The vegetation layer indeed plays a key role in thermal insulation and cooling, owing mostly to plant transpiration rates and shading. Canopy traits contribute to the green roof's overall cooling capacity by intercepting part of the solar radiation that reaches the roof and shading the soil layer (Fioretti et al. 2010, Jaffal et al. 2012, Dvorak and Volder 2013), effectively reflecting 13% and absorbing 56% of incident solar radiation (D'Orazio et al. 2012). Canopy biomass is correlated with both albedo (reflectivity), which reduces roof temperatures, and evapotranspiration, which cools the leaf and the surrounding air temperature (Fioretti et al. 2010). As a result of these characteristics, the albedo of green roofs (from 0.7 to 0.85) has a much higher value than that of bitumen, tar, and gravel roofs (from 0.1 to 0.2), according to the review by Berardi et al. (2014), and could be maximized through the selection of plants that have high reflectivity potential, like those with leaf and stem hairiness and lighter leaf colour (Sandquist and Ehleringer 1998, Vaz Monteiro et al. 2016). Alongside green roof albedo, transpiration rates could also increase as a result of these leaf morphological traits, which consequently lower leaf surface temperature and increase water loss (Vaz Monteiro et al. 2016). The vegetation layer alone can reduce green roof temperature by 4–5 °C (Onmura, Matsumoto and Hokoi 2001), with vegetation showing a 3 °C additional reduction compared to a substrate-only roof, with an overall reduction of over 16 °C for a green roof compared to a conventional asphalt roof (Lundholm et al. 2010). Moreover, vigorous growth/height, higher structural complexity (i.e. 3-dimensional vs 2-dimensional cover) and structural heterogeneity (i.e. different growth forms and heights) are equally important factors influencing shade on a rooftop (Jim 2012; Lundholm, Tran and Gebert 2015, Zhang et al. 2019), all of which are correlated with high leaf area index and greater cooling capacity (Sailor 2008, MacIvor et al. 2016b). On a larger scale, the regulating effect of vegetation on outdoor thermal environment has been shown to be seasonal, with uniform reductions in surface temperatures between April and October (highest reductions in June–August) during the vegetative season, with higher surface temperatures maintained during the winter months (Chun and Guldmann 2018). Therefore, the thermal behaviour of a green roof depends on a number of variable abiotic and biotic factors, such as local climate, weather, substrate depth, canopy architecture, foliage density and species-specific traits, the combination of which affect the release of sensible heat and long-wave radiation into the atmosphere by the roof and the heat flux through the roof deck to the building below (Vaz Monteiro et al. 2017).

When comparing the benefits provided by different green roofs systems, it is important to keep in mind the effects of both substrate and vegetation, which together significantly influence evapotranspiration rates (Berghage et al. 2007, VanWoert et al. 2005, Dunnet et al. 2008, Lundholm et al. 2010, Schroll et al. 2011, Nardini et al. 2012). In fact, two essential benefits provided by green roofs are storm water runoff reduction through soil moisture retention, and energy savings through the cooling effect provided by the esothermic reaction of soil water content depletion. Both of these essential services are driven by a combination of soil evaporation and plant transpiration rates (Berghage et al. 2007), or evapotranspiration. Evapotranspiration in fact represents the main process by which rainfall is retained by green roofs, an annual volume of retention that can range from 11 and 77% depending on weather conditions and green roof properties like substrate retention capacity, vegetation, slope and age of the green roof (Ebrahimian, Wadzuk and Traver 2019). However, deeper substrate can provide greater thermoregulatory potential compared to shallow substrate (Sookhan, Margolis and MacIvor 2018). Moreover, deeper substrates can support greater plant diversity and higher plant survival, biomass production and functionality, through 1) better water holding capacity, promoting higher evapotranspiration (Monterusso et al. 2004; Lazzarin, Castellotti and Busato 2005; Getter and Rowe 2009; Metselaar 2012; Nardini et al. 2012; Berretta, Poë and Stovin 2014; Razzaghmanesh et al. 2014; Zhang et al. 2014; Rowe 2015; Vijayaraghavan 2016; Reyes et al. 2016; Chenot et al. 2017; Soulis et al. 2017; Viola, Hellies and Deidda 2017); 2) reduced storage of heat in the substrate and transfer to the roof deck and building (Lazzarin, Castellotti and Busato 2005; Tsang and Jim 2011; Permpituck and Namprakai 2012); 3) higher buffering of daily thermal excursion/amplitude/fluctuations and a 4) bigger delay in reaching peak daily temperatures (Getter, Rowe and Cregg 2009; Rowe 2015; Reyes et al. 2016; Savi et al. 2016). Plants growing on deeper substrate have also been shown to grow taller, provide greater establishment and cover, have lower stomatal resistance to transpiration and have higher leaf water, chlorophyll and carotenoid contents (Getter and Rowe 2009; Benvenuti and Bacci 2010; Kotsiris et al. 2012; Ntoulas et al. 2013; Papafotiou et al. 2013; Razzaghmanesh et al. 2014, Nektarios et al. 2015, Rowe 2015), a combination that promotes both shading and plant fitness.

2.5 Selection criteria for green roof vegetation based on plant functional traits

Plants regulate many of the ecosystem services provided by green roofs, including building insulation and microclimate mitigation (Jim 2012, Santamouris 2014, Lundholm and Williams 2015, Cao et al. 2019), and the advantages of using a wide range of plant types in this respect are becoming more evident and crucial to choosing highly functional green roof vegetation (Benvenuti and Bacci 2010; Lundholm et al. 2010; Cook-Patton and Baurle 2012; MacIvor et al. 2013; Heim and Lundholm 2014; Simmons 2015; Van Mechelen et al. 2015; Cameron and Blanusa 2016; MacIvor et al. 2016b; Vaz Monteiro et al. 2016; Nagase, Dunnett and Choi 2017; Xie, Lundholm and MacIvor 2018; MacIvor et al. 2018; Cao et al. 2019). Optimising green roof vegetation through informed and systematic plant selection not only has the potential to improve the provisioning of thermal benefits, but can also help overcome the current socio-political and institutional barriers to the wider implementation of green roofs on buildings. Increasing building thermal performance through the use of green roofs and other green infrastructure is especially important in view of the UHI effect, climate change and momentous policy changes needed to achieve more sustainable and resilient cities (Oberndorfer et al. 2007; Jim 2012; Ng et al. 2012; Berardi et al. 2014; Wang et al. 2014; Lundholm and Williams 2015; Matthews, Lo and Byrne 2015; Peng and Jim 2015; Van Mechelen et al. 2015; Livesley, McPherson and Calfapietra 2016; MacIvor et al. 2016a; Zölch et al. 2016; Herrera-Gomez et al. 2017; Cascone et al. 2018; Catalano et al. 2018; MacIvor et al. 2018; Elmqvist et al. 2019; Lafortezza and Sanesi 2019; Voghera and Sanesi 2019).

There is an increasing number of studies focusing on criteria for green roof plant selection based on plant functional traits, ecology and phylogenetic diversity (Kotsiris, Nektarios and Paraskevopoulou 2012; Blanuša et al. 2013; Farrell et al. 2013; Starry et al. 2014; Madre et al. 2014; Van Mechelen, Dutoit and Hermy 2014; Van Mechelen et al. 2014; Razzaghmanesh et al. 2014; Caneva et al. 2015; Lundholm, Tran and Gebert 2015; Lundholm and Williams 2015; Nektarios et al. 2015; Savi et al. 2015, 2016; Heim and Lundholm 2016; MacIvor et al. 2016a; Rayner et al. 2016; Vaz Monteiro et al. 2016; Vaz Monteiro et al. 2017; Kuronuma and Watanabe 2017; Catalano et al. 2018; Du, Arndt and Farrell 2018; Payne et al. 2018; Xie, Lundholm and MacIvor 2018; Cao et al. 2019). Plant functional traits are the morpho-anatomical, physiological and phenological features and trade-offs that reflect a species' fitness and determine its strategy in responding to environmental stresses and disturbances (Lambers, Chapin and Pons 2008; Pérez-Harguindeguy et al. 2013; Lundholm and Williams 2015). Although different species may vary in their response to the rooftop environment due to the range of plant traits reflecting their species-specific adaptions (Vaz Monteiro et al. 2017), plant functional traits allow for the generalisation of behaviour in phylogenetically different species with similar ecophysiological strategies (Lambers, Chapin and Pons 2008; Lundholm and Williams 2015). In the context of green roofs they can help predict plant survival in the harsh rooftop conditions and in diverse climate regions, as well as the cooling and insulation services they can potentially provide (Van Mechelen, Dutoit and Hermy 2014; Van Mechelen et al. 2014; Caneva et al. 2015; Rayner et al. 2016; Vaz Monteiro et al. 2017; Payne et al. 2018; Sookhan, Margolis and MacIvor 2018; Xie, Lundholm and MacIvor 2018; Du, Arndt and Farrell 2019; Tran et al. 2019). These predictors can inform practitioners of simple and transferable plant selection criteria they can use to develop a broader palette of green roof vegetation and thus improve green roof design (Jim 2012, Caneva et al. 2015; Van Mechelen et al. 2015; Heim and Lundholm 2016; Catalano et al. 2018; Du, Arndt and Farrell 2018; MacIvor et al. 2018).

Selecting the best vegetation based on specific ‘cooling’ plant traits can be decisive in determining the capacity of a green roof to mitigate surface temperatures, because the type of plants used influence the rates of evapotranspiration, the albedo (i.e. reflectivity) and the levels of shading on the rooftop (Squier and Davidson 2016; Vaz Monteiro et al. 2017; Sookhan, Margolis and MacIvor 2018). At the same time, the physiological performance of green roof vegetation that enables this cooling process is highly dependent upon air and substrate temperatures on the rooftop (Kazemi and Mohorko 2017), thereby making the selection process for high functional plants tricky. The traits used as selection criteria for green roof vegetation include growth form and life strategy, certain physiological adaptive mechanisms (e.g. transpiration and photosynthetic rates, stomatal conductance, photosynthetic pathway, chlorophyll content, leaf water potential, leaf temperature), rooting depth, typical plant height, root/shoot ratio, relative growth rate and leaf area, shape, phenology, orientation, colour, longevity and succulence (Van Mechelen et al. 2014; Lundholm, Tran and Gebert 2015; Vaz Monteiro et al. 2017; Catalano et al. 2018, Du, Arndt and Farrell 2018), as well as species ecology and climate of origin, e.g. plant hardiness zones and heat moisture index (Van Mechelen, Dutoit and Hermy 2014; Razzaghmanesh et al. 2014; Caneva et al. 2015, Van Mechelen et al. 2015). Most European green roof standards and guidelines include plant functional traits as main factors for identifying suitable plant species, but recommend plant choice based on a rather simplistic lifeform–substrate depth dependency (e.g. shrubs and trees can only survive on deep substrate) without suggesting any specific lifeform or species combinations, for example, to optimise the provision of thermal benefits (Catalano et al. 2018). These guidelines also do not acknowledge the complexity of plant response to rooftop environment.

Many studies on green roof plant selection have focused on testing vegetation that will survive on very shallow substrate, as these lightweight green roofs have lower installation and maintenance costs, loading restrictions and payback periods in terms of cost-benefits to date, and therefore have a greater chance of being implemented in urban planning practices or retrofitted on existing buildings (Snodgrass and McIntyre 2010; Qiu et al. 2013; Cao et al. 2014; Li, Bou-Zeid and Oppenheimer 2014; Peng and Jim 2015; Simmons 2015; Sproul et al. 2014; Vijayaraghavan 2016; Cascone et al.

2018; Teotónio et al. 2018). Finding plants that can survive and guarantee long-term cover can also avoid replacement costs and loss of performance, thus meeting client expectations (Getter and Rowe 2009, Speak et al. 2013, Rowe 2015). However, the range of plant types and species capable of long-term survival on thin substrates is inevitably limited to drought- and wind-tolerant species with succulent leaves and shallow root systems. This is due to the exposure of green roof plants to low water and nutrient levels and extreme substrate temperatures as a consequence of high solar irradiance, wind and evaporation rates (Cao et al. 2014, Rowe 2015, Simmons 2015, Rayner et al. 2016, Savi et al. 2016, Tran et al. 2019). Succulents of the Crassulaceae family (e.g. *Sedum* sp., *Sempervivum* sp., *Delosperma* sp.) are popular choices for extensive systems as they are well-adapted to conditions of aridity, high irradiance and shallow substrate and therefore have the greatest applicability on extensive systems (Monterusso, Rowe and Rugh 2005; Oberndorfer et al. 2007; Emilsson 2008; Dvorak and Volder 2010; Rowe, Getter and Durham 2012; Farrell et al. 2013; Schweitzer and Erell 2014; Vijayaraghavan 2016; Sookhan, Margolis and MacIvor 2018). Grasses, drought-tolerant herbaceous perennials and geophytes and even some semi-woody shrubs have also been found to withstand very shallow growing media (Oberndorfer et al. 2007; Dvorak and Volder 2010; Nektarios et al. 2015; Savi et al. 2015; Van Mechelen et al. 2015; Vijayaraghavan 2016). Moreover, tall woody plants like shrubs and trees may be more vulnerable to harsh rooftop conditions, especially shallow substrate, and therefore are often not selected for green roof vegetation (Du, Arndt and Farrell 2018, 2019). Consequently, there is considerably less research on the survival and ecophysiological response of tall, long-lived and complex lifeforms like shrubs on rooftops compared to low-growing and short-lived vegetation.

Choosing plant species that can survival on shallow, drought-prone substrate is unquestionably a key factor in selecting successful green roof vegetation (Brunetti, Porti and Piro 2018; Du, Arndt and Farrell 2018; Fabiani et al. 2018). However, it is important to also consider how plant cooling mechanisms are affected by plant response to drought and other changes to atmospheric conditions. That is because a major driving factor in evaporative cooling on green roofs is transpiration by the vegetation, and the range of plant strategies aimed at either tolerating or avoiding drought can have significant effects on evapotranspiration. Transpiration is the gas exchange that occurs in plants to sustain photosynthesis, the process by which light is used to convert CO_2 into organic compounds used in carbon fixation (i.e production of sugars), which releases water vapour and oxygen as waste products into the atmosphere (Lambers, Chapin and Pons 2008). In the soil-plant-atmosphere continuum, the plant has to open its stomatal pores on the leaf surface to allow the assimilation of CO_2 from the atmosphere, thereby causing water from the xylem in the plant stem (supplied from the soil through the soil-to-leaf hydraulic system) to evaporate from the surface of the leaves (Brodribb 2009). Transpiration thereby results in water loss by the plant and transpiration rates are higher when there is high atmospheric water demand, i.e. dry, warm conditions in which there is low moisture in the air, or a high vapour pressure deficit (Lambers, Chapin and Pons 2008). In these conditions, plant response in terms of xylem water transport to declining air and soil moisture is highly dependent upon species-specific adaptations and plant size, with trees from tropical moist ecosystems presenting significantly higher maximum transpiration rates compared to those from both boreal and dry ecosystems, with plants from Mediterranean and seasonally dry tropical ecosystems showing intermediate transpiration values (Manzoni et al. 2013).

Conservative water users like succulents will tightly regulate water loss through partial or complete closure of the stomata, while drought tolerant non-succulent species and especially conifers will allow intermediate to high transpiration rates (i.e. stomatal conductance) even when there is a risk of tissue cavitation (i.e. water transport is impeded due water vapour forming in the xylem instead of a continuous water column) due to increasing leaf and water potentials in the xylem (Tyree and Cochard 1989, Johnson et al. 2011). However, even these drought tolerant plants will reach a critical point in which they too have to start closing the stomata to decrease stomatal conductance and transpiration to avoid cavitation and loss of leaf functioning (Sperry et al. 2002). Plants from Mediterranean or seasonally dry ecosystems in particular maintain higher maximum transpiration compared to boreal and arid vegetation in response to seasonal fluctuations in water availability, allowing for high transpiration when soil moisture is available while reducing it during dry spells to avoid loss of leaf function through various phenological adaptions (Manzoni et al. 2013). For example, evergreen sclerophylls develop small, thick leaves with encrypted stomata to avoid loss of water (Salleo, Nardini and Lo Gullo 1997), whereas drought-deciduous species can avoid the effects of drought by seasonally reducing leaf size or even shedding their leaves (Bucci et al. 2005). Similar responses (e.g. stomatal closure, leaf curling) have been found in plants adapted to long-term wind exposure, which avoid water loss through atmospheric turbulence at leaf level but impede photosynthesis and transpiration and reduce leaf size (Grace, Ford and Jarvis 1981; Telewski 1995; Lambers, Chapin and Pons 2008). Trade-offs between xylem safety and efficiency – survival vs transpiration – should therefore be considered carefully when choosing plant species, as the maintenance of high canopy density, transpiration and resistance to drought are all equally important to guaranteeing thermal plant performance on green roofs (Lundholm et al. 2010; Lundholm, Tran and Gebert 2015; Du, Arndt and Farrell 2018).

Plant response to soil moisture fluctuation is therefore a critical factor to survival and growth of vegetation in natural environments, but responses might be harder to predict on artificial environments such as green roofs, where thin engineered substrate, high irradiance and rooftop exposure can limit typical root growth (Savi et al. 2016) and plant height (Grace, Ford and Jarvis 1981). What is generally well established about plant-rooftop interaction is that 1) it is the combined effect of vegetation and growing media that generates the evapotranspirative cooling, shading, high albedo and insulation that drive thermal performance on green roofs (Wong et al. 2003, Castleton et al. 2010, Tsang and Jim 2011, Lundholm and Williams 2015, Raji et al. 2015, Simmons 2015, Eksi et al. 2017, He et al. 2017, Fabiani et al. 2018), and that 2) plant drought tolerance or avoidance strategies and substrate properties are both critical factors in determining plant persistence and performance on green roofs (Young et al. 2014; Simmons 2015; Savi et al. 2016; Tan et al. 2017; Brunetti, Porti and Piro 2018; Du, Arndt and Farrell 2018; Fabiani et al. 2018). However, while the properties of growing media that contribute to green roof thermal mitigation are relatively well understood (e.g. Nardini et al. 2012; Berretta, Poë and Stovin 2014; Graceson, Monaghan and Hare 2014; Stovin et al. 2015; Pianella et al. 2016; Reyes et al. 2016; Kazemi and Mohorko 2017; Pianella et al. 2017; Tan et al. 2017; Fabiani et al. 2018), the same cannot be said of plant mechanisms, which are more complex, work interdependently and would benefit from additional investigation (Jim 2012; Van Mechelen et al. 2015; Azeñas et al. 2018; Cao et al. 2019; Du, Arndt and Farrell 2019), especially from more studies directly correlating specific plant characteristics to temperature buffering (Vaz Monteiro et al. 2017). In fact, the recent study by Du, Arndt and Farrell (2019) revealed that survival of a range of shrubs on green roofs was not determined by either their drought response, water use strategy or climate of origin, but most likely by a combination of physiological traits or tolerance strategies at the *whole plant level*. This highlights the need for a deeper, more holistic understanding of the exact nature of plant-rooftop interactions and how best to exploit them to improve green roof design (Simmons 2015).

2.6 Plant thermal interaction, ecophysiology and trade-offs of tall woody plants on rooftops

Any plant coverage at all on a rooftop would certainly have a higher albedo and water retention capacity compared to a conventional roof (Berardi et al. 2014), so even the predominant use of a relatively small variety of mostly hardy, low-growing and short-lived species still contributes positively to the improvement of urban settings. Nevertheless, the passive cooling property of green roofs is not only due to higher values of albedo, but to the combined effects of soil insulation (i.e., higher substrate depth), evapotranspiration and shading created by the vegetation canopy (Bowler et al. 2010, Castleton et al. 2010, Lundholm et al. 2010, D'Orazio et al. 2012, Jaffal et al. 2012), with even wind significantly reducing temperatures at roof deck level (Jim and Peng 2012). The most important vegetation traits that influence heat transfer on green roofs are in fact plant height, leaf area index, fractional coverage, reflectivity and plant transpiration rates (Sailor 2008). Both leaf area index, LAI (or canopy foliage density), and leaf angular orientation (or phyllotaxis) are important for intercepting solar radiation and reducing its course through the canopy. LAI can range from 0 for bare ground to over 15 in conifers (Raji et al. 2015) and plant species with large, horizontal leaves have the highest solar intercepting/shading effect on a green roof (Palomo Del Barrio 1998). In fact, Jaffal et al. (2012) found that increasing the LAI on a green roof from 0.5 to 2, 3.5 and 5.0 resulted in significant reductions in indoor air temperature and cooling demand in the summer.

There are ecological advantages related to the low-growing habit, especially when combined with succulence, because it provides plants with a higher level of resistance to conditions of exposure (i.e., high insolation, wind) due to the lower transfer rates between plant surfaces and the air in plants of low stature compared to taller growth forms. However, a very important advantage in planting taller growth forms on green roofs is the fact that these can act as a natural 'windbreak', representing a means by which to slow down air flow and transfer the momentum from the atmosphere to the leaves and branches of the vegetation (Grace, Ford and Jarvis 1981). Together with higher shading and transpiration rates, taller growth forms also encourage the development of a special microclimate between the vegetation and the soil, which allows the formation of a layer of air (i.e., boundary layer) between the soil and the leaves (Lundholm et al. 2010) and therefore represents an additional buffer between rooftop and ambient conditions. With their lower shading capacity, short vegetation inevitably has lower transpiration rates compared to taller growth forms (Bond et al. 2008) and, therefore, would have a minor impact on a green roof's evaporative cooling effect and runoff reduction (Lundholm et al. 2010, Vaz Monteiro et al. 2016). On the other hand, taller growth forms are more exposed to wind and chilling and are susceptible to damage and soil moisture deficit (Jaffe 1973; Grace, Ford and Jarvis 1981; Telewski 1995; Ennos 1997). Moreover, substrate depth and irrigation needs increase with vegetation height and root system (Catalano et al. 2018).

However, as shading and evapotranspiration (Castleton et al. 2010, Heim and Lundholm 2014, Raji et al. 2015, Zölch et al. 2016, He et al. 2017), as well as high vegetation density (Olivieri et al. 2013), are key factors in daytime heat and substrate temperature mitigation on green roofs, maintaining shoot growth (Lundholm, Tran and Gebert 2015) and opting for taller growth forms like shrubs could represent a valuable strategy for optimising building thermal performance and other ecosystem services (Farrell et al. 2013; Lundholm and Williams 2015; Du, Arndt and Farrell 2018; Tran et al. 2019; Lee and Jim 2018; Cascone et al. 2019b; Zhang et al. 2019). In fact, tall plants provide higher shading, insulation and evapotranspiration (Theodosiou 2003, Monterusso et al. 2004, Farrell et al. 2013, Qiu et al. 2013, Cascone et al. 2019b), and plant canopies with high leaf density, biomass and lower absorptivity (e.g. light-coloured leaves) can significantly affect the provisioning of thermal benefits through greater reflectivity, cover and interception of solar irradiance (Wong et al. 2003; Lundholm et al. 2010; Lundholm, Tran and Gebert 2015; Raji et al. 2015; Berardi 2016; Karachaliou et al. 2016; Azeñas et al. 2018; Cascone et al. 2019b), resulting in the combined reduction of substrate temperatures (Sailor 2008; Treml, Hejda and Kašpar 2019), water loss (MacIvor and Lundholm 2011; Heim, Lundholm and Philip 2014) and weed growth, thereby lowering maintenance costs (Nagase, Dunnett and Choi 2013).

Tall, woody plants like shrubs have a greater cooling capacity compared to *Sedum* sp. and the majority of low-growing green roof plants, owing mostly to 1) their taller canopy height and thus greater shading capacity; 2) their lower leaf stomatal resistance and therefore higher stomatal conductance and transpiration rates, which cool the leaf and surrounding air temperature, and 3) to their greater evapotranspiration potential in relation to their higher water use, all of which work together to reduce substrate temperatures and stormwater runoff (Alexandri and Jones 2007; Bond et al. 2008; Lambers, Chapin and Pons 2008; Sailor 2008; Wolf and Lundholm 2008; Berretta, Poë and Stovin 2014; Stovin et al. 2015; Soulis et al. 2017; Du, Arndt and Farrell 2018; Lee and Jim 2018; Zhang et al. 2019), especially when compared to succulents (Blanusa et al. 2013, Farrell et al. 2013, Vaz Monteiro et al. 2017, Du et al. 2018, Cao et al. 2019). Succulents, through their CAM photosynthetic strategy, are highly drought tolerant because they are able to store excess water in their herbaceous tissues and to fix CO_2 during the night, allowing their stomata to remain shut during the day to avoid transpirational water loss (Lambers, Chapin and Pons 2008). Therefore, the argument against the use of CAM-photosynthesising plants would be that shifting photosynthetic activity at night, where it normally would occur during the day in regular C_3 and C_4 plants (Lambers, Chapin and Pons 2008), defeats the purpose of a green roof: the combination of extreme water use efficiency and no transpiration during the day (when evaporative cooling is *most* needed) and significant night cooling during the night (when evaporative cooling is *least* needed, especially in the winter) by CAM plants and shallow media prone to desiccation does not likely guarantee significant cooling benefits that improve green roof thermal performance (Lundholm et al. 2010, Vaz Monteiro et al. 2017, Cao et al. 2019).

The shrub form undoubtedly has several advantages over low-growing plants in terms of potential green roof functional improvement. However, plants in general are subjected to varying degrees of water stress under green roof conditions, where variations in temperature, light, water availability, and wind are accentuated on exposed sites like rooftops. High exposure and soil desiccation due to shallow substrate and intensified daily and seasonal temperature excursions causes loss of plant and soil moisture content through evapotranspiration, reducing plant growth and the number of species that can survive with limited irrigation (Snodgrass and Snodgrass, 2006, Oberndorfer et al. 2007, Luckett 2009, Nardini et al. 2012; Savi et al. 2016). Moreover, green roof design is geared towards the use of ever shallower and more lightweight substrate (Oberndorfer et al. 2007, Snodgrass and McIntyre 2010, Cao et al. 2014), thereby the combination of harsh rooftop conditions and limitations to substrate depth implies that green roof vegetation has to cope with variable water availability throughout the year (Getter, Rowe and Andersen 2007; Nagase and Dunnett 2010; Liu et al. 2012). To further stress the point, evaporation during the dry season even in natural field conditions, especially where there is shallow soil and the vegetation does not completely cover the whole surface – as can be the case on a green roof – can reduce soil water content to values as low as 5% (Villegas et al. 2010). Therefore, a careful evaluation of the ecology of plants that grow in environmental conditions similar to those found on green roofs (high wind exposure, shallow and nutrient-poor substrate, intense radiation, extreme temperatures, and periods of drought), as well as a proper understanding of the various abiotic stress factors involved, are crucial to selecting successful green roof vegetation (Nagase and Dunnett 2010; Olly et al. 2011; Cook-Patton and Baurle 2012; Rowe, Getter and Durham 2012; Caneva et al. 2015; MacIvor et al. 2016a).

In regard to what component – substrate depth or vegetation – has more influence on evapotranspiration rates and temperature on a green roof is a matter that has received mixed views from a number of authors, with some (VanWoert et al. 2005, Nardini et al. 2012) finding that vegetation aids comparatively less to water retention as opposed to substrate, while others (Berghage et al. 2007, Dunnet et al. 2008, Lundholm et al. 2010, Schroll et al. 2011) report significant effects of vegetation on water runoff, especially with higher species and plant form diversity. Moreover, Wong et al. (2003) found that the heat flux at night between a roof covered with bare soil and one with plants were similar, which would lead to conclude that plant canopies might have reduced ability to insulate during the night due to reduced plant activity. However, together with greater evaporative cooling, plants with higher transpiration rates can achieve better soil water depletion and thus higher percentages of runoff reduction on green roofs (Lundholm et al. 2010). As soil evaporation is generally restricted to the upper few centimetres of the soil profile, transpiration can often account to up to 90% of total evapotranspiration (Xiong et al. 2005, Bond et al. 2008), even in a system with relatively low canopy cover (Williams et al. 2004). The root system increases with above-ground size from annuals to shrubs and trees (Schenk and Jackson 2002), thereby woody and taller growth forms have the potential to greatly increase evaporative losses from an ecosystem because of their higher evaporative surfaces and greater access to soil water through roots compared to smaller growth forms (Bond et al. 2008). For shrubs in particular, differences in canopy transpiration and water use, in conditions of both low and high soil moisture availability, are primarily on account of foliage density in the canopy (Xiong et al., 2005; Sun, Kopp and Kjelgren 2012).

2.7 The shrub growth form – advantages & disadvantages to using shrubs on green roofs

Defining what "shrubs" actually are and elucidating their ecological adaptations in natural ecosystems can further inform of their potential survival, fitness and cooling/insulating performance on green roofs. Shrubs are loosely defined as low-growing (< 2 m) perennial plants that do not develop a distinct main trunk but have self-supporting, multiple woody stems branching at or near the ground (Orshan 1989, Rundel 2012, Götmark et al. 2016). The shrub lifeform has been shown to be successful in many diverse habitats and ecosystems (e.g. Mediterranean and desert regions, arctic and alpine tundras), due to their wide range of architectural (e.g. many stems, dual root systems), phenological (e.g. evergreen or drought-deciduous leaves), morphological and physiological (e.g. resistance to cavitation, sclerophylly) adaptations to environmental stress, especially to drought, high and low temperature and low nutrient availability (Salleo, Nardini and Lo Gullo 1997; Schenk et al. 2008; Rundel 2012; Götmark et al. 2016). In fact, their need to endure stress or chronic disturbance makes them more "thrifty" in terms of carbon use, in that shrubs do not need to rebuild as much biomass each year as herbaceous plants do (Stutz 1989), as they produce persistent woody stems that would only be shed in high stress conditions (Wilson 1995). On the basis of leaf morphology and phenology, the shrub lifeform can broadly be subdivided into evergreen or deciduous and xeromorphic or mesomorphic plants, with a wide spectrum of intermediate forms (Rundel 2012). Although all plants change form and can present more than one lifeform throughout their lives (Halloy 1990), this is especially true for shrubs and this growth form shows remarkable phenological diversity. High phenotypic plasticity is said to increase species fitness and adaptiveness (Bradshaw 1965; Lambers, Chapin and Pons 2008) and the shrub growth form, with its high phenological and ecophysiological plasticity, reflected in the numerous examples of convergence found in different biomes and ecosystems, represent the winning combination of longevity and adaptability that is needed for the hostile green roof environment.

Woody plants are generally classified as C_3 plants. The C_3 photosynthetic strategy is the most common metabolic pathway for carbon fixation in plants, whereas the CAM and C_4 strategies are more recent adaptations found in particular plant groups (e.g. succulents and grasses) that have evolved biochemical traits to resist desiccation and conserve water (Lambers, Chapin and Pons 2008) and are confined to the herbaceous growth form (Still et al. 2003). Although the studies by Kuronuma and Watanabe (2017) and Cao et al. (2019) present evidence that C_4 plants (grasses) show higher transpiration and photosynthetic rates and provide greater cooling compared to both CAM and C_3 plants growing on green roofs, their studies compared only succulents and grasses belonging to CAM, C_3 and C_4 groups, thereby excluding woody plants like shrubs and trees. Moreover, the study by Detto et al. (2006) showed that Mediterranean woody vegetation (various trees and shrub species of Sardinia, Italy) was highly tolerant to long periods of drought, transpiring at rates close to cavitation for even the driest conditions, while grass vegetation was considerably less tolerant to soil moisture deficits, transpired at lower rates compared to the woody vegetation and wilted at the beginning of the dry summer season. In fact, while CAM and C_4 plants are highly tolerant of drought compared to C_3 due to high water use efficiency, they also have lower stomatal conductance and consequently reduced transpiration in the same environmental conditions (Lambers, Chapin and Pons 2008). Therefore, shrubs not only have higher shade and evaporative cooling compared to lower-growing plants, but they are also more likely able guarantee this cooling service for longer throughout the year, especially if evergreen and drought tolerant.

The canopy characteristics of woody shrubs have the potential to provide higher levels of shading on a rooftop, compared to low-growing vegetation. In fact, both leaf area index and annual net primary productivity for shrub dominated areas, particularly in mesic habitats, have been known to exceed that of most temperate forest canopies (Huxman et al. 2005, Knapp et al. 2008). Plants growing on rooftops, however, are often exposed to high levels of irradiance and therefore have to be able to tolerate excess light. Photoprotection strategies are varied amongst the different growth forms, but the unique crown architecture of the shrub form permits the dense and homogeneous display of vertically hanging leaves through the canopy, thus minimizing self-shading (Rundel 2012) while efficiently exploiting horizontal space (Knapp et al. 2008). Especially for drought-adapted shrubs, adaptations such as small, thick and waxy leaves (Puigdefábregas and Pugnaire 1999, De Micco and Aronne 2012), encrypted stomata (Puigdefábregas and Pugnaire 1999), leaf and stem pubescence (Sandquist and Ehleringer 1998), steep leaf angles (Valladares and Pearcy 1998), leaf folding (Gulmon and Chu 1981; Pugnaire, Haase and Puigdefábregas 1996) and paraheliotropic leaf movements all provide structural photoprotection that helps maintain leaf energy balance and optimize plant growth and functioning (Puigdefábregas and Pugnaire 1999). In particular, leaf pubescence and cuticle wax can determine changes in reflectance, thus indirectly affecting leaf surface temperature and solar interception (De Micco and Aronne 2012), and ultimately increasing green roof albedo.

As described in the previous sections, shrubs have potentially greater shading and evaporative cooling capacity through their taller height, higher transpiration rates and greater water use compared to low-growing green roof vegetation (Alexandri and Jones 2007; Bond et al. 2008; Lambers, Chapin and Pons 2008; Sailor 2008; Wolf and Lundholm 2008; Berretta, Poë and Stovin 2014; Stovin et al. 2015; Soulis et al. 2017; Du, Arndt and Farrell 2018; Lee and Jim 2018; Zhang et al. 2019). There are examples of the shrub form's exceptional insulating and cooling capacity in natural environments. For example, shrub canopy cover in tundra ecosystems has been found to be the most important factor influencing soil temperatures, maintaining them significantly higher in the winter and cooler in the summer (Myers-Smith and Hik 2013). Moreover, studies comparing small shrubs and small trees either with equivalent above-ground woody volume and growing conditions (Götmark et al. 2016) or with equivalent ecological distribution (*Pinus mugo* vs *Picea abies*, Treml, Hejda and Kašpar 2016) showed that shrubs have a higher growth rate, total leaf area and lower vulnerability to drought and mortality in conditions of extreme environments compared to trees. In particular, shrubs have a larger sprouting area and faster production of twigs and canopy (Götmark et al. 2016) and maintain a lower mean soil temperature due to their higher shading capacity at ground level (Treml, Hejda and Kašpar 2016). As even slightly higher shade at ground level translates into higher substrate moisture content on green roofs (Getter, Rowe and Cregg 2009), a positive feedback can be established, where shrubs can determine their own optimal sub-canopy microclimate through self-shading (Treml, Hejda and Kašpar 2016); their ability to buffer soil temperatures can thus lead to better overall fitness and canopy growth, which in turn can improve the cooling performance of green roofs through higher surface shading, albedo and transpiration rates due to denser and healthier leaves.

Therefore, shrubs can represent a more functional growth form for green roof vegetation – an effective compromise between low vegetation that may survive on very shallow substrate but have relatively short lives and low cooling potentials, and trees that may live longer and have higher shading and transpiration rates but may struggle to survive on even relatively deep green roof substrate due to their higher vulnerability to drought and freezing. Shrubs can also provide a potentially more stable plant community on a green roof compared to succulents, forbs and grasses, achieved through: continuous presence (i.e. longevity, little or no species composition change due to competition/dominance), cover (e.g. perennial leaves and densely planted individuals or with prostrate canopies) and biomass (e.g. fast-growing shoots, high leaf density); higher structural security (i.e. multi-stemmed branching ensures survival of whole plant in case one or more stems die) and endurance in the face of environmental fluctuations (i.e. acclimation) and thus reduced vulnerability to change (especially to changes in soil water deficits), all of which would provide a more long-term provisioning of thermal and other ecosystem services (Rundel 2012; Lambers, Chapin and Pons 2008; Cook-Patton and Baurle 2012; Jim 2012, Speak et al. 2013; Rowe 2015; Götmark et al. 2016; Heim and Lundholm 2016; Eksi et al. 2017). Moreover, there is proof that drought-tolerant woody shrubs have relatively high growth and survival rates on an experimental green roof with nutrient-poor and very shallow (10-13 cm) substrate (Savi et al., 2015), with some evidence that they can even provide significantly greater thermal insulation capacity compared to herbaceous perennials (Love 2015).

Although popular in horticulture, and despite the potential advantages of using taller, woody plants on green roofs, shrubs are often neglected in ecological studies (Götmark et al. 2016), a lack of knowledge which can partly explain the resistance to testing them in green roof studies. Undoubtedly, both the lack of research and the fact that the use of deeper substrates is recommended by most, if not all, green roof guidelines to give shrubs and trees the best chance to survive, grow and provide long-term ecosystem services (Catalano et al. 2018) do not help promote the implementation of either shrubs or intensive systems by practitioners. For example, Van Mechelen et al. (2014) exclude by default both criteria ‘typical plant height’ (> 1 m) and woody ‘lifeform’ (phanerophyte) in their proposed selection process for potential green roof plants. Coupled with higher structural load and costs for intensive systems, the reason for this reluctance is most likely related to the potentially higher irrigation requirements for more water-demanding plants like shrubs. In fact, shrubs that grow on shallow green roof substrates tend to have reduced biomass and water use (Savi et al. 2015) due to lower growth rates in response to stress from high substrate temperatures and drought (Lambers, Chapin and Pons 2008; Farrell et al. 2012; Metselaar 2012; Reyes et al. 2016; Savi et al. 2016), which can ultimately translate into lower cooling capacity due to lower evapotranspiration, canopy density and shading (Lundholm, Tran and Gebert 2015).

However, the need for supplementary irrigation may be avoided if carefully-selected shrubs are tested in temperate climates like the UK, where natural precipitation throughout the year is not a limiting factor (Vaz Monteiro et al. 2017), especially if the substrate and other green roof components are adjusted for greater moisture retention, for example with the use of a water retention layer, a higher percentage of organic and/or porous, lightweight substrate and hydrogel- or biochar-based soil amendments (Nagase and Dunnett 2011; Ntoulas et al. 2013; Farrell, Ang and Rayner 2013; Cao et al. 2014; Graceson, Monaghan and Hare 2014; Young et al. 2014; Rowe 2015; Savi et al. 2013, 2014, 2015; Raimondo et al. 2015; Simmons 2015; Farrell et al. 2016; Young, Cameron and Phoenix 2017; Chen et al. 2018; Cipolla et al. 2018; Sookhan, Margolis and MacIvor 2018). In fact, the study by Raimondo et al. (2015) comparing the water use strategies of two Mediterranean shrubs growing on green roof modules found that even subtle differences in substrate properties, in particular particle size, had significant effects on the water retention capacity of the substrate and hence the soil water potential reached and the amount of water available to the shrubs. If the aim is to increase green roof thermal performance, it is essential to not base plant choice solely on which species survive on shallow substrate with little or no irrigation, but also on the features that can potentially optimise the delivery of thermal benefits (Nardini et al. 2012, Blanuša et al. 2013, Simmons 2015, Vaz Monteiro et al. 2017) – namely, deeper substrate and taller plants with higher water use and transpiration rates (e.g. Lee and Jim 2018) – especially when the local climate is favourable.

2.8 The use of shrubs in green roof research

There are many studies that have used either sub-shrubs, woody shrubs or even trees as part of a vegetation mixture on both extensive and intensive systems. For example, Nardini et al. (2012) compared the effects of substrate depth and vegetation (herbaceous perennials vs shrubs) on stormwater runoff reduction; Payne et al. (2018) looked at plant selection for stormwater biofiltration; Heim and Lundholm (2016) investigated phenological complementarity in different plant types and Xie, Lundholm and MacIvor (2018) concluded that phylogenetic diversity and traits in different plant types can predict substrate cooling. There are currently no studies testing shrubs or even vegetation mixes that include shrubs specifically in winter conditions. A number of studies have monitored the thermal behaviour of intensive green roofs, for example a few on the effect of native woodland vegetation on rooftop temperatures in humid subtropical climate (Jim and Tsang 2011, Lee and Jim 2018, Peng et al. 2019), or the effect of mixed vegetation that includes shrubs on air temperature and the effects of drought damage on the vegetation's cooling capacity in the northern UK (Speak et al. 2013). However, only about a dozen studies have tested the survival, growth, cooling performance, morpho-anatomical and/or physiological response of shrubs. In these studies, shrubs were tested either in a vegetation mixture with herbaceous perennials and/or trees (Wong 2003; Jim and Tsang 2011a, 2011b; Nagase and Nomura 2014; Lee and Jim 2018) or on their own to compare the growth of semi-woody subshrubs (Papafotiou et al. 2013), to be compared with other plant genotypes (Huang Chen and Liu 2018) or to assess particular canopy or leaf traits for cooling services (Jim 2012, Vaz Monteiro 2017). In a few studies, one specific shrub species (Kotsiris et al. 2012) or two shrub species were compared (Raimondo et al. 2015, Savi et al. 2015) in terms of survival, growth, morpho-anatomical and/or ecophysiological responses to substrate depth and type, water use and drought and temperature stress. Lastly, the studies by Du, Arndt and Farrell (2018, 2019) and Savi et al. (2016) provide the most complete 'picture' of how the shrub growth form interacts, morpho-anatomically and ecophysiologically, with the rooftop environment, despite not correlating directly with below-canopy temperatures or rooftop thermal behaviour. To date, no studies have yet looked at the effects of spatial variation, density and canopy structure of shrubs on rooftop temperature mitigation.

The following are short summaries of the most relevant studies that have tested shrubs for either their cooling capacity, their ability to survive on rooftop environment or a combination of the two.

Papafotiou et al. 2013 – Growth of small semi-woody shrubs on extensive systems

Six **s**mall Mediterranean semi-woody subshrubs (*Helichrysum italicum*, *H. orientale*, *Origanum majorana, O. dictamnus, Santolina chamaecyparissus, Artemisia absinthium*) were planted on 7.5-cm or 15-cm green roof substrate depth on a rooftop, with two different substrate mixtures (either with peat or with compost), and were either sparsely or normally irrigated. The main result was that all shrubs except *O. dictamnus* showed higher dry weight (biomass) in deeper substrate with compost.

Kotsiris et al. 2012 – Monitoring of a single shrub species for certain morphological and physiological responses to semi-intensive substrate depth/type in field containers

Lavandula angustifolia growth and physiological response in Mediterranean climate conditions were monitored in field containers (1.2 x 1.2 m, 4 shrubs per container), planted in either 20 cm or 30 cm deep substrate and with three different lightweight substrate mixes. The deeper substrate (30 cm) provided higher growth and root dry weight, higher chlorophyll content and reduced leaf stomatal resistance compared to the shallower substrate.

Nagase and Nomura 2014 – **Long-term monitoring of tree and shrub survival and growth on intensive green roof system**

An intensive green roof (50 cm of lightweight green roof substrate) that had been neglected for eight years was used to study and identify trees and shrubs that could survive low levels of irrigation and maintenance. In 2002, twelve species of trees and eighteen of shrubs, all commonly used in gardens, parks and amenity landscapes in Japan, were planted and found to have a survival rate of about 70% for both growth forms after eight years. Most surviving trees (e.g., *Cornus florida*, *Quercus glauca*) showed little growth, while a few, like *Ilex rotunda* and *Styrax japonica*, showed severe stress symptoms (few leaves and numerous dead branches). The most successful tree species were *Myrica rubra*, which showed vigorous growth and no symptoms of stress, *Cinnamomum camphora* and *Osmanthus fragrans*. As for the shrubs, half of the species showed vigorous growth and flowering, including: *Abelia* x *grandiflora*, *Camellia sasanqua*, *Forsythia suspense, Hydrangea macrophylla*, *Hypericum chinense*, *Spiraea thunbergii*, and *Viburnum dilatatum*. However, all the species belonging to the Rutaceae family died, while *Eurya japonica*, *Loropetalum chinense*, and *Photina* x *fraser* showed high mortality rates. Overall, the authors noted that shrubs grew successfully without irrigation or maintenance on the 50-cm deep substrate, and particularly that a high density planting seemed effective in increasing wind resistance, which contributed to their survival.

Jim and Tsang 2011a, 2011b – Thermal behaviour of woodland vegetation through the different seasons and growing on an intensive green roof in subtropical climate

Jim and Tsang (2011b) examined the thermal behaviour of an intensive green roof (100 cm depth) with woodland vegetation native to Hong Kong (subtropical climate, rooftop on a 14-m, 4-storey building). Environmental sensors monitored microclimate and soil parameters for 14 months, along with transpiration, wind, light and energy flux. They found that the woodland vegetation formed a stable sub-canopy environment, with only about 20% of solar irradiation reaching the substrate surface on sunny days and a reduction of energy flux into the substrate of 300 W m^{-2}. On the same experimental site, Jim and Tsang (2011a) also found that just 10 cm of substrate is enough to reduce heat penetration into building and that seasonal variations heavily dictates transpiration. They also found that the tree canopy can both intercept solar irradiation and trap air temperature near the substrate surface.

Lee and Jim 2018 – Cooling by woodland native vegetation on intensive green roof in subtropical climate

Using detailed microclimatic monitoring, the study investigated the thermal behaviour of an intensive (100 cm substrate depth) green roof in subtropical Hong Kong (14-m, four-storey building) with native woodland vegetation with herbaceous perennials, shrubs and trees. Three specific summer days (sunny, cloudy and rainy) were chosen to compare with control. Shading and evapotranspiration by the woodland vegetation significantly reduced roof surface temperature and air temperature, with a maximum surface and air temperature reduction of 19.80 °C and 6.21 °C, respectively, achieved in daytime sunny conditions and by filtering 90% of incoming irradiance and with cooling effect extending into night-time. Surface cooling was driven by daily patterns of solar irradiance, whereas air cooling was affected more by substrate surface dynamics. The substrate showed limited heat flux at 50-cm depth and therefore maintained a stable temperature.

Wong et al. 2003 – Effect of woody vegetation on temperature abatement in intensive green roof system in tropical climate

A field experiment on an intensive green roof in tropical climate (Singapore) covered with grass, shrubs and trees (on a low-rise building) was carried out to measure the impact of the vegetation on roof surface temperature and heat flux. Maximum surface temperature under dense vegetation was 25.6 °C compared to 42 °C on bare soil and 57 °C on bare roof during conditions of high irradiance (1400 W m^{-2}). There was also both no heat gain under the dense shrub foliage as well as maximum heat loss with shrubs.

Huang, Chen and Liu 2018 – Comparison of the cooling capacity of different plant growth forms (shrub vs herbaceous perennial)

The temperature at the bottom of herbaceous perennial, shrub, vine and groundcover green roof modules grown on 15-cm substrate were compared, and the study found that they were 17.75, 12.57, 11.55 and 9.31 °C lower than the bare rooftop, respectively. The herbaceous perennial (*Impatiens walleriana*, vigorous growth, good cover) therefore surpassed the shrub (*Aglaia odorata*, evergreen, fast growing) in cooling capacity. The lower cooling capacity of the shrub could be related to the substrate depth (15 cm), which would have been ideal for the herbaceous perennial but not so much for the shrub.

Jim 2012 – Comparison of the cooling capacity of different plant growth forms (shrub vs herbaceous perennial vs grass) in relation to biomass structure complexity

The cooling effect of extensive green roofs in humid tropical climate was investigated with reference to three vegetated plots vs control: grass (*Zoysia tenuifolia*, 3.5 cm depth), groundcover herb (*Arachis pintoi*, 5 cm) and shrub/climber hedge (*Duranta repens*, 8 cm), with contrasting growth form and biomass structure. All vegetation buffered diurnal minimum and maximum air temperature but did not cool the air at night compared to control. The grass plots showed greater air cooling than both groundcover and shrub plots. The shrubs (70 cm tall, with the densest and most complex biomass structure) showed the most extreme diurnal air temperature regime, while grass (with the simple biomass structure) cooled the air more effectively than both groundcover herb and shrub. Of the three vegetated roofs, the shrub plots had the widest temperature amplitude, with the highest maximums and lowest minimums. The authors related this odd thermal behaviour of the shrub plots to the ‘stagnant’ air within the shrub biomass, which trapped heat. However, it could also be related to the extremely shallow substrate (8 cm) on which the shrubs were growing on, which would generate extreme temperature fluctuations and high substrate temperatures.

Du, Arndt and Farrell 2018, 2019 – Shrub survival, water relations, water use and drought adaptations in glasshouse experiments vs extensive green roof modules in hot dry climate

Du, Arndt and Farrell (2018) carried out a glasshouse experiment to determine the possible trade-offs between shrub water use for stormwater management and their response to drought conditions. Twenty shrubs (6-month old seedlings in tube stock, potted in individual 6-L pots containing green roof substrate, 19-cm depth, scoria & coir) were selected from a wide range of climates of origin (all Australian native species: *Derwentia*, *Prostanthera*, *Daviesia*, *Hardenbergia*, *Indigofera*, *Eremophila*, *Calytrix*, *Grevillea*, *Olearia*, *Dillwynia*, *Cheiranthera*, *Correa*, *Goodenia*, *Dodonaea*, *Eutaxia*). Either under well-watered or water-deficit conditions, the shrubs were evaluated in terms of their response to water availability, evapotranspiration rate and midday water potential to determine species water use and drought response. All species adjusted their transpiration rates and water potentials in conditions of water deficit. However, there were no species that simultaneously achieved high rates of water use under well-watered conditions and high drought tolerance under water deficit, although some species that did have high water use under well-watered conditions could avoid drought stress. Water use was strongly related to plant biomass, total leaf area and leaf traits (specific leaf area and leaf area ratio), and therefore these traits could be used for the selection of shrubs for green roof stormwater mitigation. Du, Arndt and Farrell (2019) further found that the same species planted in 20 replicated green roof modules with 13-cm substrate depth in the field had a survival rate that ranged between 10% and 100%, even though plant drought response, water use strategy and climate of origin were not strongly related to survival. The authors suggest survival on green roofs is likely determined by a combination of physiological traits

Vaz Monteiro et al. 2017 – Cooling services provided by specific leaf traits

The canopies of two succulent (*Sempervivum*, *Sedum*) and four broad-leaved plants (*Heuchera* sp., *Salvia officinalis*, *Stachys byzantina*,) with contrasting plant traits were monitored in small field plots for two summers in the UK. Non-succulent canopies, in particular light coloured ones, with high leaf stomatal conductance and high LAI, provided the highest potential for substrate insulation and cooling in the summer. These results suggest that succulent plants may be less suited for significant summertime cooling and substrate insulation.

Raimondo et al. 2015 & Savi et al. 2015 – Physiological response of shrubs in relation to substrate depth/properties, water deficit and temperature stress in Mediterranean climate

In the study by Raimondo et al. (2015), *Arbutus unedo* and *Salvia officinalis* were grown on 18-cm deep green roof modules in southern Italy. *Arbutus* was considered a better candidate for green roof vegetation for its isohydric behaviour in dealing with drought stress (i.e. progressive reduction of stomatal conductance, or stomatal closure) under water stress, which allowed it to limit water loss and maintain relatively stable leaf water potential values under both well-watered and drought stress conditions. In contrast, *Salvia* maintained high stomatal conductance until substrate water potentials reached critical values (i.e. anisohydric behaviour), below which it reduced its gas exchange rates by 50% and shed its leaves. The authors concluded that *Arbutus* could better overcome intense drought condition, although only regular, minimum irrigation would guaranteed survival. Savi et al. (2015) monitored the water status, growth and evapotranspiration of drought-adapted shrubs (*Cotinus coggygria* and *Prunus mahaleb*) growing on experimental green roof modules with 10 or 13 cm deep substrate. Shallower substrate depth was found to promote lower water consumption by the shrubs as a likely consequence of reduced plant biomass.

Savi et al. 2016 – Survival, growth and morpho-anatomical and ecophysiological response of shrubs in relation to drought, substrate depth and substrate temperature stress

Water status, growth, survival and plant indicators of drought and heat stress tolerance of 11 drought-adapted shrubs growing on shallow green roof modules (10 and 13 cm deep substrate) were monitored and analysed in relation to substrate temperature fluctuations. The shrub species used were: *Cistus salviifolius*, *Cotinus coggygria, Emerus majus, Ligustrum vulgare, Paliurus spina-christi, Phillyrea angustifolia, Pistacia lentiscus, Prunus mahaleb, Prunus spinose, Pyrus pyraster, Salvia officinalis, Spartium junceum.* The plant traits analysed were leaf turgor loss point, osmotic potential at full turgor, water potential inducing 50% loss of conductivity, leaf water potentials, and stomatal conductance. These plant traits influenced plant water status and can be used to predict plant water use and growth rates on green roofs. The more drought-tolerant species had lower water use and growth rates, while survival on the green roof was significantly correlated to root resistance to substrate heat stress.

3 Purpose and aims of the research project

The main purpose of the research project was to use potential findings from experiments carried out at whole-plant level to demonstrate how the unique qualities of the shrub lifeform can provide greater cooling and insulation mechanisms compared to more commonly used low-growing green roof plants, with the hope of further encouraging their use in green roof technology and other green infrastructure.

3.1 Aims and structure of the research project

To carry out its objectives, for greater clarity to the reader and for better comprehension of the findings, the research project was split into two studies, each one examining a different aspect of the issue that unites them:

- **Study ‘A’** – The effect of species traits, plant density, population size and species mixture on the morphological and physiological performance of six woody shrubs growing on rooftops, and
- **Study ‘B’** – The effect of species traits, plant density, population size and species mixture on the thermal performance of six woody shrubs growing on rooftops.

Each study will have a chapter dedicated to: 1) describing the materials and methods used, 2) the presentation of the results and 3) the discussion of the findings.

Study ‘A’ and Study ‘B’ are deemed by the author as ‘two sides of the same coin’, the ‘coin’ being the main factors determining the relationship between plant functional traits and temperature abatement. The final Conclusions chapter of the thesis will therefore analyse the findings from Study ‘A’ and Study ‘B’ as a whole, with the aim of underpinning the cooling/insulating mechanisms of woody shrubs and how these affect shrub survival and performance as potential green roof vegetation for intensive systems in a temperate climate. Findings from this research project could potentially improve the plant selection process for functional green roofs, promote the use of woody shrubs in green infrastructure and contribute to the knowledge of what characteristics and conditions make for high-performing green roof vegetation in terms of thermal insulation, fitness and longevity.

3.2 Hypotheses and research questions

The following research questions guided the research project:

1) ***How important are species choice and plant spacing in reducing temperature extremes on rooftop environment in different seasons?*** In order to answer this question, it was necessary to determine if species choice and spacing (i.e. plant density and population size) could significantly affect temperature profiles on the rooftop in both winter and summer scenarios in terms of insulation and cooling, respectively. Results may shed light on the implications of using shrubs and different spacing arrangements on building energy management.
2) ***How important is 'species mixture', or the combination of species, in potentially optimizing the cooling and insulating properties of green roofs in the warm and cold seasons, respectively?*** In order to answer this question, it was necessary to investigate how 'monospecific' populations (i.e. composed of only one single species) affected rooftop temperatures differently compared to 'polyspecific' populations (i.e. composed of more than one species) of shrubs, and how this could affect their overall cooling/insulating potential.
3) ***Do plants provide a range of 'energy savings options' for green roofs through their specific adaptive strategies?*** Both field and semi-controlled experiments measuring a range of morphological and physiological parameters were used to determine whether different shrub species could provide microclimatic cooling or insulating properties via similar physiological and morphological adaptations, or if there were species-specific adaptations that could hinder or promote cooling/insulating mechanisms. Survival, growth and fitness of the study species were also evaluated in terms of how these factors could affect their potential cooling/insulating capacity in rooftop environment.

The following hypotheses will be tested in order to answer the research questions above:

- Shrubs arranged in a spatially-dense communities on a rooftop have temperature profiles with reduced variation compared to those of sparsely-arranged shrubs;
- Shrubs arranged in spatially-sparse communities on a rooftop provide more opportunity for warming the rooftop surface compared to a dense community of shrubs;
- Shrubs with an evergreen foliage perform in a similar manner when intercepting solar irradiance in winter and summer, and
- The interaction between specific canopy and foliage traits and abiotic factors such as air temperature and irradiance are the main drivers of potential differences in the temperature profiles of the study species.

3.3 Objectives

To answer the research questions, project was designed around experiments that would monitor above- and below-canopy substrate temperatures in relation to rooftop microclimate and the relative growth, survival and fitness (i.e. water relations, transpiration, photosynthesis rate and performance, leaf temperature and water content), water use efficiency and morphological plant traits (i.e. leaf area, canopy density and architecture) of a number of shrub species growing on rooftops. The species chosen for the experiments was based on varying degrees of drought tolerance and other traits that would be advantageous for rooftop conditions.

The objectives of the present study were:

- To evaluate the performance and survival of selected shrub species on rooftops – how rooftop conditions affect different shrub species and how specific plant traits can predict plant fitness on green roofs,
- To examine how the shrub canopy characteristics affect rooftop microclimate and determine which traits (or combination of traits) have the greatest impact on rooftop thermal behaviour,
- To identify co-factors that may be required to ensure the delivery of cooling benefits (species-specific traits, irrigation, spacing, wider abiotic tolerances, etc.), and
- To determine how points above could be used to maximize green roof functionality and optimize cooling capacity and energy savings through the use shrubs and more generally through a refined plant selection process.

The effects of the shrub growth form on rooftop thermal properties were therefore measured and analysed in relation to:

1) Daily and seasonal changes in rooftop abiotic conditions (i.e., irradiance, air temperature, wind speed, precipitation, relative humidity),
2) Daily and seasonal changes in temperature and relative humidity beneath the plant canopy at substrate level compared to controls,
3) Arrangement of plant population density (dense vs sparse),
4) Different combinations of shrub species (populations of monospecific vs mixed species),
5) Plant responses that indicate temperature or drought stress (e.g. transpiration rates, photosynthetic performance, leaf water potential), assess drought tolerance or avoidance strategies (e.g. transpiration rates, water use, leaf mass per area, leaf water content and temperature) or suggest general fitness (e.g. mortality, growth, canopy biomass), and

6) Differences in canopy architecture (branching, leaf density, total leaf area, stem growth).

The correlation between the points above may highlight the significant relationships between rooftop-plant interactions, thermal mitigation and plant cooling/insulating mechanisms, and the possible significant differences in the potential cooling capacity of shrubs at the whole plant level when considering species, spacing and plant combination type.

4 Study area, research sites and experimental design

4.1 Study area and local climate

The study was carried out between December 2015 and August 2018 in two nearby locations within the University of Sheffield, United Kingdom (S10 2TN): on the roof of the Lower Hicks building (Department of Physics and Astronomy) and on the roof garden at the Sir Robert Hadfield building (Department of Materials Science and Engineering). Both sites were equipped with control units with a data acquisition system for weather and climate data, which logged data every 30 and 60 minutes on Hicks and Hadfield roofs, respectively. The Lower Hicks rooftop additionally had solar panels that measured total irradiance at high resolution (every 2 minutes). The Lower Hicks building is considerably taller (15 m) and has a greater roof area (1060 m^2) compared to the Hadfield roof garden (8 m and 750 m^2 in height and area, respectively). However, the area utilised for the experiments was the same on both rooftops (approximately 25 m^2), with the experiments positioned away from the margins of the rooftop and from possible shading by surrounding buildings.

The city of Sheffield (South Yorkshire, England; 53°23’01”N, 1°28’01”W) is located on the eastern slopes of the Pennines at the confluence of the River Sheaf and the River Don, decreasing in altitude by more than 400 m a.s.l. going from the city’s western to eastern limits. The western perimeter bordering the Peak District National Park is considered the city’s ‘greenbelt’, which is interlaid by smaller rivers that trace green valleys and allow the presence of numerous parks near the urban centre (Watts 2004). Sheffield is characterized by a temperate oceanic climate, *Cfb* (Peel et al. 2007), with mean annual temperatures and precipitation in the last decade (2006-2016) averaging 10.3 °C (highest 21.4 °C in July, lowest 2.14 °C in February) and 828.3 mm (highest 93.9 mm in June, lowest 47.8 mm in September), respectively. Over the same period, mean annual sunshine was 1443 h, with July the sunniest month (199 h) and January the cloudiest (53 h). Wind is strongest in winter, with prevailing south-westerly winds.

4.2 Comparability of the two research sites

Weston Park (S10 2TP) is the nearest ground-level weather station to the experimental rooftops, located at a distance of 0.3 km and 1.1 km from the Hicks and Hadfield buildings, respectively. The main variables used for recording and monitoring weather conditions on the three sites were mean, maximum and minimum temperature; relative humidity; solar irradiance; wind speed and rainfall. Unfortunately, the three sites are fully and directly comparable only for mean temperature, wind speed and relative humidity, as the Hadfield roof does not record minimum and maximum temperature and rainfall, and Weston Park does not record solar irradiance. Over the three experimental periods (1/2016 to 12/2016, 1/2017 to 12/2017 and 1/2018 to 8/2018), the amount of mean solar irradiance (W m^{-2}) received on the Hicks roof (123.5 ± 2.2) was significantly higher (P = 0.004) than the amount received on the Hadfield roof (96.0 ± 4.2) over the same period. This difference is most likely due to the building height difference. Values of relative humidity (%) were also likely influenced by building height in that same 3-year period. While the difference in relative humidity between the Hicks and Hadfield roofs (65.5 ± 0.1 and 77.8 ± 0.1, respectively) and that between the Hicks roof and Weston Park (65.5 ± 0.1 and 77.6 ± 0.1, respectively) were both statistically significant ($P < 0.001$), no significant difference could be found between Weston Park and the Hadfield roof, both of which are situated at a lower height compared to the Hicks roof.

Building height also clearly had an effect on mean temperature (°C) – again, the differences between mean temperature during the same 3-year period on the Hicks roof (10.45 ± 0.03) compared to both Weston Park (10.30 ± 0.04) and Hadfield roof (10.28 ± 0.04) were statistically significant (P = 0.006 and P = 0.003, respectively), while the difference between the mean temperatures of Weston Park and Hadfield roof was not significant. Although the mean maximum temperature during the same period on the Hicks roof (10.55 ± 0.03) was not statistically different to that reached in Weston Park (10.57 ± 0.04), the mean minimum temperature was ($P < 0.001$), with Hicks presenting a higher mean minimum temperature (10.17 ± 0.03) compared to Weston Park (9.86 ± 0.04). This last difference may be due to indoor heating seeping through the roof deck during the winter and to the difference in surface material (concrete vs. grass). A highly significant difference ($P < 0.001$) was also found between all sites in terms of mean wind speed (m s^{-1}) of the overall study period, with highest wind speeds found in Weston Park (6.30 ± 0.02), closely followed by the Hicks roof (4.34 ± 0.02), but with much lower wind speeds on the Hadfield roof (1.72 ± 0.01). The stark difference in wind speed between the three sites is most likely related to the higher openness, lower building density and smaller rooftop area found going from Weston Park, Hicks building to the Hadfield building. Possibly for similar reasons, Weston Park (64.0 ± 1.0) received greater amounts of mean monthly rainfall (mm) throughout the study period compared to the Hicks roof (61.3 ± 1.6), but the difference was only marginally significant (P = 0.165).

4.3 Experimental design

4.3.1 Experimental units, growing media and irrigation

In December 2015, 57 free-draining, round plastic containers (40 L, 32.5-cm height, 44 cm Ø diameter, Fig. 2a & 2b) were positioned on each of the two rooftops of the university buildings, Lower Hicks and Hadfield (Fig. 1). Each container was filled with a mixture of 50% green roof substrate and 50% compost (Verve Multipurpose Compost, Bord na Móna, Co. Kildare, Ireland; contains: < 80% Sphagnum moss peat, > 20% non-peat composted organic material, 0–7 g/L limestone, and 0-3 g/L fertiliser) to ensure survival of the shrubs after transplant. The green roof substrate was a blend of two substrates made available by the Green Roof Centre (www.thegreenroofcentre.co.uk), both containing large- and fine-grained crushed brick and mineral aggregates: the ZinCo 'Heather with Lavender' substrate (ZinCo GmbH, Nurtingen, Germany) and the Boningale GreenSky 'Superstrate' (Boningale Ltd., Wolverhampton, UK). The ZinCo 'Heather with Lavender' is a substrate suitable for intensive green roof systems, made from recycled material and can support shrubs, bushes and trees (Dry bulk weight: 1000 g/L ± 100, saturated bulk weight: 1500 g/l ± 100 g/L; Maximum water-holding capacity: 50%; pH: 6.5–8.0; Organic content: < 90 g/L). Boningale GreenSky 'Superstrate' (Class Sky-2) is a relatively lighter substrate (Dry bulk weight: 884 g/L, saturated bulk weight: 1412 g/L) with a slightly lower water-holding capacity (43.9%) and low nutrient content (0.40 mg/g N, 0.002 mg/g P) and high porosity (18.3%). Each container was filled to 30 cm in depth with the substrate mixture described (Fig. 1).

The ratio of inorganic and organic matter used for the growing media stems from the fact that increasing organic content such as peat, mulch and other composts, or reducing particle size of the aggregates, improve volumetric water content and the substrate's water holding capacity, as well as increase insulation and thus protection of the roots from high temperatures (Rowe 2015, Simmon 2015). Compost also provides nutrients and enhances plant growth (Nagase and Dunnett 2011, Vijaraghavan 2016). Despite using a higher than recommended ratio of organic content (Vijaraghavan 2016) and the higher microbial oxidation of organic carbon content, which can lead to substrate shrinkage, compaction and altered porosity and longevity over time (Cao et al. 2014, Rowe 2015), organic matter is an important factor in roof cooling due to its higher evapotranspirative qualities (MacIvor et al. 2016) and is essential for the successful survival and growth of the experimental plants, both immediately after transplant and for the entire duration of the study. A substrate depth of 30 cm was chosen as a compromise between what is generally recommended by green roof guidelines for supporting woody species (≥ 50 cm, Catalano et al. 2018) and shallower substrate, in which studies have related survival of certain shrub species but also stress due to high substrate temperatures and drought (10-13 cm, Savi et al. 2016; Du Arndt and Farrell 2019). The deeper substrate of 30 cm is generally recommended for optimising energy savings (Zeng et al. 2017), as it increases water holding capacity and insulation (Rowe 2015), promotes shoot growth for higher shading and delays the reaching of peak maximum temperature more compared to shallower substrate (Savi et al. 2016). Specifically, a study by Kotsiris et al. (2012) showed that 30-cm substrate in large pots promoted higher growth and tolerance of shrubs to green roof conditions, especially in summer, compared to 20-cm depth.

Figure 1. Experimental design. The arrangement of the experimental units on the Hicks Lower roof (top) and the Hadfield Roof Garden (bottom) during the first experimental year (01/2016-12/2016).

With the exception of summer during the second experimental year, in which specific watering regimes were applied to determine water use by the different species, only emergency irrigation was carried out to avoid mortality during the hottest days of the year when plants showed clear signs of stress. A hose with a nozzle that adjusted for spray intensity was used for watering. During emergency irrigation or watering regimes, each unit was sprayed with the same amount of water (i.e. same watering time), and this amount was calculated by clocking the time it took for a certain amount of water to be filled in a graduated bucket at a certain spray intensity.

Figure 2. Experimental units. A) Above: Diameter of experimental units (plastic containers), showing drainage holes; Below: ‘Control’ unit with temperature and relative humidity sensor placed at the centre and on top of the substrate surface. B) Each unit is 32.5 cm in height and filled with 30-cm deep substrate mix. Tall species were pruned back to level height with shorter species in winter at the beginning of each experimental year, but natural growth in height was allowed throughout the study year to ensure survival and normal physiological responses, so plant stature could be between 30 and 120 cm depending on species. C) Example of a vegetated unit, in this case planted with three evenly-spaced individuals of *V. tinus*.

4.3.2 The shrub species used and the selection criteria

A total of 324 individual shrubs were used in this study, belonging to six different species (Fig. 3) and ordered from a local wholesale nursery (James Coles & Sons, Ltd., Leicester) as two-year old saplings. Each rooftop hosted 162 individual plants belonging to three phenological types (deciduous, evergreen and semi-deciduous), with 54 individuals per species. A species belonging to each phenological type was grown on each roof, with Hicks hosting *Elaeagnus angustifolia* (deciduous), *Viburnum tinus* (evergreen) and *Cistus × hybridus* (semi-deciduous) and Hadfield hosting *Cotinus coggygria* (deciduous), *Ceanothus thyrsiflorus repens* (evergreen) and *Buddleja davidii* (semi-deciduous). Each experimental unit was comprised of a plastic container planted with three evenly-spaced individuals of the same species (Fig. 2c), except for the three 'Control' containers (one for each species), which were left bare with only substrate (Fig. 4). A total of 57 experimental units were placed on each roof, 54 of which were vegetated units and 3 were bare (control) units.

The species were selected for their known resilience to harsh environments, their ruderal nature and for their range of drought-tolerant characteristics thought to facilitate their survival in rooftop environment. The following are brief descriptions of the six woody shrub species. See Table 1 for a summary and Appendix A for an in-depth description of the characteristics of the different species.

***Viburnum tinus* L.**, known as the Laurustinus, belongs to the Adoxaceae family and is an evergreen shrub with a dense growth form (multi-stemmed base) reaching 1.5-2.5 m in height, occasionally more (Clennett 2004). Shoots are adventitious, pubescent when young, becoming glabrous, smooth, with a reddish bark at maturity (Kollman and Grubb 2002). Leaves are sclerophyllous or coriaceous to the touch (Salleo et al., 1997), opposite (Kollman and Grubb 2002), shortly petiolated, narrowly ovate to oblong (3-10 cm long), acute at both ends, entire, dark green and glossy above but lighter beneath with some axillary pubescence (Clennett 2004). Flowers have a white to pinkish funnel-shaped corolla with five lobes (Kollman and Grubb 2002), are somewhat fragrant, and are borne in convex terminal umbel-like cymes (5-7 cm wide). Fruits (single-seeded drupes) are ovate, deep blue and turn black at maturity in early autumn. *V.* tinus has a long, winter flowering period that goes from November to April both in the wild and in cultivation (Clennett 2004). The Laurustinus is distributed throughout southern Europe and North Africa in the Mediterranean-climate region. It is a constituent of *garrigue*-type scrub and forest fringes, often in association with *Laurus nobilis* and *Myrtus communis* as understory components of woodland *maquis* (Clennett 2004). The distributional range of *V. tinus* reflects the adaptation of this species to living under two different types of light condition: under high irradiance as a part of the Mediterranean *maquis* and in the partially shaded environments of the understory (Fini et al. 2010). *V. tinus* is therefore well adapted to semi-arid environments that experience summer drought and high temperatures (Nardini 2002), but that also have high winter rainfall and little frost (Clennett 2004). The Laurustinus was introduced to the British Isles for cultivation in the late 16th century and is today observed to perform well in southern and western parts of Britain, being frost hardy in all but the worst conditions and tolerant of a variety of soil types.

***Cistus* × *hybridus* Pourr.** (syn. *Cistus* x *corbariensis* var. *grandiflorus* Pau) is a spontaneous hybrid of the species *Cistus populifolius* L. and *Cistus salviifolius* L. (Martín Bolaños and Guinea López 1949, Tela Botanica 2016). It is a member of the Rockrose family (Cistaceae) composed of well-branched, perennial shrubs of small dimensions with characteristically showy flowers and covered in fine to dense pubescence (Martín Bolaños and Guinea López 1949). The morphological traits of *Cistus* × *hybridus* are intermediate between those of parents *C. populifolius* (tall, upright and very aromatic shrub with large glabrous, cordate, smooth-surface and flat-margined leaves) and *C. salviifolius* (small, sprawling and slightly aromatic shrub with small felted, ovate-lanceolate, rough-surfaced and crispate-margined leaves), both of which are highly branched, glabrous shrubs with slightly different ecologies and distributions (Guzmán et al. 2009, Abreu et al. 2012). Martín Bolaños and Guinea López (1949) describe *Cistus* × *hybridus* as being an erect shrub (0.5-1 m in height) with dark or blackish, elongated, glabrous and viscous stems. The leaves are petiolate, opposite, cordate to ovate at the base, elongated to oblong-lanceolate and slightly sharp or obtuse at the apex, generally rather small (20-30 mm × 10-20 mm up to 30-40 mm × 15-35 mm) but sometimes relatively large (70-80 mm × 25-40 mm) when mature. The leaf laminas are coriaceous on the adaxial surface and rough and reticulated on the abaxial side with prominent venation, partly stellate-hairy or subglabrous on both sides with tomentum only on younger leaves, and have a slightly undulate margin. The inflorescences appear at the tip of branches and carry 1 to 3 large (40-50 mm Ø), white, briefly pedunculated, axillary, 5-symmetry monoecious and many-stamened flowers that have one pair of ovate-lanceolate, tomentous bracts and 5 sepals characterized by a central bulge. The fruit is a pentagonal (5-valved) and slightly hairy dehiscent capsule about 8 mm long. Flowering occurs from May to the first week of June, while fructification begins immediately afterwards and maturation is completed by August, when seeds are released from the open capsule (Correia et al. 1992, De Lillis and Fontanella 1992). *Cistus* species are pioneering, highly thermophilous and xeric woody shrubs with shallow and markedly planar root systems (Amato and Sarnataro 2001). They are commonly found in Mediterranean *maquis* and scrubland (*garigue*), usually as a result of the degradation of oak and pine scrubland (Bosch 1992, De Dato et al. 2013). The hybrid's area of distribution is limited to the southern part of the Mediterranean Basin: Spain, S France, Italy (except for the NE region), the Balkans, Asia Minor and the coast of N Africa (Martín Bolaños and Guinea López 1949).

***Elaeagnus angustifolia* L.** is known as the Russian olive and belongs to the family *Elaeagnaceae* (Stannard et al. 2002). It is generally a large, spreading, multi-stemmed, spiny, fast-growing shrub with a reddish shredding bark, often obtaining 3.5 to 5.5 m in height and the same in width, forming extensive, dense thickets (Dirr 1998, Katz and Shafroth 2003). The abaxial side of leaves (alternate, lanceolate, simple and entire), petioles, and current-year branches are covered in distinctive, silvery-grey peltate hairs or scales. Flowers are apetalous, 4-symmetrical, small, with a cylindrical to campanulate yellow calyx, clustered in axillary umbels produced in the spring (Graham 1964, Katz and Shafroth 2003). The drupe-like fruit is oval-shaped, 1-1.5 cm long, and has a fleshy pericarp containing a hard-coated achene primarily dispersed by birds (Graham 1964, Katz and Shafroth 2003). *Elaeagnus* sp. thrives in both disturbed areas and undisturbed habitats including the understory of pre-existing forests (Yates et al. 2004, Brym et al. 2011), and the Russian olive readily propagates from vegetative structures (Stannard et al. 2002). The Russian olive was introduced in the early 1900s in semi-arid and saline environments of western United States because of its adaptability, for use as shelterbelts, food, wildlife cover, roadside reclamation, and soil stabilization (Knof and Olsen 1984). Today, *E. angustifolia* is ranked as the fourth most dominant riparian tree species in western United States (Nagler et al. 2011). This and other species of the same genus (e.g., *E. umbellata*) occur across a range of environments with different light and moisture conditions, showing tolerance to drought, high pH soils, and pollutants (Stannard et al. 2002; Yates et al. 2004, Brym et al. 2011, Zinnert et al. 2011). These characteristics, combined with the ability to fix nitrogen, make *Elaeagnus* species successful invaders, capable of displacing co-occurring native species (Ahmad et al. 2005). The Russian olive is also invasive of wet-saline and certain riparian environments and tolerates infrequent fire, temporary flooding, browsing, and mechanical cutting (Stannard et al. 2002).

Ceanothus thyrsiflorus* Eschsch. var. *thyrsiflorus (syn. *Ceanothus thyrsiflorus* var. *repens* McMinn, according to NBCI 2016 and Jepson eFlora 2016b) belongs to the cosmopolitan Buckthorn family (Rhamnaceae) and is commonly known as the common Blue blossom. Plants of this variety are medium or large mat- to mound-like shrubs, generally < 1 m in height, with an open habit and subglabrous, flexible, and ascending to spreading stems. When in thickets in their native environment, individuals can be 1-4 m in height and have stems ascending to erect. Stipules are scale-like, thin and early deciduous. Branches are green, not spinose or papillate, angled distally and with ridged internodes. Leaves (0.5-4.5 × 0.3-2.5 cm, or at least < 2 × width) are alternate, evergreen, petioled (3-9 mm) and glandular, with stomata on lower epidermis and never encrypted. The leaf lamina is oblong-ovate to elliptic, firm, adaxially dark green, smooth, glossy and glabrous, abaxially paler and glabrous to minutely pubescent, with only a few coarse hairs along the prominent veins, which are 3-ribbed from the base. The tip of the leaf is obtuse to rounded and the margin slightly revolute, thick, and minutely gland-toothed, with teeth paler and glands dark. Inflorescences (1.5-7.0 cm) generally in subcompound racemes or panicles (termed ‘thyrsoid’), axillary, with light to deep blue (rarely white) flowers (< 5 mm) and white to deep blue pedicels. Flowers are bisexual, radial, 5-stamened, with 5 hood-shaped petals and 5 lance-deltate and incurved persistent sepals, colored like petals. Ovary ½-inferior, 3-lobed and 3-chambered (each 1-ovuled). The fruit (2.5-4.0 mm) is a sticky, spherical, generally 3-lobed capsule, smooth and without horns but often with 3 ridges or crests, producing 3 seeds (2-5 mm). The growth of new leaves, flower buds, and branch elongation in this species are all observed to begin in February, while leave buds form at the end of June. Fruit development begins in April and maturation and dispersion occurs by June. Although evergreen, *Ceanothus thyrsiflorus* loses a major portion of its foliage during the summer, beginning in June and continuing until water stress persists. The common Blue blossom is a native to northern California and a component of northern coastal scrub and prairie. The variety *thyrsiflorus* can be found along bluffs, slopes and canyons as part of chaparral, coastal scrub and closed-cone pine forest vegetation of California’s coastal range, at altitudes lower than 800 m. Its distribution outside California includes SW Oregon and northern Baja California, Mexico (Watson 1875, McMinn 1930, Jepson eFlora 2016b). *C. thyrsiflorus* is known to be a rapid pioneer and temporary dominant of post-fire and degraded areas.

***Buddleja davidii* Franchet** is known as the Orange Eye Butterflybush and is a semi-deciduous, fast-growing, multi-stemmed shrub that forms canopies of dense foliage and fragrant, showy flowers (Leeuwenberg 1979) belonging to the family Scrophulariaceae (EOL 2015). The habit of *B. davidii* is unique in that it has no main trunk: the main meristem (four-angled) grows underground, while the aboveground biomass is comprised of several stems that originate from the main meristem (Tallent-Halsell and Watt 2009). Leaves (5-20 cm × 1-7 cm) are usually ovate (less commonly lanceolate), serrated, wedge-shaped, and shortly petiolate, with the adaxial surface dark green and glabrous and the abaxial side whitish to greyish tomentose with stellate and glanduliferous hairs that extrude crystals, giving them a characteristic sheen (Leeuwenberg 1979, Webb et al. 1988, Tallent-Halsell and Watt 2009). Leaves are described as ‘semi-deciduous’ in that they are shed in the autumn and immediately replaced with a set of new, smaller leaves covered in downy hairs that persist until the following spring. Both spring shoots and leaves are pubescent but become glabrous as the year progresses (Tallent-Halsell and Watt 2009). Flowers (5-8 mm) are zygomorphic, four-symmetrical, with petals fused into a lilac or purple corolla tube that opens at the top to form four separate petals and has an orange interior with a series of yellow nectar guides (Leeuwenberg 1979). Flowers, borne in long corymbose panicles that can extend up to 30 cm in length, mature from late spring to mid-summer from the base to the top of the inflorescence (Findley et al. 1997). The fruit is a brown, narrowly ellipsoid to ovoid cylindrical, two-valved capsule (5-9 × 1.5-2 mm) with an acute apex, an impressed line along the dehiscence zone, and containing many small (3-4 × 0.5 mm), thread-like and long-winged seeds that disperse with wind (Leeuwenberg 1979, Norman 2000). *B. davidii* depends on insects and other wildlife for pollination (Norman 2000), attracting many species of butterflies, moths, bees, wasps, hornets, hoverflies, beetles and even hummingbirds in the New World (Stuart 2006, Chen et al. 2011) with both the scent and nectar it produces in abundance (Houghton et al. 2003). *Buddleja davidii* is native to central and southwestern China up to 3500 m and was introduced to Europe as an ornamental in the late 19th century (Owen and Whiteway 1980), thus becoming naturalized and a successful invader of the European continent (Ebeling et al. 2008, Wittig 2012). Since 1920, seven subspecies of *B. davidii* have been described and 90 different cultivars have been bred (Stuart 2006). These have long escaped cultivation and in the United Kingdom has spread to every angle of the British Isles (Owen and Whiteway 1980). The invasiveness and expansion of *B. davidii* to such a wide range of climates is certainly related to its high adaptability and tolerance of many different types of soils and environmental conditions. However, *B. davidii* seems to prefer open dry, disturbed sites, like roadsides, abandoned areas, quarries, pastures, scree slopes, open woodlands, riverbanks, and forestry plantations (Binggeli 1998, Ebeling et al. 2012).

Cotinus coggygria **Scop.** belongs to the cosmopolitan family Anacardiaceae and is an upright, spreading and multi-stemmed tall shrub (30-70 cm), rarely small tree (1-4 m), with smooth, greyish bark that smells of sap due to its production of resins and tannins (Pignatti 1982). A characteristic terpene-like fragrance can also be detected in leaves and inflorescences, which produce essential oils composed of limonene, α-pinene, terpinolene, various monoterpenes and many other organic compounds (Tzakou et al. 2005). Leaves are opposite, simple, entire, glabrous, glaucous and without stipules; those found near the base of the plant have rounded laminas (5-7 cm ø) and long petioles (3-7 cm), while the leaves near the apex become progressively more ovate (22-35×35-60 cm), with a maximum width at one-third of the lamina and a pointy base. In its venation architecture one may distinguish 8-10 veins diverging at almost 90°, becoming dichotomous at the apex. Flowers are usually infertile and monoecious, radially pentamerous, free and reduced, with 5 stamens, long peduncles and pale yellow to yellowish-green petals, borne in polygamous, erect, loose, terminal, and plume-like panicles (10-20 cm) that bloom between May and July and often persist through September. The fruit is a dry, one-seeded, reticulate, sclerenchymous and pseudomonomerous drupe (3-4 mm), light-reddish brown in color and ripening to near black between August and October (Pignatti 1982; Greuter et al. 1984, 1986, 1989; Diamantoglou et al. 1989; Wannan and Quinn 1991;

Dirr 1998; Tzakou et al. 2005; Pijut 2008; Gilman and Watson 2014; Schönfelder and Schönfelder 2014). Leaves are produced in March and undergo growth and a natural defoliation process until about 25% of its foliage is dropped by June, leaf senescence starting late August and persisting until September and October when leaves turn a vivid yellow-orange and are completely shed (Diamantoglou et al. 1989). The western distribution area of *C. coggygria* extends mostly to the southern part of Europe, including Spain, France, Italy, the Balkan Peninsula, Lebanon, Syria and Crimea (Greuter et al. 1984, 1986, 1989), growing in thickets especially on dry, rocky limestone soil in brush and cliffs (0-900 m) (Pignatti 1982, Tzakou et al. 2005, Gilman and Watson 2014). *C. coggygria* is among the typical pioneer species that develop during the natural encroachment of abandoned rural and degraded areas. *C. coggygria* is considered to be highly drought-tolerant (Nardini et al. 2003) and is a drought-deciduous species (i.e. avoids unfavourable conditions through the shedding of leaves, Kozlowski 1991). Leaves may display symptoms of water stress, but plants tend to replace them by sprouting new ones (Savi et al. 2015) and by decreasing leaf size during the summer to tolerate these conditions (Nardini et al. 2012).

Figure 3. Species of woody shrubs used in the study. From top left and clockwise: *Ceanothus thyrsiflorus repens*; *Cistus* x *hybridus*; *Cotinus coggygria*; *Elaeagnus angustifolia*; *Buddleja davidii* 'Black Knight' and *Viburnum tinus* 'Eve Price'.

4.3.3 The experiments

The study was divided into three experimental years (1/2016 to 12/2016, 1/2017 to 12/2017 and 1/2018 to 8/2018), in order to monitor the temperature profiles and the physiological and morpho-anatomical responses of the shrubs within different combinations of both spatial arrangement and species groupings. The experimental units were designed to be easily moved around each year (i.e. lightweight containers with handles) in order to rearrange the units for these specific investigations. The three main categories of experiments are ‘Control’ (C), ‘Dense population’ (DP) and ‘Sparse population’ (SP), in which ‘C’ represents a bare green roof unit, with only substrate and no vegetation, while ‘DP’ and ‘SP’ represent small populations of vegetated green roof units. ‘DP’ represents a spatially-dense arrangement of shrubs on a green roof, with no space between the experimental units, while ‘SP’ represents a spatially-sparse arrangement of shrubs, with containers evenly distributed around each other (i.e. about half a metre of space between each unit, Fig. 4).

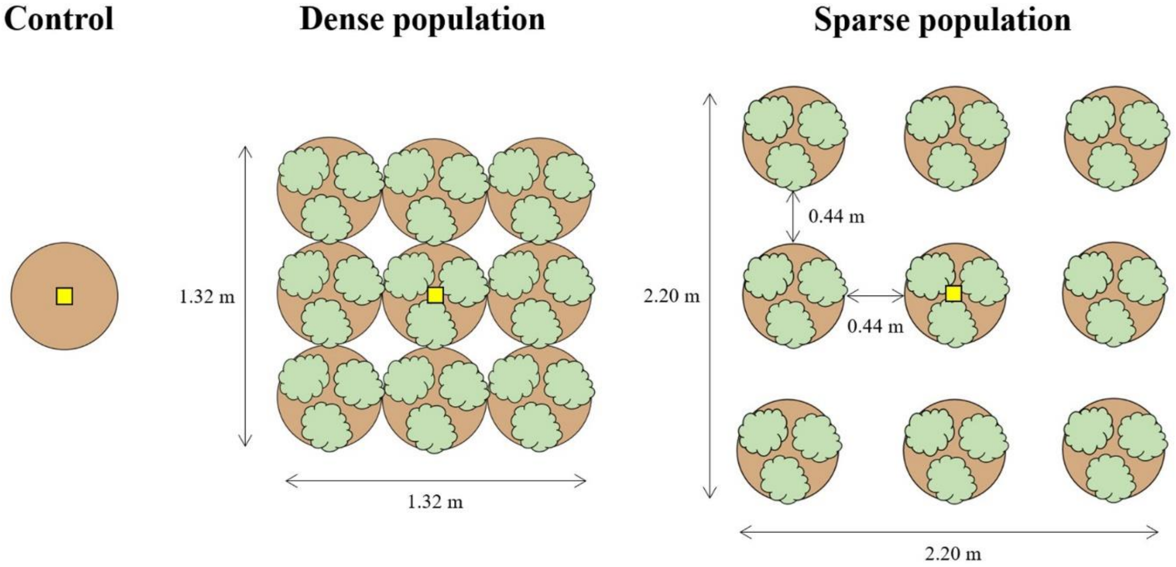


Figure 4. The arrangement of experimental units into populations with different plant density. The three experimental unit types are ‘Control’ (C), ‘Dense population’ (DP) and ‘Sparse population’ (SP). Throughout the study, the species were divided into two populations with distinct spatial arrangements: 1) in a ‘Dense’ population, with no space between containers, and 2) in a ‘Sparse’ population, with 0.44 m of space between them. The yellow squares represent the position in which the T and RH sensors were placed on control or under the plant canopies.

The following paragraphs describe the different combinations per experimental year.

Year 1: Monitoring the effects of plant density

For the first experimental year (1/2016 to 12/2016), all shrub units were placed in ‘monospecific’ (i.e. single-species) populations. For each shrub species on both research sites, half of individuals (27 plants, planted in 9 containers) were arranged in a high-density (‘dense’) population, while the other half (27 plants, planted in 9 containers) were arranged in a low-density (‘sparse’) population (Fig. 5). This combination was used to investigate the effects of plant density on the physiological and morpho-anatomical responses and the temperature profiles of the six woody shrubs.

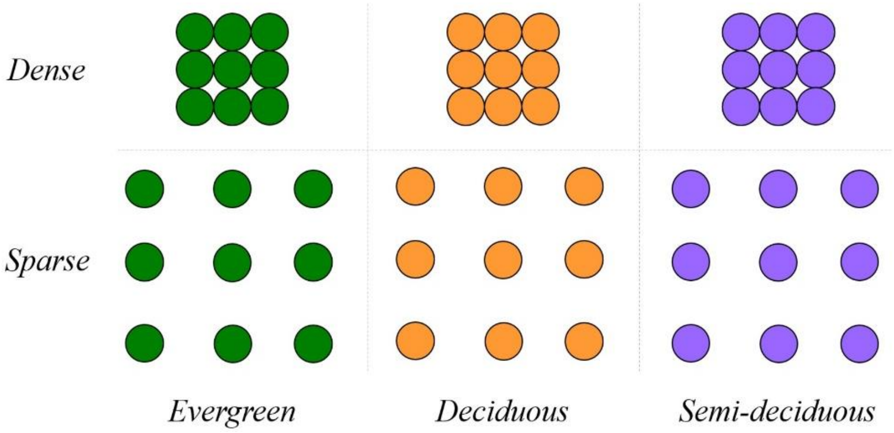


Figure 5.
Year 1 experimental design. Combination of species and spatial arrangement during the first experimental year: species vs plant density vs phenology.

Year 2: Monitoring the effects of plant density and population size

For the second experimental year (1/2017 to 12/2017), all shrub units rearranged on both research sites into ‘polyspecific’ (i.e. mixed-species) populations. These populations were divided into four different groupings (Fig. 6): 1) a small (9-unit) ‘dense’ population; 2) a small (9-unit) ‘sparse’ population; 3) a large (16-unit) ‘dense’ population and 4) a large (16-unit) ‘sparse’. This combination was used to investigate the combined effects of plant density and population size on the physiological and morpho-anatomical responses and the temperature profiles of the six woody shrubs.

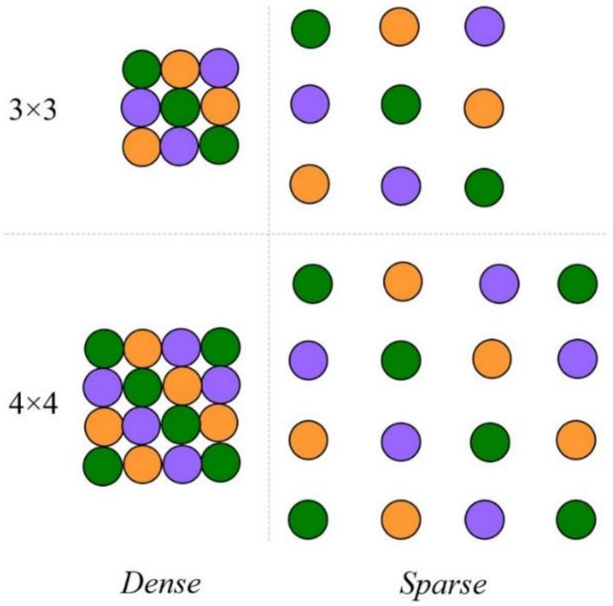


Figure 6.
Year 2 experimental design. Combination of species and spatial arrangement during the second experimental year: plant density vs population size.

Year 3: Monitoring the effects of species mixture

For the third and last experimental year (1/2018 to 8/2018), the units were rearranged again on both research sites so that half of the units were placed in 'monospecific' (i.e. single-species) populations and the other half were placed in 'polyspecific' (i.e. mixed-species) populations (Fig. 7). This combination was used to directly compare the effects of species mixture on the physiological and morpho-anatomical responses and the temperature profiles of the six woody shrubs.

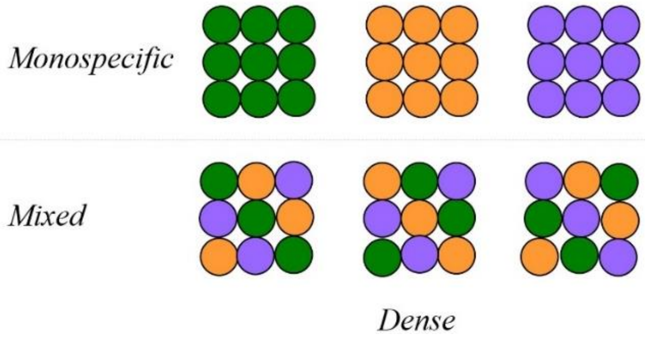


Figure 7.
Year 3 experimental design. Combination of species and spatial arrangement during the third experimental year: monospecific vs polyspecific (mixed) populations.

4.4 Limitations of the study

The limitations to this field study are many. To start, it would have been ideal for all species to have been placed on a single experimental rooftop rather than on two separate ones, as the two locations present slightly different weather conditions. However, the actual space available on the bigger roof (Lower Hicks roof), for example, was limited, as it was equally limited on the Hadfield Roof Garden. That is because they were not bare rooftops – the areas surrounding the experiments were used for other purposes (e.g. solar panels, observatory, roof apparatus, other green roof studies, hard landscaping for amenity). Certain health and safety measures on the Hicks Lower roof also did not allow me to go beyond a certain area of the roof space available, limiting the experimental space even more. The advantages of using these two rooftops that were limited in available space were that they were both easily accessible in terms of transportation of material and everyday use and that they already had fully functional weather stations with ongoing data collection. The choice of these two sites was therefore a compromise between ideal conditions and practical needs. The analysis of the weather data collected by the two roofs was also laborious, as the two weather stations have different resolutions of data logging.

The microclimate of a green roof (in this case a rooftop with experimental plants) can be affected by: 1) the height of the roof, 2) the presence of surrounding buildings that can provide shade and shelter from wind, and 3) the characteristics of the underlying building (Brown and Lundholm 2015). Therefore, not only are the two rooftops different in terms of height and presence of surrounding buildings (the Hadfield rooftop is closely surrounded by equally tall buildings, while the Hicks rooftop is not as packed in), heat from from the indoor environment directly underneath the rooftop could potentially present a factor influencing the temperature profiles of the experimental units, which are placed directly on the roof surface. This influence obviously depends on the level of the building's insulation. However, if this heat flux from indoor to outdoor environment was present on both rooftops (both rooftops are placed over heated indoor spaces), then this effect would at least have been applied to all experimental units.

Surprisingly, despite all species being drought tolerant and ruderal, some turned out to be considerably less hardy than others and needed replacements, especially during the first year. Particularly problematic was *C.* x *hybridus*, which needed hefty replacements throughout the study. It was badly affected by aphids in summer 2017 (but fully recovered after the application of a pesticide spray) and was equally negatively affected by the snow cover in the 2017-2018 winter, never fully recovering and causing many individuals (mainly in the MP) to rapidly shrivel up in the summer of 2018 despite emergency irrigation. *C. coggygria* was also quite delicate. It was targeted by slugs during the wetter spring days and the strong winter winds could sometimes cause breakage of the more brittle branches.

Among the most time-consuming and laborious processes were the measuring of the RGR, which often required standing in the cold in awkward positions to avoid damaging the plants, the counting and scanning of canopy leaf area, and the harvesting of plant biomass. The rapid deciduousness of a *E. angustifolia* and *C. cotinus* also made it difficult to harvest the leaves and do the post-field work investigations.

Although most equipment used worked reliably throughout the entire study, some (in particular the IRGA) could be temperamental. Although working correctly throughout the summer of 2016, the leaf cuvette (chamber) of IRGA became loose and required sending it abroad to Italy and a rather expensive two-month repair. Data was collected normally again in 2017, but at the beginning of summer 2018 the IRGA could not calibrate on any day during the summer in which measurements were attempted and no data could be collected. This malfunctioning was probably due to unstable weather conditions, as the IRGA calibrated and worked reliably indoors on the same test days. Sending it abroad again for a check-up would probably not have made a difference, as there was nothing physically wrong with the equipment, and the summer would have been over by the time the IRGA would have been sent back. Another equipment issue was the use of the pressure chamber. In 2016, permission to use a portable pressure chamber in the Plant Identification of the Arts Tower (main point of reference for the study), owned by the Department of Landscape Architecture, was denied for health and safety reasons. In order to carry out measurements of bulk leaf water potential, an agreement was made with the Department of Animal and Plant Sciences for a temporary use of their pressure chamber in their plant physiology laboratory. Training for special access and use of this laboratory was needed. However, this agreement was not renewed for the following year and therefore measurements of bulk leaf water potential were only carried out in the summer of 2016.

STUDY 'A'

The effect of species traits, plant density, population size and species mixture on the morphological and physiological performance of six woody shrubs growing on rooftops

A.1 Overview and aims of the study

Study 'A' of the research project was dedicated to assessing the morphological and physiological performance of six distinct species of woody shrubs placed in populations of varying plant density, population size and type of species mixture during the summer months of three consecutive years (2016–2018). The aim was to observe the effects of species, plant density, population size and species mixture on the shrubs' morphological and physiological responses. The study measured a range of morphological and physiological plant parameters and were used to identify and test differences between species and to quantify the effect that plant density, population size and species mixture had on the shrubs' fitness and survival on the rooftops.

The sections that follow describe:

1) the equipment and methods used to measure the responses of the six woody shrub species in a range of morphological and physiological plant parameters through the three years of the study (Section A.2.), and
2) the statistical analysis ('Results') of the effects of plant density, population size and species mixture on shrub morphological and physiological performance (Section A.4).

A discussion of the results for Study 'B' concludes this second part of the thesis (Section A.5).

A.2 Material and Methods

As described previously (Chapter 4), the experiments for Study ‘B’ were the same as those used for Study ‘A’, therefore placed on the same two research sites (Lower Hicks rooftop and Hadfield roof garden, Section 4.1) and the two studies were carried out simultaneously over the same period. However, while the morphological and physiological plant parameters measured in Study ‘A’ were carried out primarily in the summer months, the monitoring of plant microclimate in Study ‘B’ was carried out during both the winter *and* summer months.

A.2.1 Volumetric substrate moisture content (SMC)

The importance of measuring substrate moisture content (SMC) and evapotranspiration (ET) lies in the fact that these parameters can have a significant impact on green roof thermal performance, in particular on heat and mass transfer (Cascone et al. 2019). In fact, an increase in volumetric SMC from 30 to 60% can lead to a similar reduction (24%) in the heat stored by a green roof (Tsang and Jim 2011). ET is a complex process that depends on the combined effects of local climate conditions and their seasonal variations (e.g. solar irradiance, wind speed, air temperature, relative humidity, precipitation), substrate characteristics (e.g. SMC at substrate surface, depth, porosity, particle size, permeability, compaction, drainage) and plant traits (e.g. growth form, leaf area and density, shading by the canopy, height, transpiration rates, stomatal resistance and conductance). Both the level of plant development and species have a considerable influence on the rate of water consumption, as transpiration increases with development, cover and reduced stomatal resistance (Cascone et al. 2019).

Throughout the summer months of all three experimental years of the present study, spot measurements of substrate moisture content (SMC) were conducted with a soil moisture metre (see Table 2 for full description) on the same days in which plant water status and gas exchange measurements were conducted, in order to support the data collected. Measurements of SMC were carried out alongside each physiological measurement taken throughout the study. SMC was measured by inserting the full length of the sensor probe (30 mm diameter, 60 mm long) in six different areas (three in the margins, three in the centre) of the substrate of each experimental unit, so as to get an average across the entire surface.

A.2.2 Plant response to rooftop conditions, species mixture and plant spatial arrangement

Functional plant traits are any morpho-anatomical, physiological or phenological feature of a plant, measureable at the cell to the whole-plant level, that affects its fitness (McGill et al. 2006, Violle et al. 2007). The study of plant traits in relation to plant performance under environmental stress is key to understanding plant functional ecology (Catro-Dìez et al. 2000), assessing plant drought tolerance (Bartlett et al. 2012) and identifying the underlying mechanisms in the relationships between morpho-anatomical and physiological parameters (Scoffoni et al. 2014) and plant–atmosphere interactions (Pérez-Harguindeguy et al. 2013). Trait-based responses and relationships can be used as predictors of plant function, not only in ecological and evolutionary studies (Brodribb et al. 2007) but also in many contexts and fields, including agronomy, forestry, conservation, horticulture and landscape studies (Pérez-Harguindeguy et al. 2013).

In the present study, a number of morpho-anatomical and physiological plant traits were measured during the summer months (June–August) of each experimental year, with the intent of correlating them with the different shrub species' cooling/insulating capacities (i.e. below- and above-canopy temperature). The outcomes of these correlations can help bring about a better understanding of plant cooling/insulating mechanisms and their potential use as predictors of temperature mitigation. Table 2 summarises the plant parameters measured in the study, detailing the units they were measured in, the equipment used, and their significance to the study. The following subsections describe the methods used for the sampling and measuring of these parameters.

A.2.3 Morpho-anatomical plant traits

A.2.3.1 Mortality (*M*) and relative growth rate (RGR)

Every plant in the study was identifiable by unique waterproof labels attached to the trunk with thick string, which identified them by a code with species and number (e.g. CC18, *C. coggygria* no. 18). Mortality (*M*) of individual plants was determined by direct observation throughout the entire study on both experimental sites. Plants with browning/curling of the leaves, coupled with reduced stem flexibility, density and greenness and a loss in rooting strength/stability, would generally be considered dead. Unless presenting these signs, it may be difficult to determine the vitality of a deciduous plant dying over winter without waiting for the appearance or absence of leaves in the spring. However, terminal and adventitious buds on the stems would generally show signs of stress (e.g. much smaller, shrivelled) or even drop off in case of low vitality. These individuals usually also appeared stunted in growth compared to others belonging to the same species.

Relative growth rate (RGR) is an indicator of plant productive strategy in response to environmental stressors. RGR is usually measured by destructively harvesting a group of plants at the beginning and a group at the end of a study, in order to compare their dry biomasses (Pérez-Harguindeguy et al. 2013). However, the present study required the shrubs to be alive throughout the three experimental years and so their RGR was monitored by measuring the diameter of each individual trunk at the stem-root transition level with a digital caliper, and taking the mean of two measurements at 90° angles. This process was carried out for every individual plant, at the start of the study and then repeated after a certain growth period. RGR was measured in three occasions – initial values of RGR were taken a few weeks after planting (1/2016), the second ones after 12 months of growth (1/2017) and the last values at the end of the study (9/2018).

A.2.3.2 Leaf density, leaf mass per area (LMA) and leaf, plant & population leaf area (A_L)

Leaf area (A_L) is the most commonly used metric for leaf size and is the one-sided projected area of an individual leaf, whereas leaf mass per area (LMA), or specific leaf mass, is the dry weight of a leaf divided by its fresh one-sided area. Interspecific variations in A_L are associated with environmental stresses and adaptive strategies that predispose towards the selection of small leaves, whereas LMA is often correlated with RGR, photosynthetic rate and leaf longevity. For all experimental years, leaves for both A_L and LMA were sampled on 2–4 different days in late summer (mid-August to early-September), when shrubs were assumed to have reached maximum foliage maturity and before leaf senescence occurred in the deciduous species. A total of 42 leaves per species were sampled for A_L and LMA in 2016 on both experimental sites (21 for DP, 21 for SP); a total of 28 leaves per species were sampled for for A_L and LMA in 2017 on both roofs (6 for '3x3 DP'; 6 for '3x3 SP'; 8 for '4x4 DP' and 8 for '4x4 SP') and a total of 41 leaves per species were sampled for A_L and LMA in 2018 on both roofs (14 for MP; 9 for PP1; 9 for PP2; 9 for PP3).

Leaves used for A_L and LMA measurements (Fig. 8) were sampled by removing each leaf from the plant, covered it cling film, placing it in a sealed bag labelled by experimental category and transported to the Plant Identification laboratory (Arts Tower, Department of Landscape Architecture) in a thermal cooler. The petioles of each leaf was first removed with a razor blade, then placed on a graphic scanner next to a small sheet of millimetric graph paper for scaling. The image produced (300 dpi image) was then analysed with the image analysis software package IMAGEJ (National Institute of Health, Bethesda, MD, USA, available online at http://rsbweb.nih.gov/ij/index.html) to find A_L. Finally, samples were left in a drying cabinet at 70

°C for 24 hours to dry. The dry weight (DW) of each sample was then divided by its A_L to calculate LMA for that sample.

Between October 2018 and March 2019, after the end of the study, all plants were harvested for above-ground biomass (Section 2.5.1.5). The leaves belonging to the monospecific population (9 units, or 27 individual plants) of each species were removed, counted for leaf density and scanned for A_L before drying for both LMA and biomass measurements, so as to find both total and mean single plant canopy A_L and LMA and overall population A_L and LMA. A complete examination of this type was achievable for only three out of the six species (*Buddleja*, *Ceanothus* and *Viburnum*), however, as *Cistus* suffered from high mortality rates throughout that summer (only 8 healthy individuals), while *Elaeagnus* (14) and *Cotinus* (21) faced increasing levels of leaf drop and some mortality by the end of the study.

Figure 8. Leaf morphology of experimental species. Examples of leaves (to scale and without petioles) of the six experimental species (from left to right): *V. tinus*, *C.* x *hybridus*, *E. angustifolia*, *C. thyrsiflorus*, *B. davidii* and *C. coggygria*.

A.2.3.3 Branching architecture (ADI)

Branching architecture is defined as the intensity of how a plant branches (i.e. number of ramifications per stem length). In natural environments, branching architecture can be affected by grazing, fire, wind, access to light, disease and other stresses affecting fitness, as well as by age (Pérez-Harguindeguy et al. 2013). As the experimental plants in the present study all came from the same nursery, arrived as saplings of the same age and were exposed to the same conditions relative to each rooftop, one can assume that the branching developed throughout the study period was primarily influenced by genetic predisposition and the rooftop environment alone. A comparison of the different shrub species' branching architecture (Fig. 9) could be analysed in relationship to plant height, leaf count, leaf area and light interception (*I*, only for *B. davidii*, Section 2.51.4) to determine if and how this adaptive trait affects the various species' shading and ability to form an insulating microclimate. An indicator of branching architecture is apical dominance index (ADI), which is the number of ramifications per unit length of the branch, identified in this study through image analysis. A description of the method used to find ADI and the units of measurement can be found in Table 2.

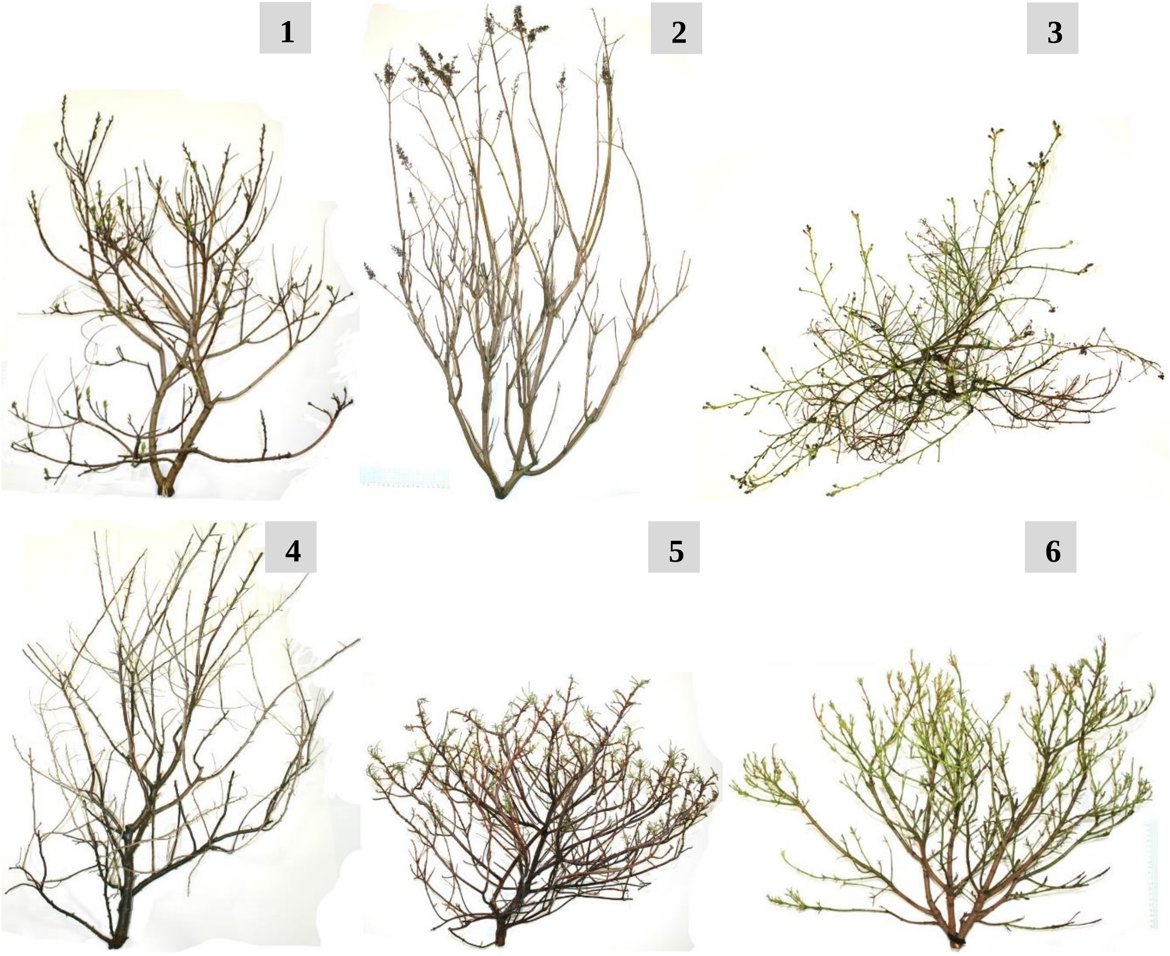


Figure 9. Branching architecture of the experimental species. The leafless plant canopies of the six shrubs (to scale): (1) *C. coggygria*, (2) *B. davidii*, (3) *C. thyrsiflorus*, (4) *E. angustifolia*, (5) *C.* × *hybridus* and (6) *V. tinus*.

A.2.3.4. Canopy interception of irradiance (*I*)

After the end of the field study in early September 2018, 27 shrubs belonging to the *B. davidii* monospecific population (9 units) were selected for investigations into canopy interception of irradiance. *B. davidii* was selected based on its height and peculiar characteristics – despite experiencing no mortality, high levels of fitness and an average plant height of about 113 cm at full maturity, *B. davidii* demonstrated the lowest performance in terms of extreme temperature mitigation (See Results in Section 3). This species' ability to intercept irradiance, in relation to leaf density and canopy leaf area, LMA, above-ground biomass, branching architecture and temperature profiles, could help identify the relationship between plant traits and cooling and insulating properties in this and more generally in other shrubs. The 27 *B. davidii* plants were transported live (dug out of their experimental units on the roof and maintained alive by keeping part of the substrate and by watering) to the Plant Identification lab and placed in containers similar to those used on the roof, with some padding to hold the plants in place and in the same disposition as in their original units (e.g. BD40-42-43, BD22-23-24). A powerful strobe light (flash light energy: 1500 W) at maximum intensity and in full darkness of the room was flashed through 3 sections of the plant canopy (bottom, middle and top) for 10 seconds, at the end of which a value (in W m^{-2}) was taken using a solar metre placed on the other side of the canopy (Fig. 10). This was repeated 3 times per section. The entire process was repeated 6 times, one for every angle of the unit (which was turned every 60°) and for every unit of the monospecific population (9), for a total of 486 measurements. Both the strobe light and the solar metre were kept in place at the same height for bottom (0.32 m), middle (0.72 m) and top (0.96 m) to allow for repetition of measurements.

Fig. 10 Measuring interception of irradiance. Strobe light, strobe controller and solar metre (bottom left to right) used in lab experiments. Top left and right: disposition of equipment and units with live *B. davidii* plants.

A.2.3.5 Above-ground biomass (B_W and B_L)

Photosynthesis is the process by which light energy reduces CO_2 to organic compounds (carbon), or chemical energy (Lambers, Chapin and Pons 2008). Plants either store this energy or use it to grow, producing biomass in the latter case. Plant biomass is defined as the weight of living plant material contained above and below a unit of ground surface area at a given time (Roberts et al. 1985), measured in g m^{-2}. In this study, only above-ground plant material (i.e leaves, main stem and branches) was harvested and therefore only above-ground woody (B_W) and leaf (B_L) biomass was determined. At the end of the study, above-ground plant material was harvested for each individual plant during the autumn-winter dormancy period (i.e. in which little or no growth occurs) between October 2018 and March 2019. The woody components (main stem and branches) were separated from the leaves and were placed into separate, labelled envelopes. These envelopes were then left to dry at 70 °C in a drying cabinet, for 24 h in the case of leaves and 48h for woody components, and weighed. The values of dry weight found for each individual plant was then divided by the area of the experimental unit in which they grew (0.15 m^2), obtaining B_A.

A.2.4 Physiological plant traits

A.2.4.1 Plant water status

Determining the water status of the experimental shrubs was essential for understanding the effects of water stress on their growth and physiology, their adaptive response to this stress and their range of drought tolerance. Leaf water status is regulated by stomatal closure and changes in stomatal conductance, which in turn are dependent on species-specific adaptive mechanisms, and changes in leaf water status can represent stress factors for plant physiological processes (Jones 2007). The following sections describe the different water-related physiological parameters measured in the present study.

A.2.4.2 Leaf relative water content (RWC_L)

Leaf relative water content (RWC_L) is defined as the water content (%) found in the leaf tissue at the time of sampling relative to the water content at full hydration, or saturation. It is a widely-used and reliable trait for describing plant water status at a given time and correlates closely with other physiological activities, SMC and drought tolerance (Jones 2007; Tanentzap, Stempel and Ryser

2015). The leaves for measuring RWC_L in the present study were sampled on different days in late summer (mid-August to early-September), when all species are assumed to have reached maximum foliage maturity and before leaf senescence occurs in the deciduous species. A total of 42 leaves per species were sampled for RWC_L in 2016 on both experimental sites (21 for DP, 21 for SP); a total of 28 leaves per species were sampled for for RWC_L in 2017 on both roofs (6 for ‘3x3 DP’; 6 for ‘3x3 SP’; 8 for ‘4x4 DP’ and 8 for ‘4x4 SP’) and a total of 41 leaves per species were sampled for RWC_L in 2018 on both roofs (14 for MP; 9 for PP1; 9 for PP2; 9 for PP3).

Once removed from the plant, the samples were covered in cling film, placed in a sealed bag labelled by experimental category and transported to the Plant Identification laboratory (Arts Tower, Department of Landscape Architecture) in a thermal cooler. After removing the cling film, each sample was weighed for fresh weight (FW) on a precision balance and placed in a small plastic tube containing deionised water, with only the petiole inside the water (Fig. 11). The tubes were carefully labelled with the code identifying the plant from which the leaf was sampled. These tubes were then placed in a box to rehydrate overnight. The next morning, each rehydrated sample was weighed again to find its rehydrated weight (RHW). They were then placed individually in labelled oven-proof cases and left to dry in a drying cabinet for 24 hours at 70 °C, after which the samples were weighed again for the last time to obtain their dry weights (DW). See Table 2 for the formula used to find RWC_L.

Figure 11. Determining leaf relative water content (RWC_L). It requires the rehydration of sampled leaves (top left) after obtaining their fresh weight (top right). Samples are then closed in a box to rehydrate overnight and re-weighed in the morning. Leaves are then left to dry in a drying cabinet for 24 h at 70 °C (bottom left), after which samples are weighed again for dry weight (bottom right) and for the calculation of RWC_L.

A.2.4.3 Bulk leaf water potential

A reliable method for assessing the degree of physiological drought experienced by a plant is that of measuring its bulk leaf water potential (Ψ_L). It is an indicator of leaf water status that, when measured during the day, can give an indication of the species' drought tolerance. In fact, Ψ_L measures the negative hydrostatic pressure reached within the xylem vessels at the time of sampling – the xylem tension that a species must tolerate – and the more negative the value, the more dehydrated the leaf (Lambers, Chapin and Pons 2008; Pérez-Harguindeguy et al. 2013). This parameter is controlled by SMC and transpiration and is influenced by soil properties, climate, rooting depth and diurnal stomatal physiology (Tyree et al. 2002, Bhaskar and Ackerly 2006, Sade et al. 2009, Hernandéz et al. 2010). In the present study, Ψ_L was measured only in the first experimental year, using a pressure chamber on two consecutive days in 2016 – on 10 August for plants growing on the Hicks roof and 11 August for those growing on the Hadfield roof. These particular dates were chosen because the plants had experienced two weeks of continuous and relatively high temperatures (mean midday temperature: 18.9°C), minimal precipitation (10.1 mm total) and no additional irrigation. Leaves were sampled at three different times of the day: in the morning (8.30am), at midday (12.30pm), and in late afternoon (16.30pm). For each time slot, 12 leaf samples were measured per species, with three leaves arbitrarily selected from two individuals belonging to DP and SP. A total of 36 leaves per species were measured throughout the investigation, totalling 216 leaves overall.

Sampling involved the removal of a healthy and mature sun leaf (i.e. leaf in full exposure to sunlight) from an individual, very quickly covering the leaf with cling film to avoid loss of water from the leaf surface, placing it in the appropriate sealed bag labelled by experimental category and placing the bag in a thermal cooler. For each sampling cohort (8.30am, 12.30pm, 4.30pm), the cooler was then quickly transported to the plant physiology lab at the Sir David Read Facility (Department of Animal and Plant Sciences, University of Sheffield) for the measurement of Ψ_L of each sample, using a pressure chamber (see Table 2 for more details). The sample is removed from the bag and its cling film and quickly inserted through the rubber gasket of the chamber lid with the petiole facing outward while the leaf is placed within the chamber with the lid sealed, leaving the petiole exposed outside of the chamber. Air pressure is then applied slowly through a pressure gauge until the petiole is observed via a microscope to exude a small droplet of xylem sap. The pressure (in –MPa) indicated by the pressure gauge at the moment sap flows out of the petiole is then recorded as the value of Ψ_L for the particular sample.

A.2.4.4 Gas exchange: Transpiration rate (*E*), stomatal conductance (g_s) and assimilation (*A*)

A powerful analysis of photosynthetic performance can be deduced when the following gas-exchange parameters (in photosynthesis) are measured: 1) transpiration rate (*E*), the rate at which water is lost from leaves due to evaporation from within the leaf to the atmosphere; 2) stomatal conductance (g_s), the conductance for transport of CO_2 through the stomata (i.e. depends on stomatal control, SMC and air vapour pressure), and 3) assimilation (*A*), the rate of CO_2 assimilation (carbon gain) per unit leaf area. In particular, g_s can also be another measure of plant water status, in that it determines the gradient for transpirational water loss (Lambers, Chapin and Pons 2008).
These parameters are measured using gas-exchange systems. The gas-exchange system used in the present study was a portable Infra-Red Gas Analyzer or IRGA (See Table 2 for description). This complex system uses a transparent chamber (i.e. a leaf cuvette: a head attached to a tube inserted inside a gas analyser) that encloses a leaf. Air enters the chamber through the tube at a specified flow rate (f_m, 300 cm^3 min^{-1}) and the leaf enclosed by the chamber changes the concentration of CO_2 and H_2O inside the chamber. This change is recorded by the gas analyser, which uses this difference in concentration in both CO_2 (C) and H_2O (W) between air entering (C_e and W_e) and leaving (C_o and W_o) the chamber to calculate gas-exchange activity.
A is directly calculated by the analyser and expressed per unit leaf area (A_L) (µmol CO_2 m^{-2} s^{-1}) using the following formula:

$$A = f_m/A_L\{C_e - C_o\,(1 - W_e)/(1 - W_o)\}.$$

E is then calculated by substituting and W_e and W_o with C_e and C_o.

Leaf temperature (T_L) is also a parameter measured by the gas analyser. Once *E* and T_L are obtained during the measurement, the gas analyser can also calculate g_s. Once g_s is calculated, then intercellular CO_2 (C_i) can be calculated as well (Lambers, Chapin and Pons 2008). *A*, *E* and g_s are all expressed in µmol CO_2 m^{-2} s^{-1}.

It was necessary to choose summer days that were strictly cloudless, calm and sunny in order to carry out this kind of investigation, due to the complicated (and often temperamental) nature of the gas analyser. Before any day of measurements began, the IRGA would be turned on and left in a sheltered area of the rooftop to “warm up” for about 20 min and was then calibrated for atmospheric CO_2 concentrations (generally 410 ppm). For each species in 2016 (June 9, July 27 and August 18), three leaves per plant (10 plants per species) were measured, for a total of 30 leaves per species (15 for DP, 15 for SP). Summer days in 2017 were a bit more unstable and more days were needed for measurements. For each species in 2017 (July 17; August 10, 13, 15, 17 & 27; September 1), 6 leaves per plant (10 plants per species) were measured, for a total of 60 leaves per species (15 for DP 3x3, 15 for SP 3x3, 15 for DP 4x4 and 15 for SP 4x4). Carrying out each measurement with the IRGA took a relatively long time (5 minutes per leaf, to allow for stabilisation of leaf gas exchange); in order to have a sufficiently large sample size per species, measurements were conducted throughout the entire day (10:00 to 17:00), alternating between species and populations/categories.

A.2.4.5 Photosynthetic performance (Maximum Quantum Yield, QY)

Quantum yield is a term that describes the efficiency with which light is converted into fixed carbon in a leaf, or the ‘maximum quantum yield’ (QY) after dark incubation of PS II, i.e. photosynthetic system. This parameter is used to quantify the effects of stress on photosynthetic performance. F_v is the variable fluorescence and is equal to the difference between maximal (F_m) and minimal (F_0) fluorescence ($\Delta F_\mathrm{m} - F_0$), and QY is simply the ratio between F_v and F_m. (Lambers, Chapin and Pons 2008). In the present study, a chlorophyll fluorimeter (Table 2) was used to determine the QY of sampled mature sun leaves for every experimental year, throughout the summer months and on sunny and calm days. On nine different days between late July and early September 2016, 114 measurements of QY were conducted (57 for DP and 57 for SP) per species (3 measurements per plant, 38 plants per species), for a total of 684 measurements. On four different days between late August and early September 2017, 84 measurements were conducted (18 for DP 3x3, 18 for SP 3x3, 24 for DP 4x4 and 24 for SP 4x4) per species (3 measurements per plant, 28 plants per species), for a total of 504 measurements. On five different days between late June and early July 2018, 78 measurements were conducted (24 for MP and 54 for PP) per species (6 measurements per plant, 13 plants per species), for a total of 468 measurements. For each sampled leaf, a leaf clip was attached (i.e. clipped so as to cover both upper and lower surface) and left for 20 min with the shutter closed, to allow a small area of the leaf surface to remain in complete darkness and adjust to that condition (F_0). After that time had elapsed, the chlorophyll fluorimeter probe was attached to the clip and the shutter of the clip was opened to allow a single flash of light, lasting 10 s (intensity: 3000 µMol m^2 s^{-1}), to reach the surface of the leaf (F_m). The chlorophyll fluorimeter automatically calculated the QY after each flash.

A.2.4.6 Extrapolated plant parameter: Photosynthetic water-use efficiency (WUE_P)

Intrinsic water use efficiency (WUE_i) is the ratio between the gain of CO_2 in photosynthesis (*A*, assimilation rate) and transpiration rate (*E*). The higher the stomatal conductance to CO_2 (g_S), the greater the water lost through transpiration and the lower the WUE_P (Lambers, Chapin and Pons 2008). In general, drought tolerant species have high WUE_P in that they progressively reduce g_s (i.e. close the stomata) as water availability decreases in order to avoid water loss and related physiological consequences. In the present study, both *A* and *E* are parameters that were measured using the IRGA (Section 2.5.3) and therefore can be used to extrapolate WUE_P, i.e. *A*/*E*. The best conditions for measuring WUE_P would be in a laboratory with constant vapour pressure difference and leaf temperature, while *A* and *E* were measured in the field and therefore in an uncontrolled environment. However, as it is a ratio, WUE_P can be used in this case as indicator of drought tolerance purely for the comparison between the study species.

A.3 Statistical analysis

Statistical analysis was performed using the software SigmaPlot v. 13.0 (Systat Software Inc., San Jose, CA, USA). Comparisons between species or groups were made by testing the significance of differences, using Student's t-test and one-way ANOVA followed by Tukey's post hoc comparisons. Linear regression analysis was used to test for pairwise relationships between key inter-specific traits, while the significance of trait correlations was determined using the Pearson product-moment coefficient. Regressions or differences were considered to be significant if $P < 0.05$. Regressions or differences with a *P*-value between 0.05 and 0.2 were considered marginally significant. All mean values for each parameter are followed by their standard error (SEM).

Table 1. Summary of study species' ecological and morphological characteristics. List of the six study species and relative family, canopy type, leaf habit (E, evergreen; D, Deciduous; SD, Semi-deciduous) and traits, and the species' characteristics, habitat and distribution. See Appendix A for more detailed information on each study species.

Roof	Species	Family	Canopy type	Leaf habit	Leaf traits	Characteristics	Habitat & Distribution	References
Hadfield	*Buddleja davidii*	Scrophulariaceae	Multi-stemmed, dense foliage	SD	Wedge-shaped, dark green, underside of lamina covered in white-grey hair	Seasonal dimorphism, abundant nectar production, fast-growing, tolerant of broad range of environmental conditions	Invasive of open, dry disturbed sites in all of Europe, native of C and SW China	Leeuwenberg 1979; Owen and Whiteway 1980; Webb et al. 1988; Binggeli 1998; Houghton et al. 2003; Feng et al. 2007; Kriticos et al. 2010; Tallent-Halsell and Watt, 2009; Ebeling et al. 2012
Hadfield	*Ceanothus thyrsiflorus*	Rhamnaceae	Mat-forming, open habit, flexible spreading stems	E	Small, dark green, smooth, glossy, glabrous, gland-toothed	Nitrogen-fixing, shallow root system, seasonal self-pruning, high WUE, sensitive to small changes in soil moisture	Rapid post-fire pioneers of California's "soft" chaparral	Watson 1875; McMinn 1930; Poole and Miller 1975; Axelrod 1978; Burk 1978; Conrad et al. 1985; Franklin et al. 1985; Mahall and Wilson 1986; Tenhunen et al. 1994; Kennedy et al. 1999; Pugnaire et al. 2006; Ford and Hayes 2007; Harvey and Holzman 2014; Jepson eFlora 2016
Hadfield	*Cotinus coggygria*	Anacardiaceae	Multi-stemmed, spreading, upright	D	Large, simple, ovate to rounded lamina, glabrous	Drought-deciduous, highly drought tolerant, tight stomatal control, high WUE	Pioneer of abandoned and degraded areas, grows in thickets in S Europe on rocky limestone	Pignatti 1982; Greuter et al. 1984, 1986, 1989; Diamantoglou et al. 1989; Wannan and Quinn 1991; Dirr 1998; Nardini et al. 2003; Tzakou et al., 2005; Pijut 2008; Liu et al. 2010; Li et al. 2014, 2015; Gilman and Watson 2014; Schönfelder and Schönfelder 2014
Hicks	*Cistus × hybridus*	Cistaceae	Highly branched, erect, dense foliage	SD	Small, coriaceous, subglabrous, undulated margin, can roll under drought stress	Seasonal dimorphism, shallow root system, intermediate strategies between evergreen sclerophylls and drought-deciduous shrubs	Post-fire pioneer of S Mediterranean wood- and scrubland; colonizer of strongly degraded, exposed, and extreme environments	Martín Bolaños and Guinea López 1949; Harley et al. 1987; Gratani and Amadori 1991; Bosch 1992; De Lillis and Fontanella 1992; Grammatikopoulos 1999; Gratani and Bombelli 2000; De Micco and Aronne 2009;Guzmán et al. 2009; Abreu et al. 2012; Catoni et al. 2012; Schaffhauser et al. 2012; De Dato et al. 2013; Bartoli et al. 2014
Hicks	*Elaeagnus angustifolia*	Elaeagnaceae	Multi-stemmed, spreading, upright	D	Lanceolate, simple, underside of lamina covered in grey scales	Nitrogen-fixing, high resprouting capacity, strong root system, distinct sun- and shade-leaf cohorts	Vigorous pioneer of steppe regions in S Europe and C Asia, highly invasive in W USA	Graham 1964; Dirr 1998; Klich 2000; Stannard et al. 2002; Katz and Shafroth 2003; Yates et al. 2004; Gong et al. 2006; Brym et al. 2011; Carro et al. 2013; Zinnert et al. 2013
Hicks	*Viburnum tinus*	Adoxaceae	Multi-stemmed, dense foliage	E	Sclerophyllous, coriaceous, simple, dark green	Both shade and drought tolerant (high adaptive plasticity), high WUE and hydraulic safety	Native of S Mediterranean scrubland and typical understory component of woodland	Salleo et al. 1997; Kollman and Grubb 2002; Nardini 2002; Sack et al. 2003; Clennett 2004; García-Navarro et al. 2004; Fini et al. 2010

Table 2. Summary of morphological and physiological plant parameters measured in the study. Presented from left to right are the abbreviations of the parameters, units of measurement, relative equipment used to measure the parameters and the methods and significance of the parameters in the study.

Symbol	Parameter	Units	Equipment	Significance
SMC	Soil moisture content	$m^3\ m^{-3}$	ML3 ThetaProbe Soil Moisture Sensor with HH2 Moisture Meter, Delta-T Devices, Cambridge, UK	Volumetric soil moisture content, normalized by the container area and the total foliage count of the individuals planted in the container. Both stomatal conductance and transpiration depend on soil moisture, as the difference in leaf water potential and soil water potential is the driving force for water transport in the plant.
M	Plant mortality	%	Observation	Indicative of general plant fitness and tolerance to various stress factors on the rooftop.
RGR	Growth rate	$mm\ y^{-1}$, %	Digital caliper (DML, Sheffield, UK)	Annual diametric growth at stem-root transition level: Final growth (G_f) – initial growth (G_i) value, or (G_f – G_i)/G_i * 100. Can be indicative of how the plant invests carbon assimilates (on respiration vs new biomass) – fast vs slow-growing species. Unfavourable environmental conditions tend to reduce growth (i.e., canopy height, branch elongation, leaf size).
$\boldsymbol{A_{\mathrm{L}}}$	Leaf surface area (single & total canopy)	cm^2	Scanner (12000XL, Epson), Image J software (NIH, Bethesda, USA)	Leaf size is closely correlated with the size of terminal twigs and with branching spacing – it expresses scaling of the shoot architecture, but the ecological significance remains poorly understood. It also indicates if leaves are more sun- or shade-adapted and/or are more or less affected by wind exposure.
LMA	Leaf mass per area (single & total canopy)	$mg\ cm^{-2}$	Scanner, drying cabinet (LEEC Ltd., Nottingham, UK), Image J	Specific leaf mass, leaf dry mass per unit area. Indicator of cell wall thickness and sclerophylly (thickness). Species with low LMA tend to have short leaf life-spans, high leaf nutrient concentrations and high potential photosynthesis, therefore a fast turnover of plant parts which in turn permits a more flexible response to variations in light and soil resources. Species with high LMA have slow turnover of plant parts (long leaf life-span), expensive leaf construction, low nutrient concentration and lower photosynthetic rates.
$\boldsymbol{B_{\mathrm{W}}, B_{\mathrm{L}}}$	Woody and leaf above-ground biomass	$g\ m^{-2}$	Drying cabinet, precision balance (ME103TE/00, Mettler-Toledo Ltd., Leicester, UK)	Grams of above-ground dry plant material (leaves, main stem and branches) divided by experimental unit area (0.15 m^2). Plants are harvested and stems and leaves are divided. Leaves and stems are put in separate envelopes and dried at 70 °C in a drying cabinet for 24 h (48h for stems) and then weighed.
ADI	Apical Dominance Index	m^{-1}	Image J	No. ramifications / total length of branch, 5 images per species. The length of the branch is the distance from the base of a terminal, leaf-bearing branch that bears leaf-bearing secondary branches to the tip. Going from the base to the tip (following the main branch), the secondary ramifications in the images are counted along the way as the number of ramification points that lead to living branches.
I	Canopy interception of irradiance	$W\ m^{-2}$	Strobe light and controller (1500 DMX, Thomann GmbH, Germany), solar meter (TPI 510, TPI, Beaverton, OR, USA)	A powerful strobe light (flash light energy: 1500 W) at max intensity and in full darkness is flashed through 3 sections of the plant canopy (bottom, middle and top) for 10 seconds, at the end of which a value is taken by an irradiance metre placed on the other side of the canopy. This is repeated 3 times per section. The entire process is repeated 6 times, one for every angle of the plant (every 60°).
$\mathbf{RWC_{L}}$	Leaf relative water content	%	Plastic tubes for leaf rehydration, digital balance, drying cabinet	RWC_L = (FW-DW)/(RHW-DW) × 100; water content of leaf tissue relative to the water content at full hydration. Measure of plant water status, drought tolerance and leaf succulence.
$\boldsymbol{\Psi_{\mathrm{L}}}$	Bulk leaf water potential	MPa	Cling film, air-tight bags, cooler, pressure chamber (Model 1000, PMS Instruments, Albany, OR, USA)	Water potential of leaves reached during the warmest part of sampling day (11 -15 h). It is defined as the gradient between leaf and air, which indicates leaf water status, and depends on soil moisture, transpiration rate, stomatal control, and species-specific osmotic or elastic adjustments. The lower (more negative) the water potential that a species can tolerate before stomatal closure and turgor loss, the lower the level to which it can reduce soil moisture (e.g., drought-tolerant species and plants with high hydraulic safety).
E	Transpiration rate	$mmol\ CO_2\ m^{-2}\ s^{-1}$	Infrared Gas Analyser (TPS-2, PP Systems, Amesbury, MA, USA)	Gas exchange parameter that measures water loss from leaves due to evaporation from within the leaf. It is the major avenue of water loss to the atmosphere and therefore of soil drying.
$\boldsymbol{g_{\mathrm{s}}}$	Stomatal conductance	$mmol\ CO_2\ m^{-2}\ s^{-1}$	Infrared Gas Analyser	Gas exchange parameter that measures the conductance for transport of CO_2 or water vapour through the stomata, which in turn depends on stomatal control, soil moisture and vapour pressure in the air.
A	Assimilation	$\mu mol\ CO_2\ m^{-2}\ s^{-1}$	Infrared Gas Analyser	Gas exchange parameter that measures the rate of CO_2 assimilation (carbon gain) per unit leaf area, used for plant growth analysis.
$\mathbf{WUE_{P}}$	Photosynthetic Water-Use Efficiency	$mmol\ \ mol^{-1}$	Extrapolated using data collected with the Infrared Gas Analyser	A/E, ratio between assimilation and transpiration rate. Since transpiration is approx. linearly related to g_s, this ratio is used as an approximation of WUE, described as carbon gain per water lost.
QY	Maximum quantum yield	ratio	Handy PEA Chlorophyll Fluorimeter, Hansatech Instruments, Norfolk, UK	Ratio between F_v ($\Delta F_m – F_0$) and maximal fluorescence (F_m), defined as the maximum quantum yield after dark incubation of PS II and used to quantify effects of stress on photosynthetic performance. Quantum yield describes the efficiency with which light is converted into fixed carbon.
$\boldsymbol{T_{\mathrm{L}}}$	Leaf temperature	°C	Infrared Gas Analyser (TPS-2, PP Systems, Amesbury, MA, USA)	Can be indicative of the plant's capacity to lower temperatures when irradiance and temperatures are high; wind exposure also tends to lower leaf temperature

A.4 Results

A.4.1 The effects of plant density, population size and species mixture on the morphology and fitness of six woody shrubs

The ecological distribution of woody shrubs is determined by species-specific plant traits, which regulate fundamental plant functions and determine productivity and performance both in natural and in managed or manmade ecosystems within agriculture, forestry and urban contexts (Garnier and Navas 2012, Reich 2014). As manifestation of inherent adaptive strategies, the shrub species in the present study have been diversely affected by rooftop conditions and therefore have inevitably displayed species-specific morphological and physiological behaviour. The analysis of the plant parameters measured throughout the study, as well as their effects on temperature profiles, are therefore essential to understanding the variation in performance within different shrub species or ecological groups and to translating and transferring these findings into more informed methods of plant selection for the urban or semi-natural environments, such as those represented by green roofs.

A.4.1.1 Long-term survival and growth

A.4.1.1.1 Mortality (*M*)

Mortality for each study species (Table 3) is presented as both the specific number and as the percentage of plants that died in relation to the total number of individuals per species (i.e. 54 plants). Mortality rate is further divided into: mortality after 12 months from transplant (M_1), during the first study year; after a further 21 months (M_2) during the second and third study years and finally as total mortality over the entire study period (M), which lasted about 33 months.

Table 3. Species mortality over time. The mortality rate for each species presented as specific number (n° plants, out of 54) and percentage (%) of plants that died after 12 months (M_1), after 21 months (M_2) and after a total of 33 months (M).

Species	M_1 **(n° plants)**	M_1 **(%)**	M_2 **(n° plants)**	M_2 **(%)**	M **(n° plants)**	M **(%)**
Viburnum tinus	2	3.70	0	0	2	3.70
Cistus × hybridus	13	24.07	43	79.63	56	103.70
Elaeagnus angustifolia	2	3.70	7	12.96	9	16.66
Ceanothus thyrsiflorus	0	0	0	0	0	0
Buddleja davidii	0	0	0	0	0	0
Cotinus coggygria	5	9.26	11	20.37	16	29.63

When taking into account all species (i.e. a total of 324 individual plants), the average M_{1+2} was 25.62%, therefore a little over a quarter of shrubs in the present study died over a period of 33 months, with a progressive increase in *M* going from only 6.79% in the first 12 months (less than 2 plants per month) to almost three times the rate at 18.83% in the following 21 months (nearly 3 plants per month), with an overall average of 2.5 plants dying per month. It would then seem that 1 out of 4 plants in the study died, however, 70.49% of total *M* belonged to individuals of *Cistus* × *hybridus*. Therefore, species-specific causes of mortality need to be taken into great consideration, in that more than one unsuitable selection in this case could have resulted in a much higher total *M*.

In fact, despite selecting it based on its stellar ʽCV’ (see Appendix A for detailed descriptions of all study species), *Cistus* has undoubtedly faired the worst in this study, ranking as the species with the absolute highest *M*. The *M* of 103.70% signifies that the entire population of *Cistus* has had to be completely replaced in the space of 33 months, plus 2 individuals on top of that, at an average rate of almost 2 plants per month. It is also clear that the species’ fitness progressively decreased with time, going from an average *M* of about 1 plant per month in the first 12 months to about 2 plants per month in the remaining study period. *Cistus* was the only species to suffer an aphid outbreak during the first summer season of the study, but more generally during the study it appeared stressed by snow and frost in the winter months and would visibly deteriorate much quicker in fitness after prolonged spells of drought in the warmer months compared to the other species. In particular, the *Cistus* individuals placed in the category of dense population (DP) during the first study year had more than double the mortality (33.33%) compared to those placed in the sparse population, SP (14.81%), whereas mortality was only somewhat higher in the category of monospecific population, MP (88.89%) during the third study year compared to the polyspecific population, PP (70.37%).

Though not nearly as many as *Cistus*, some of the other species also saw losses in their populations. The two deciduous shrubs, *Cotinus coggygria* and *Elaeagnus angustifolia*, have had slightly higher *M* than both *Buddleja davidii* and their evergreen counterparts (*Viburnum tinus* and *Ceanothus thyrsiflorus*) and showed a similar progressive deterioration in fitness over time to that of *Cistus*. *Cotinus* in particular lost nearly a third of its population by the end of the study (29.63%), at a rate of about 1 plant every 2 months, however without any remarkable difference in *M* between the various categories (i.e. DP vs SP; MP vs PP). Instead, *Elaeagnus*’ decline in fitness was concentrated in the final study year and most of the plants that died then belonged to the MP category. While the cause of increased stress displayed by *Elaeagnus* plants in the final year is not entirely known (perhaps the limited growing space), the brittle branches of *Cotinus* plants would occasionally be gnawed on by slugs in the spring months, probably attracted by the strong-smelling resin they would start producing in that time of year, which, on top of the various other stresses, undoubtedly added to the progressive decline in the shrub's vigour. The evergreen *Viburnum tinus* only had two plants die in total, all during the first study year due to mechanical damage from transplant and wind, while all individuals belonging to *Buddleja davidii* and to the other evergreen shrub (*Ceanothus thyrsiflorus*) survived the entire study period. At the time of harvest, all *Viburnum*, *Buddleja* and *Ceanothus* plants were in relatively good health and showed no particular signs of stress.

A.4.1.1.2 Growth (G) and relative growth rate (RGR)

Closely linked to M should be the relative rate at which shrubs grow over a period of time (RGR). As survival and reproduction in all plants depend on the physical size of the individual, and therefore on RGR, growth is a particularly important activity in shrubs. However, RGR is determined by the combined differences in physiological (e.g. net assimilation rate), morphological (e.g. leaf area and mass) and biomass partitioning processes (e.g. plant mass) that all contribute to plant growth (Shipley 2006), all of which will be discussed in more detail further on in the chapter. Table 4 below lists the mean growth in trunk diameter at stem-root transition level per species, organised as: 1) the increase (ΔG_1-G_0) that occurred in the first 12 months of the study (G_{12}), in terms of both millimetres of biomass growth and as a percentage (ΔG_1-G_0 / $G_2 \times 100$); 2) as the increase (ΔG_2-G_1) that occurred in the following 21 months (G_{21}), expressed in millimetres and as percentage (ΔG_2-G_1 / $G_2 \times 100$) and 3) as the increase (ΔG_2-G_0) that occurred throughout the entire study, or total growth (G), presented in millimetres and as percentage (ΔG_2-G_0 / $G_2 \times 100$).

Table 4. Species growth over time. Mean growth of the six study species divided into G_{12} (growth in the first 12 months), G_{21} (growth in the following 21 months) and G (total growth over 33 months). Growth is presented as the increment in trunk diameter at stem-root transition level, both in millimetres (mm) and as percentage (%).

Species	**G_{12} (mm)**	**G_{12} (%)**	**G_{21} (mm)**	**G_{21} (%)**	**G (mm)**	**G (%)**
Viburnum tinus	**16.34**±0.68	36.61	**15.61**±1.07	34.98	**31.95**±1.33	71.60
Cistus × hybridus	**5.00**±0.31	28.79	**2.53**±0.42	14.58	**7.53**±0.51	43.38
Elaeagnus angustifolia	**5.83**±0.33	23.79	**4.21**±0.46	17.19	**10.04**±0.67	40.98
Ceanothus thyrsiflorus	**3.02**±0.30	20.69	**3.43**±0.29	23.45	**6.45**±0.31	44.14
Buddleja davidii	**6.29**±0.43	25.67	**3.79**±0.35	15.45	**10.06**±0.49	41.03
Cotinus coggygria	**7.30**±0.44	33.19	**4.61**±0.44	20.96	**11.91**±0.69	54.15

From here, the mean relative growth rate for each species can be calculated by dividing growth as shown above in Table 4 by unit of time. For each species, Table 5 below presents: 1) the growth per month that occurred in the first 12 months of the study (RGR_1), calculated as G_{12} / 12; 2) the growth per month that occurred in the following 21 months (RGR_2), calculated as G_{21} / 21, and 3) the growth per month across the entire 33 months of the study (RGR), calculated as G / 33, all of which is expressed in both millimetres of biomass growth per month and as percentage growth per month.

Table 5. Species relative growth rate over time. Mean relative growth rate for the six study species, presented as growth per month in the first 12 months (RGR_1), growth per month in the following 21 months (RGR_2) and total growth per month (RGR). Results are presented in both millimetres (mm) and as percentage (%) of growth per month.

Species	**RGR_1 (mm)**	**RGR_1 (%)**	**RGR_2 (mm)**	**RGR_2 (%)**	**RGR (mm)**	**RGR (%)**
Viburnum tinus	**1.36**±0.06	3.05	**0.74**±0.05	1.67	**0.97**±0.04	2.17
Cistus × hybridus	**0.42**±0.03	2.40	**0.12**±0.02	0.69	**0.23**±0.02	1.31
Elaeagnus angustifolia	**0.49**±0.03	1.98	**0.20**±0.02	0.82	**0.30**±0.02	1.24
Ceanothus thyrsiflorus	**0.25**±0.03	1.72	**0.16**±0.01	1.12	**0.20**±0.01	1.34
Buddleja davidii	**0.52**±0.04	2.14	**0.18**±0.02	0.74	**0.30**±0.01	1.24
Cotinus coggygria	**0.61**±0.04	2.77	**0.22**±0.02	1.00	**0.36**±0.02	1.64

When comparing the different study species in terms of the various categories presented in Tables 4 and 5 (i.e. G_{12}, G_{21}, G; RGR_1, RGR_2, RGR), all differences were found to be highly significant ($P<0.001$), therefore the six shrubs have significantly different mean G and mean RGR values. *Viburnum* also clearly had the highest mean G and mean RGR, in all categories, followed by *Cotinus* and *Ceanothus*. Mean G and mean RGR were positively and significantly correlated ($P=0.007$ and $R=0.929$, See Table A in Appendix B) with mean leaf biomass (or dry weight) per plant, B_L (See Section 3.1.2.2). However, this correlation is highly skewed by the presence of *Viburnum* – without *Viburnum*, the correlation would not be significant.

When comparing the values of G_{12} and G_{21} for each species, all shrubs presented a significantly lower mean growth in the second phase (i.e. the last 21 months) compared to the first 12 months of the study, except for the two evergreen shrubs (*Viburnum* and *Ceanothus*). In fact, although not a significant increase, *Ceanothus* even had a slightly higher growth in the second (3.43 mm) compared to the first phase (3.02 mm) of the study. All this could indicate that the evergreen shrubs might have had a slightly greater ability to adapt to rooftop environment in the long-term, especially when compared to the semi-deciduous shrubs *Cistus* and *Buddleja*, where G_{21} was almost exactly 2 times and about 1.66 times lower than G_{12}, respectively. The deciduous shrubs, *Cotinus* and *Elaeagnus*, had intermediate decreases in G over time, with G_{21} about 1.58 times and about 1.38 times lower than G_{12}, respectively. Based on their overall mean G, the different species can thus be ranked (from highest to lowest): *Viburnum* > *Cotinus* > *Ceanothus* > *Cistus* > *Buddleja* > *Elaeagnus*; however, based solely on their mean G_{21}, the species can be ranked: *Viburnum* > *Ceanothus* > *Elaeagnus* > *Cotinus* > *Buddleja* > *Cistus*, or essentially: Evergreen > Deciduous > Semi-deciduous. In fact, *Ceanothus* made the highest leap up in the ranks, going from last in terms of G_{12} to just behind *Viburnum* in terms of G_{21}, whereas *Cistus* made the worst change in growth pattern, going from third in terms G_{12} to very last in terms of G_{21}. This is in line with the mortality rates of *Cistus* described previously, especially in the second phase of the study – clearly, this species struggled to grow and therefore survive long-term. However, despite perhaps an intuitively close link between mortality and growth, the parameters M and G were not found to be significantly correlated (See Table A in Appendix B). In fact, in spite of being classified as a semi-deciduous species like *Cistus* and having one of the worst growth patterns, *Buddleja* had zero mortality throughout the entire study. There must therefore be complex underlying factors influencing the shrubs' ability to survive and adapt to rooftop environment.

Values of mean G for the different categories of population adopted throughout the study were also analysed. In the final year of the study (i.e. the last 9 months), all plants were divided into the two categories of monospecific (only one species) and polyspecific (mixture of species) populations, in order to observe the effect of species mixture on the different plant parameters; however, G was not significantly affected by this. What did affect growth appreciably was the division of each study species into "sparse population" and "dense population" in the first 12 months of the study, to replicate conditions of low and high plant density. Table 6 shows that, in all species, values of mean growth were lower in the dense population (G_{DP}) compared to the sparse one (G_{SP}) and this difference between G_{SP} and G_{DP} was even significant for *Viburnum*. The p-values of the other species (Table 6), despite not representing significant differences, still show what can be described as "marginal" significance in plant ecophysiology and thereby can reveal interesting "trends". For example, the ranking of the species from highest to lowest p-value is: *Viburnum* > *Ceanothus* > *Elaeagnus* > *Cotinus* > *Buddleja* > *Cistus*, or again: Evergreen > Deciduous > Semi-deciduous. Could this be an emerging trend? In this case, it applies to the effect of plant density on growth, which may or may not have a greater impact on the evergreen shrubs compared to the others. These findings and direct observation of the shrubs would logically lead to the assumption that a higher plant density could hamper the infiltration of irradiance through the canopy due to the physical nearness of each plant to one another, thereby impacting on photosynthesis and growth. Moreover, the evergreens might be more affected by plant density compared to other types of shrubs because, as they photosynthesis year round, the combination of seasonally lower irradiance levels and less irradiance penetrating the dense canopies could negatively affect photosynthesis levels in the winter.

Table 6. The effect of plant density on growth. Mean growth for the six study species as divided into the sparse (G_{SP}) and the dense population (G_{DP}), with respective *p*-values indicating the differences between G_{SP} and G_{DP} for each shrub.

Species	**G_{SP} (mm)**	**G_{DP} (mm)**	***P*-value**
Viburnum tinus	**17.36**±0.84	**14.08**±1.27	**0.037**
Cistus × hybridus	**5.34**±0.36	**4.65**±0.49	0.259
Elaeagnus angustifolia	**6.28**±0.43	**5.37**±0.49	0.168
Ceanothus thyrsiflorus	**3.53**±0.27	**2.52**±0.53	0.097
Buddleja davidii	**6.82**±0.66	**5.77**±0.53	0.223
Cotinus coggygria	**7.87**±0.67	**6.74**±0.57	0.204

As RGR is simply *G* divided by time elapsed, or in this case the rate of growth per month, the same exact trends and rankings per species in relation to mean values of *G* as described previously can be observed for RGR as well. The only point to add would be that, despite having a slightly higher mean G_{21} compared to G_{12}, *Ceanothus* still showed signs of slowing down in terms of RGR in the second part of the study (0.16 mm/month) compared to the first part (0.25 mm/month, Table 5). In fact, all shrub species showed significant signs of slowing RGR ($P<0.001$) between the first 12 months (RGR_1) and the next 21 months (RGR_2), however *Ceanontus* had the lowest rate of slowing growth overall – RGR_1 was only 1.57 times higher than RGR_2 in *Ceanothus*, whereas *Cistus* had the highest decline in RGR with RGR_1 being 3.5 times higher than RGR_2. The following is a ranking of the study species based on their rate of slowing growth (RGR_1 vs RGR_2), from lowest to highest: *Ceanothus* > *Viburnum* > *Elaeagnus* > *Cotinus* > *Buddleja* > *Cistus*. Again, we have a ranking of this type: Evergreen > Deciduous > Semi-deciduous.

On the other hand, this type of assessment might be too simplistic and not take into account fundamental physiological differences between the different species or categories within which they fit. For example, decidous shrubs have a natural pause in growth in the winter months, a period of no or minimal metabolic activity called dormancy, in which branches are bare and leaves reappear only in the spring to again start contributing to photosynthesis and growth in the summer. This would account for the lower mean values of both *G* and RGR in the deciduous compared to the evergreen shrubs. By this logic, the semi-deciduous shrubs (i.e. shrubs that do not shed leaves in the summer but have a change in habit between summer and winter leaves) should have intermediate values of *G* and RGR. *Cistus* and *Buddleja* effectively did have intermediate values of *G* and RGR in the first 12 months, but then had a steep decline in both parameters in the latter part of the study. More investigation is therefore needed to ascertain the underlying factors in what can essentially be considered a decline in fitness over time, as will be discussed further in this chapter.

A.4.1.1.3 Leaf mass per area (LMA)

Despite not being the best indicator of plant performance, leaf mass per area (LMA) is an easy plant trait to measure, as it is simply the ratio between the dry weight of a leaf and its leaf area (mg cm^{-2}). Nutrient, water and especially light and temperature levels significantly influence LMA, thereby reflecting species fitness in its environment (Poorter et al. 2009). The structure of a leaf, in particular the palisade mesophyll layer in the lamina, stands between sunlight acquisition and the chloroplasts that carry out photosynthesis, therefore LMA is often regarded as the physical connection between light capture and biomass gain (Kattge et al. 2011). In fact, it often correlates with assimilation and growth rate and can be an indicator of leaf lifespan, leaf tissue density, leaf decomposition rate, resistance to herbivory and drought tolerance (de la Riva et al. 2016). Higher LMA is often found in woody trees and shrubs from nutrient-poor environments that allocate greater resources in support and defence structures, such as sclerified tissues for mechanical support and smaller vessels to avoid embolism (Castro-Díez, Puyravaud and Cornelissen 2000). Succulent, woody evergreen and slow-growing species tend to have the highest values of LMA and leaf tissue density, and evergreen species will tend to have thicker leaves (i.e. larger volume of tissue per leaf area) than deciduous species (Poorter et al. 2009).

Measurements of LMA in the present study were conducted both in terms of yearly sampling at the end of each summer and as an overall last sampling after harvesting. For each species, Table 7 below presents: 1) the mean values of leaf mass per area as measured separately in the three years of the study (LMA$_1$, LMA$_2$ and LMA$_3$), to evaluate possible changes in this parameter over time; 2) the *p*-values associated to the One-Way ANOVA applied to test the differences in leaf mass per area in the three separate years; 3) the average leaf mass per area for the entire study (LMA$_T$), in terms of yearly sampling at the end of each summer, and 4) mean values of LMA based on above-ground biomass measurements carried out after harvesting the shrubs at the the end of the study (LMA$_B$). LMA$_B$ is the ratio between total leaf dry weight (B_L) and total leaf area (A_L) of the entire canopy of each plant belonging to the monospecific population of each species, as obtained at the end of Summer 2018 (See Section 3.1.2.2).

LMA$_T$ was found to be statistically different among the woody shrubs ($P<0.001$), with the sclerophyllous evergreen *Viburnum* presenting the highest mean LMA (14.98 mg cm^{-2}) and the deciduous *Elaeagnus* and *Cotinus* displaying the lowest mean LMA (6.82 and 9.01 mg cm^{-2}, respectively). Despite the expected association between LMA and *G*, the two parameters were not found to be significantly correlated ($P=0.148$, See Table A in Appendix B). LMA$_B$ was also found to be statistically different among the woody shrubs ($P<0.001$) and to be similar to LMA$_T$ in almost all species. The difference between LMA$_T$ and LMA$_B$ was statistically significant for only *Buddleja*

(*P*<0.001) and *Cotinus* (*P*<0.001), perhaps due to a greater differentiation between sun and shade leaves in these species compared to the others, as measurements of LMA_T were only based on samples of sun leaves (i.e. normally thicker than shade leaves).

Although LMA_B was also not significantly correlated to *G*, it was instead significantly and negatively correlated to branch length (*P*=0.033, See Table A in Appendix B and Section 3.1.2.1), perhaps because the two parameters were measured at the same time (i.e. above-ground biomass after harvesting) – this means that, as mean branch length increased, mean LMA_B decreased. In fact, it would seem that the shrubs with the shortest branches (*Viburnum*, *Ceanothus* and *Cistus*) had the highest mean LMA_B. A possible explanation for this correlation (unless completely random) could be that the allocation of carbon likely went preferentially into leaves rather than into branch growth in the short shrubs, whereas the tall shrubs preferred to distribute more biomass into branch growth and therefore into canopy height.

Table 7. Changes in leaf mass per area over time. Mean values of LMA for each year of the study (LMA_1, LMA_2 and LMA_3); the *p*-values of the differences tested between study years; total leaf mass per area (LMA_T) for each species, based on yearly measurements, and leaf mass per area based on biomass measurements after harvesting (LMA_B).

Species	**LMA_1 (mg cm^{-2})**	**LMA_2 (mg cm^{-2})**	**LMA_3 (mg cm^{-2})**	***P*-value**	**LMA_T (mg cm^{-2})**	**LMA_B (mg cm^{-2})**
Viburnum tinus	**14.40**±0.35	**14.94**±0.46	**15.78**±0.37	**0.031**	**14.98**±0.23	**14.35**±0.40
Cistus × hybridus	**11.27**±0.31	**13.86**±0.50	**11.69**±0.32	**<0.001**	**11.99**±0.22	**13.08**±0.66
Elaeagnus angustifolia	**5.84**±0.15	**7.75**±0.21	**7.52**±0.17	**<0.001**	**6.82**±0.13	**6.47**±0.44
Ceanothus thyrsiflorus	**12.12**±0.21	**11.46**±0.40	**8.31**±0.28	**<0.001**	**10.72**±0.22	**11.36**±0.47
Buddleja davidii	**10.44**±0.18	**13.44**±0.26	**9.38**±0.18	**<0.001**	**10.74**±0.17	**5.91**±0.21
Cotinus coggygria	**8.67**±0.28	**9.83**±0.32	**8.90**±0.27	**0.032**	**9.01**±0.17	**6.85**±0.28

The difference between LMA_1, LMA_2 and LMA_3 was found significant to highly significant for all study species. This means that LMA varied significantly over the course of the three years, with only *Viburnum* (highest LMA) and *Elaeagnus* (lowest LMA) maintaining the same position in the ranking throughout the study. The following ranks the species from highest mean LMA_1 to lowest during the first study year: *Viburnum* > *Ceanothus* > *Cistus* > *Buddleja* > *Cotinus* > *Elaeagnus*, which can be converted into a ranking of functional groups: Evergreen > Semi-deciduous > Deciduous. Therefore, at full health and at presumably low stress levels, the shrubs presented the classic subdivision of evergreen (high LMA), semi-deciduous (intermediate LMA) and deciduous (low LMA) in terms of leaf structure. However, by the third year of the study *Ceanothus* showed a notable and constant decrease in mean LMA, going from 12.12 mg cm^{-2} in Year 1 to 8.31 mg cm^{-2} in Year 3. Whether down to a general reduction in fitness or a shuffle in resource allocation from leaf to other structures, *Ceanothus* displayed the greatest decrease in LMA through the years and the lowest overall *G* among the species (See Section 3.1.1.2), while *Viburnum* displayed one of the highest and continuous increases in LMA and the highest overall *G* among the species, thereby indicating at least a connection between the two parameters within the evergreen shrubs. *Cistus*, despite having one of the lowest *G*, had one of the highest values of LMA throughout the study, potentially denoting the species' preferential allocation of carbon to leaf rather than woody biomass growth. Finally, the semi-deciduous and the deciduous species all showed an increase in mean LMA going from Year 1 (LMA_1) to Year 2 (LMA_2), but then a slight dip in mean LMA going from Year 2 to Year 3 (LMA_3). The same variation was found in values of maximum quantum yield (See Section 3.2.1.1 further on), however the two parameters were not significantly correlated when comparing overall mean values (P=0.326, See Table A in Appendix B) or when testing the correlation by year (e.g., LMA_1 vs QY_1).

During the first year of the study, all six shrub species were arranged into monospecific (MP) populations, but each species was divided into sparse (SP) and dense (DP) populations, to evaluate the effect of plant density on various plant parameters. The year after, the shrubs were rearranged into four polyspecific populations (PP) that were further arranged into one of the following combinations: a) SP 3×3; b) SP 4×4; c) DP 3×3 or d) DP 4×4 (See Section 2.2.3.2 for more details). For each study species, Table 8 below highlights the differences between mean values of LMA in terms of the effects of species mixture (MP vs PP) and therefore has these values divided into study year. Year 3 was dedicated to directly compare (i.e. same year, same exact conditions) the effects of species mixture on LMA and other plant parameters. All data in Tables 8–11 are presented in units of mg cm^{-2}.

Table 8. The effect of species mixture on leaf mass per area. Comparison of mean LMA between populations of MP ($\mathrm{LMA}_{\mathrm{MP}}$) and PP ($\mathrm{LMA}_{\mathrm{PP}}$) shrubs, divided by species and year of study (Year 1, 2 & 3). *P* is the *p*-value of the test (within each species) between $\mathrm{LMA}_{\mathrm{MP}}$ in Year 1 and $\mathrm{LMA}_{\mathrm{PP}}$ in Year 2, and the test between $\mathrm{LMA}_{\mathrm{MP}}$ and $\mathrm{LMA}_{\mathrm{PP}}$ in Year 3.

	Year 1	**Year 2**		**Year 3**		
Species	**$\mathrm{LMA}_{\mathrm{MP}}$**	**$\mathrm{LMA}_{\mathrm{PP}}$**	***P***	**$\mathrm{LMA}_{\mathrm{MP}}$**	**$\mathrm{LMA}_{\mathrm{PP}}$**	***P***
Viburnum tinus	**14.40**±0.35	**14.94**±0.46	0.367	**15.79**±0.64	**15.78**±0.47	0.993
Cistus × hybridus	**11.27**±0.31	**13.86**±0.50	**<0.001**	**12.51**±0.45	**11.27**±0.40	0.060
Elaeagnus angustifolia	**5.84**±0.15	**7.75**±0.21	**<0.001**	**7.02**±0.23	**7.79**±0.22	**0.033**
Ceanothus thyrsiflorus	**12.12**±0.21	**11.46**±0.40	0.110	**9.67**±0.18	**7.61**±0.35	**<0.001**
Buddleja davidii	**10.44**±0.18	**13.44**±0.26	**<0.001**	**8.92**±0.25	**9.63**±0.22	0.053
Cotinus coggygria	**8.67**±0.28	**9.83**±0.32	**0.014**	**9.15**±0.54	**8.77**±0.31	0.514

When comparing Year 1 ($\mathrm{LMA}_{\mathrm{MP}}$) with Year 2 ($\mathrm{LMA}_{\mathrm{PP}}$) data in Table 8, it can be observed that all species except for *Ceanothus* showed higher mean LMA (significantly so in all shrubs except

Viburnum) when growing in the PP compared to the MP. However, the importance of having direct comparisons for different categories can easily be observed in the same table – while the difference between the effects of species mixture (MP vs PP) on LMA is significant in almost all the shrubs when comparing data from Year 1 (MP) against data from Year 2 (PP), the same cannot be said when directly comparing the same categories in Year 3 (MP vs PP), where only *Elaeagnus* and *Ceanothus* showed a significant difference in mean LMA. While that is true, it should also be taken into account the fact that Year 3 had a smaller number of plants dedicated to each category compared to Years 1 and 2 and therefore may have contributed to the reduced significance of the results. The only species that showed a significant difference between LMA_{MP} and LMA_{PP} in both cohorts of data (i.e. Year 1 vs Year 2 and Year 3) was *Elaeagnus*, a deciduous shrub that also had the lowest mean LMA in the study.

While mean LMA in Year 3 was significantly lower in *Ceanothus* shrubs growing in a PP (7.61 mg cm^{-2}) compared to those growing in a MP (9.67 mg cm^{-2}), species mixture had the opposite effect on *Elaeagnus*, with LMA slightly lower in the shrubs placed in a MP (7.02 mg cm^{-2}) compared to those in a PP (7.79 mg cm^{-2}). Although the differences between LMA_{MP} and LMA_{PP} in Year 3 for *Buddleja* (*P*=0.053) and *Cistus* (*P*=0.060) fall just below the significance level, the two semi-deciduous shrubs present, like *Elaeagnus* and *Ceanothus*, the same opposed results: *Buddleja* had higher mean LMA in PP (9.63 mg cm^{-2}) compared to MP (8.92 mg cm^{-2}), while *Cistus* had higher mean LMA in MP (12.51 mg cm^{-2}) compared to PP (11.27 mg cm^{-2}).

These results could support the hypothesis that LMA might be influenced by light exposure, which inevitably will be different for the taller shrubs (*Buddleja*, *Elaeagnus*, *Cotinus*) compared to the shorter shrubs (*Cistus*, *Ceanothus*, *Viburnum*) when these are placed in populations composed of individuals with heterogeneous heights as in polyspecific (PP) ones. With the exception of *Viburnum* and *Cotinus*, which showed no significant difference, mean values were found to be higher in LMA_{MP} than in LMA_{PP} within the short shrubs, whereas the opposite was true for the tall shrubs. This polarisation could signify a need by the shorter shrubs to increase leaf thickness and tissue density (i.e. higher LMA) when placed in a population composed of individuals with homogeneous heights, as in a monospecific population (MP), due to the greater exposure to light; inversely, the same shrubs would need to allocate less carbon resources and thereby have thinner leaves (i.e. lower LMA) when growing in a PP, surrounded by taller shrubs that create more shade and therefore less exposure to both light, wind and other environmental stresses. As the taller shrubs are more exposed to light when placed in a PP than in a MP (i.e. self-shading by all individuals having tall canopies), the opposite effect is observed: thinner leaves in tall shrubs placed in PP and thicker leaves in those placed in MP. While not entirely supported by results in Table 8, this hypothesis may be backed by results in Table 10 (explained in the next paragraphs), which show that the short shrubs (*Viburnum*, *Ceanothus* and *Cistus*) placed in a PP were significantly affected by plant density (i.e. they had lower mean LMA in DP) whereas the tall shrubs are not.

Unlike species mixture, plant density unequivocally affected leaf mass per area in all study species except the deciduous ones. The best way to observe the effects of plant density and population size on LMA is to present the data in a series of tables, with relative *p*-values for the tests applied to identify the differences between categories. Below are: 1) Table 9, presenting the values of mean LMA per species as divided into sparse ($\mathrm{LMA}_{\mathrm{SP}}$) and dense ($\mathrm{LMA}_{\mathrm{DP}}$) population within Years 1 and 2 of the study; 2) Table 10, presenting the values of mean LMA per species in Year 2 as divided into both population size 3×3 ($\mathrm{LMA}_{3\times3}$) and 4×4 ($\mathrm{LMA}_{4\times4}$) and into plant density sparse ($\mathrm{LMA}_{\mathrm{SP}}$) and dense ($\mathrm{LMA}_{\mathrm{DP}}$), and finally 3) Tables 11a and 11b, presenting results and *p*-values, respectively, for mean LMA per species in Year 2 as divided into the various different combinations of categories ($\mathrm{LMA}_{\mathrm{SP+3x3}}$, $\mathrm{LMA}_{\mathrm{DP+3x3}}$, $\mathrm{LMA}_{\mathrm{SP+4x4}}$ and $\mathrm{LMA}_{\mathrm{DP+4x4}}$).

Table 9. Direct comparison of the effect of species mixture on leaf mass per area. Comparison of mean LMA per species between sparse ($\mathrm{LMA}_{\mathrm{SP}}$) and dense ($\mathrm{LMA}_{\mathrm{DP}}$) populations. Data divided by: Year 1 (shrubs in MP & 3×3 size) and Year 2 (shrubs in PP & only in 3×3 size). *P* is the *p*-value of the test between $\mathrm{LMA}_{\mathrm{SP}}$ and $\mathrm{LMA}_{\mathrm{DP}}$ in Year 1 and in Year 2 of the study.

	Year 1 (MP, 3×3)			**Year 2 (PP, 3×3)**		
Species	$\mathbf{LMA}_{\mathbf{SP}}$	$\mathbf{LMA}_{\mathbf{DP}}$	***P***	$\mathbf{LMA}_{\mathbf{SP}}$	$\mathbf{LMA}_{\mathbf{DP}}$	***P***
Viburnum tinus	**15.63**±0.49	**13.21**±0.40	**<0.001**	**16.76**±1.08	**14.29**±0.74	0.088
Cistus × hybridus	**11.43**±0.42	**11.16**±0.46	0.660	**14.87**±0.94	**13.53**±1.25	0.414
Elaeagnus angustifolia	**6.05**±0.21	**5.60**±0.21	0.146	**8.19**±0.52	**7.66**±0.54	0.497
Ceanothus thyrsiflorus	**12.60**±0.25	**11.61**±0.31	**0.016**	**13.25**±0.56	**10.37**±0.60	**0.006**
Buddleja davidii	**10.92**±0.23	**9.95**±0.23	**0.004**	**13.61**±0.54	**13.34**±0.45	0.427
Cotinus coggygria	**8.78**±0.37	**8.56**±0.43	0.694	**9.44**±0.37	**10.22**±0.87	0.706

Table 10. The effect of increasing population size and plant density on the leaf mass per area of shrubs in polyspecific populations. Comparison of mean LMA per species in Year 2 (comprised of only PP), between: 1) small population size ($\mathrm{LMA}_{3\times3}$) and big population size ($\mathrm{LMA}_{4\times4}$), and 2) low ($\mathrm{LMA}_{\mathrm{SP}}$) and high ($\mathrm{LMA}_{\mathrm{DP}}$) plant density. *P* is *p*-value per species of the test between $\mathrm{LMA}_{3\times3}$ and $\mathrm{LMA}_{4\times4}$ and between $\mathrm{LMA}_{\mathrm{SP}}$ and $\mathrm{LMA}_{\mathrm{DP}}$.

	Year 2 (PP)					
Species	$\mathbf{LMA}_{3\times3}$	$\mathbf{LMA}_{4\times4}$	***P***	$\mathbf{LMA}_{\mathbf{SP}}$	$\mathbf{LMA}_{\mathbf{DP}}$	***P***
Viburnum tinus	**15.53**±0.73	**14.51**±0.58	0.277	**16.09**±0.67	**13.80**±0.46	**0.009**
Cistus × hybridus	**14.20**±0.77	**13.61**±0.67	0.567	**15.29**±0.46	**12.43**±0.73	**0.003**
Elaeagnus angustifolia	**7.93**±0.37	**7.61**±0.24	0.458	**7.97**±0.31	**7.53**±0.26	0.296
Ceanothus thyrsiflorus	**11.81**±0.58	**11.20**±0.55	0.461	**12.99**±0.36	**9.92**±0.41	**<0.001**
Buddleja davidii	**13.48**±0.34	**13.41**±0.38	0.896	**13.59**±0.33	**13.28**±0.41	0.564
Cotinus coggygria	**9.83**±0.47	**9.82**±0.44	0.988	**10.06**±0.37	**9.59**±0.52	0.471

Table 11a. The combined effect of population size and plant density on leaf mass per area. Mean values of LMA as combinations of the different categories tested in Year 2 ($LMA_{SP+3\times3}$, $LMA_{DP+3\times3}$, $LMA_{SP+4\times4}$, and $LMA_{DP+4\times4}$).

Species	$\mathbf{LMA_{SP+3\times3}}$	$\mathbf{LMA_{DP+3\times3}}$	$\mathbf{LMA_{SP+4\times4}}$	$\mathbf{LMA_{DP+4\times4}}$
Viburnum tinus	**16.76**±1.08	**14.29**±0.74	**15.59**±0.88	**13.43**±0.59
Cistus × hybridus	**14.87**±0.94	**13.53**±1.25	**15.61**±0.41	**11.61**±0.80
Elaeagnus angustifolia	**8.19**±0.52	**7.66**±0.54	**7.80**±0.41	**7.43**±0.26
Ceanothus thyrsiflorus	**13.25**±0.56	**10.37**±0.60	**12.80**±0.50	**9.59**±0.57
Buddleja davidii	**13.61**±0.54	**13.34**±0.45	**13.57**±0.44	**13.24**±0.66
Cotinus coggygria	**9.44**±0.37	**10.22**±0.87	**10.52**±0.55	**9.12**±0.62

Table 11b. Results of statistical tests comparing the effects of plant density and population size on leaf mass per area. *P*-values of the tests between categories of mean LMA in Year 2, in terms of: 1) the effect of plant density within each population size, 3×3 ($LMA_{SP+3\times3}$ vs $LMA_{DP+3\times3}$) & 4×4 ($LMA_{SP+4\times4}$ vs $LMA_{DP+4\times4}$); and 2) the effect of population size within each type of plant density, SP ($LMA_{SP+3\times3}$ vs $LMA_{SP+4\times4}$) & DP ($LMA_{DP+3\times3}$ vs $LMA_{DP+4\times4}$).

Species	**Plant density**		**Population size**	
	$\mathbf{LMA_{SP+3\times3}}$ **vs** $\mathbf{LMA_{DP+3\times3}}$	$\mathbf{LMA_{SP+4\times4}}$ **vs** $\mathbf{LMA_{DP+4\times4}}$	$\mathbf{LMA_{SP+3\times3}}$ **vs** $\mathbf{LMA_{SP+4\times4}}$	$\mathbf{LMA_{DP+3\times3}}$ **vs** $\mathbf{LMA_{DP+4\times4}}$
Viburnum tinus	0.088	0.060	0.409	0.374
Cistus × hybridus	0.414	**<0.001**	0.446	0.200
Elaeagnus angustifolia	0.497	0.455	0.554	0.677
Ceanothus thyrsiflorus	**0.006**	**<0.001**	0.567	0.373
Buddleja davidii	0.427	0.682	0.953	0.910
Cotinus coggygria	0.706	0.113	0.155	0.310

It can be evinced from Tables 9 and 10 that, in almost all cases, mean LMA was always higher in shrubs placed in a SP than in a DP and that this difference – when comparing the SP and DP categories of Year 1 in Table 9 to the same categories of Year 2 in Table 10 – was always significant in *Viburnum* and *Ceanothus*. It would seem that the evergreen shrubs were the most affected by plant density. The evergreens also had the highest mean LMA in both SP and DP in Year 1, which increased in Year 2 for *Viburnum* as well as for the semi-deciduous species, but showed a reduction in *Ceanothus* in the DP. If plant density definitely affected mean LMA in at least two shrub species in the first two years of the study, population size was instead clearly not a significant factor in determining LMA (See Table 10).

In fact, when taking into consideration only Year 1 of the study, in which all shrubs were divided into monospecific populations (MP) and were further split into either sparse (SP) or dense (DP) populations within each species, Table 9 shows that all species presented higher mean LMA in SP than in DP, but that this difference was only significant in the evergreen shrubs (*Viburnum* and *Ceanothus*) and in the semi-deciduous *Buddleja*. Based on their mean LMA, the species in Year 1 of the study, in both SP and DP categories, can therefore be ranked as follows (from highest to lowest): *Viburnum* > *Ceanothus* > *Cistus* > *Buddleja* > *Cotinus* > *Elaeagnus*, or better Evergreen > Semi-deciduous > Deciduous. As predicted, even within different categories of plant density, shrubs in Year 1 of the study, at full health and potential, presented the anticipated trend of thicker, denser leaves in the evergreen group and of thinner ones in the deciduous group, with the semi-deciduous species in the middle as expected. This ranking remained essentially the same in the following years of the study, with only *Ceanothus* progressively decreasing in LMA from Year 2 to Year 3.

Table 9 is useful to compare the effects of plant density on shrubs growing in a MP compared to those growing in a PP, whereby Year 2 data in this table relates to leaves obtained from shrubs growing in polyspecific populations (PP) but solely from those of the same size as the ones in Year 1 (i.e. 3×3). It would seem in this case that, in Year 2, only *Ceanothus* showed a significant difference between SP and DP (*P*=0.006), again with SP showing higher mean values (13.25 mg cm^{-2}) compared to DP (10.37 mg cm^{-2}). However, the lower significance levels in Year 2 may be due to the smaller number of plants dedicated to each category (i.e. SP, DP, 3×3 and 4×4) compared to Year 1 (just SP and DP). In all cases except for the category of *Ceanothus* shrubs placed in a DP, mean values of LMA for each species increased going from Year 1 to Year 2 within both the SP and the DP (e.g. from SP in Year 1 to SP in Year 2). This increase, however, was significant only for 3 species (*Cistus*, *Buddleja* and *Elaeagnus*). This signifies that, even though mean values of LMA were always higher in shrubs placed in a SP than in a DP, all leaves increased in thickness over the course of a full year atop a rooftop as a likely reaction to an increase in environmental stress.

Despite almost all species experiencing a decrease in mean LMA when placed in a physically larger population of shrubs (4×4) in Year 2, none were significantly affected by population size (See Table 10). However, like in Year 1, all species placed in a PP had higher mean values of LMA when placed in a SP than in a DP, but again this difference was only significant in the evergreen shrubs (*Viburnum* and *Ceanothus*) and the semi-deciduous *Cistus*. When further subdivided into the four combined categories of plant density and population size (i.e. LMA_{SP+3x3}, LMA_{SP+4x4}, LMA_{DP+3x3} and LMA_{DP+4x4}) in Table 11a, it is clear that only *Ceanothus* was affected by plant density in Year 2 within the 3x3 (*P*=0.006) and the 4x4 (*P*=<0.001) populations, whereas no species was significantly affected by population size within the SP and the DP (See Table 11b).

A.4.1.2 Canopy morphology

A.4.1.2.1 Woody aboveground biomass: Branching architecture (ADI) & woody biomass area (A_W) and weight (B_W)

The apical dominance index (ADI) is used to describe branching architecture in plant ecophysiology and can range anywhere between 0 m^{-1} (no branching) and >100 m^{-1} (extreme branching). This wide range of branching indicates that ADI is most likely used to determine the branching architecture of trees rather than of woody shrubs, where undoubtedly branches in the former will be longer and more ramified. However, this index is much better suited for evaluating the branching architecture in shrubs compared to the apical dominance ratio (ADR), for example, which is the ratio between apical leading shoot length (i.e. main trunk) and the mean length of lateral twigs forming the first upper whorl or node. ADR is clearly intended for tree canopies, especially of conifers, as was the case for the study by Ripullone et al. (2016), where values of ADR were used to establish ideal growth performance of silver fir saplings growing under different levels of irradiance as affected by surrounding mature tree stands. In the present study, the scope of determining branching architecture was to understand how this parameter can influence the performance of shrubs in buffering extreme temperature on rooftops, in terms of how light is intercepted through the canopy. The aim was to determine the level of impact that branching architecture has on temperature mitigation compared to other morphological parameters (e.g. leaf density/area, LMA) and whether there are any correlations between this and other parameters (e.g. canopy interception of irradiance) that can help predict the ideal shrub form/type for optimal performance.

The characterisation of the study species' 'physicality' or morphological structures could help explain the findings in this section and better understand how branching architecture can contribute to the reduction of temperature extremes and lead to more informed plant selection. In terms of diversity in shrub form, *Cotinus coggygria* and *Elaeagnus angustifolia* under optimal environments can grow to be small trees, with *Buddleja davidii* also potentially reaching several metres in height, but the other study species are lower growing shrubs (See Appendix A for more detailed descriptions of the study species). *Ceanothus thyrsiflorus* in particular has a predominantly spreading habit rather than a vertical development. Consequently, the different study species will unquestionably be less ramified than trees and will most likely have more varied habits and degrees of ramification. Invariably, despite the annual trim in the autumn prior to the growing season to reduce height differences, the taller shrubs (*Buddleja*, *Cotinus* and *Elaeagnus*) grew to be between 0.80 m and 1.20 m in height in the summer throughout the three growing seasons, while the shorter shrubs (*Ceanothus*, *Cistus* and *Viburnum*) remained between 0.50 and 0.70 m in height. As plant height and habit may play important roles on extreme temperature abatement, it could prove useful to divide the shrub species into two loose categories – tall shrubs and short shrubs – and take into consideration their canopy 'shape' or structure. In this sense, *Buddleja* can be described as having a tall and narrow canopy, with very slender but rigid branches; *Elaeagnus* has a tall and more oval shape with stiff, heavy branches and *Cotinus* is tall and round with brittle branches. *Viburnum* and *Cistus* are both short shrubs with similar canopies, but *Viburnum* is often more cylindrical to fan-like in shape with thick, sturdy branches, whereas *Cistus* is more rounded, chalice-shaped, with supple branches. *Ceanothus* is in a category of its own – it develops into a short and prostrate shrub with bendy branches.

The ADI for each species was found after harvesting, once all the leaves were removed for biomass evaluation, but before all aboveground biomass material was dried to determine dry weight. The "skeleton" (i.e. bare trunk and branches) of 5 plants per species were thus selected and photographed to later determine their branching architecture through ImageJ. Each plant was positioned onto a flat, white backdrop with a millimetric ruler and photographed in its entirety and at a perpendicular angle to the surface, in order to ensure ease of analysis and maximum accuracy of scale. Each photo was subsequently analysed to establish total woody biomass area (A_W) and to measure both branch length and ramification of 15 branches per plant, for a total of 75 branches per species. The level of ramification of each branch was determined as by Pérez-Harguindeguy et al. (2013), in which ramification points are counted starting from a terminal, leaf-bearing branch (e.g. major branch stemming from the trunk) towards secondary branches until reaching the tip. ADI was then calculated by dividing the number of ramification points by the length of each branch in metres. The results can be viewed in Table 12 below.

Table 12. Mean values of branching parameters. Mean woody biomass area (A_W), ramifications, branch length and apical dominance index (ADI) of the six study species. ADI is calculated by dividing ramifications by unit length of branch.

Species	**A_W (m^2)**	**Ramifications**	**Branch length (m)**	**ADI (m^{-1})**
Viburnum tinus	**9.27**±0.78	**4.72**±0.12	**0.48**±0.01	**10.02**±0.18
Cistus × hybridus	**10.83**±0.73	**5.99**±0.12	**0.49**±0.01	**12.22**±0.22
Elaeagnus angustifolia	**7.50**±1.18	**6.67**±0.18	**0.69**±0.01	**9.76**±0.26
Ceanothus thyrsiflorus	**5.63**±0.32	**8.09**±0.24	**0.41**±0.01	**19.76**±0.42
Buddleja davidii	**6.19**±0.75	**7.85**±0.18	**0.78**±0.02	**10.29**±0.24
Cotinus coggygria	**7.68**±1.06	**4.73**±0.14	**0.59**±0.02	**8.14**±0.21

Mean A_W (P=0.002), mean ramifications (P<0.001), mean branch length (P<0.001) and mean ADI (P<0.001) have all been found to be significantly different amongst the six study species. Notably, *Ceanothus* had the most ramified branches (an average of about 8 ramification points) and the highest mean value of ADI (19.76 m^{-1}), but it also had the lowest mean values in both A_W (5.63 m^2) and branch length (0.41 m). In comparison, *Cistus* had almost double the A_W (10.83 m^2) and the second highest mean value of ADI (12.22 m^{-1}) despite having one of the lowest mean branch lengths (0.49 m). *Buddleja* was found to have nearly twice the branch length (0.78 m) but a comparatively similar ADI (10.29 m^{-1}) to that of *Viburnum* (10.02 m^{-1}, which only had a mean branch length of 0.48 m), as well as the second lowest A_W (6.19 m^2). Lastly, *Cotinus* had the lowest mean value of ADI with 8.14 m^{-1}, less than half that of *Ceanothus*.

It could prove useful at this stage to know the mean values of woody biomass weight (B_W) for each species to explain the above findings and hone the characterisations of the different species' branching architecture. After harvesting, B_W was measured at the final stage of biomass measurements, when all aboveground biomass was dried to obtain the final dry weights of both leaves and woody biomass for each individual plant. Mean values of total B_W for each species are listed in Table 13 and further divided into two separate categories, monospecific (MP) and polyspecific (PP) population, into which the species were placed during the last growing season of the study. The difference in mean values of total B_W amongst the six species was found to be statistically significant ($P<0.001$) and underlines the contrast between the B_W of *Ceanothus* (69.19 g) and that of the other species (i.e. all above 100 g), which could potentially explain the low values of A_W and branch length in this particular shrub despite its high ADI. However, upon testing ADI against B_W, the two parameters were found not to be significantly correlated (P=0.08, See Table A in Appendix B).

Table 13. The effect of species mixture on woody biomass. Mean values of woody biomass (B_W) for total, monospecific and mixed populations of the six study species. *P*-values are in relation to monospecific vs polyspecific population.

Species	Total B_W (g)	MP B_W (g)	PP B_W (g)	*P*-value
Viburnum tinus	**141.49**±5.44	**148.91**±7.49	**133.79**±7.76	0.167
Cistus × hybridus	**117.11**±5.80	**117.23**±8.28	**116.99**±8.28	0.984
Elaeagnus angustifolia	**112.33**±9.62	**101.15**±9.87	**120.20**±14.82	0.335
Ceanothus thyrsiflorus	**69.19**±2.94	**70.15**±3.52	**67.19**±5.52	0.644
Buddleja davidii	**129.27**±3.14	**130.93**±3.99	**127.23**±5.07	0.564
Cotinus coggygria	**104.39**±8.58	**94.26**±8.87	**115.59**±15.02	0.219

On a final note, B_W between the two populations was not statistically significant for any of the shrubs, despite a seemingly noteworthy difference in three of the species (*Cotinus*, *Elaeagnus* and

Viburnum). It is interesting to point out, however, that the deciduous species (*Cotinus* and *Elaeagnus*) both showed a reasonably higher B_W in the PP compared to the MP, whereas species mixture had the opposite effect on *Viburnum*. One could speculate that, due to their deciduousness and taller height, *Cotinus* and *Elaeagnus* may have been positively affected by their positioning in a PP where they would be surrounded by plants with heterogeneous heights that would allow for greater exposure to light and therefore greater seasonal photosynthesis and growth. *Viburnum*, a short evergreen shrub surrounded by taller shrubs in the PP, on the other hand may have been negatively affected by a situation in which it was less exposed to irradiance year-round compared to the more homogeneous MP.

A.4.1.2.2 Leafy aboveground biomass: Canopy density (CD), leaf biomass (B_L) and area (A_L), leaf area index (LAI) and canopy interception of irradiance

Foliage represents the boundary where energy is received and is exchanged with the surrounding environment and where canopy interception, evapotranspiration and photosynthesis happen (Fang and Liang 2014). For this reason, foliage plays a major role in both plant productivity and below-canopy microclimate. Foliage density of a plant canopy can therefore be an important ecological parameter to quantify, either directly or indirectly, with the use of the leaf area index, or LAI (Bréda 2003). There are various ways of defining and measuring LAI, depending on the scale and purpose of its application. In forestry and other large-scale studies, LAI is defined as the projected area of leaves over a unit of land (m^2 m^{-1}), often referring to units of 10,000 m^2 of leaf area per hectare (Waring and Running 2007). In this case, LAI would be used for modelling primary production and exchange of carbon dioxide, water vapor and nutrients from a stand to whole region scale. However, for smaller investigations, as often carried out in agricultural or smaller ecological studies (especially on broadleaf canopies), LAI can be defined as the one-sided green leaf surface area per unit soil or ground surface area, and it is a dimensionless quantity (m^2 m^{-2}) that can range from 0 for bare ground to over 10 for dense forests (Bréda 2003). One of the aims in crop science, for example, is to maximise crop yield through the production of higher growth crops that have a greater ability to intercept incident radiation (Sparkes 2003). This concept has been applied in landscape studies for many years. In fact, there are numerous recent studies that identify LAI as one of the key parameters influencing green roof energy performance in terms of temperature abatement (e.g. Kumar and Kaushik 2005, Vera et al. 2015, Ferrante et al. 2016, Vaz Monteiro et al. 2017, Gomes et al. 2019), along with vegetation height and soil depth.

LAI can be estimated either directly with ground-based methods or indirectly through remote-sensing. Indirect methods are useful for large-scale studies and long-term seasonal monitoring of LAI. One such indirect method is carried out by measuring the attenuation of photosynthetically active radiation (PAR) by the canopy, estimating the PAR extinction coefficient and then calculating LAI using the Beer-Lambert law (Saitoh et al. 2012). Another indirect method estimates LAI via canopy transmittance or reflectance models using satellite sensors, e.g. ENVI-met modelling (Fang and Liang 2014). For example, Morakinyo et al. 2018 studied the shading effect of street trees by using a mixture of hemispherical photography and ENVI-met modelling, the latter of which applies LAI as one of the input parameters. They found that species-specific analysis was crucial, and that LAI was the most important factor influencing temperature regulation, thermal comfort and energy savings by trees, followed by tree height and crown diameter. Other non-destructive tools include hemispherical photography, plant canopy analysers and LAI meters. Hemispherical photography estimates LAI by analysing upward fisheye photographs taken beneath the canopy; plant canopy analysers determine LAI through canopy light interception as quantified by an optical sensor that measures solar radiation above and below the canopy, and LAI meters calculate the difference between light levels above and below the canopy and factor in the leaf angle distribution, solar zenith angle and light extinction coefficient (Blanco and Folegatti 2003).

Direct methods of estimating LAI include the destructive sampling of evergreen species and the collection of leaf litter in deciduous species. In the first case, foliage can be sampled from a plant canopy to measure the leaf area per sample plot and then divide that area by the plot surface area. Leaf area can be measured using a leaf area meter, an image scanner plus an image analysis software (e.g. ImageJ) or mobile applications like Leafscan (www.leafscanapp.com) and Easy Leaf Area (www.quantitative-plant.org). A less destructive method can be used on deciduous species by collecting senescent leaves in traps below the canopy and dividing their leaf area by the area of the traps (Bréda 2003). Although time consuming, the destructive sampling method was thought to be more appropriate for a small-scale study involving a mixture of evergreen and deciduous woody shrub saplings with varying but essentially low plant height, such as in the present study – all study plants used were far from having the full trunk height and crown characteristics of a mature tree, which is the typical unit for most indirect studies of LAI. For example, the results from the study by Zhang, Zhan and Lan (2018), which used ENVI-met modelling, indicated that tall evergreen trees with large LAI and canopy diameter situated in a dense planting pattern were the best combination for both temperature mitigation in the summer and wind speed reduction in the winter at ground level in a highly urbanised residential area in Wuhan, China. As even intensive green roof systems rarely support the growth of tall trees, woody shrubs (all < 2 m tall) were chosen as the next best alternative for the present study. Indirect methods also often underestimate LAI when most leaves in the canopy lie one on top of the other, as in very dense canopies (Wilhelm, Ruwe and Schlemmer 2000), which will most likely have been the case for *Viburnum tinus* if not for all study species. For these reasons, the direct and destructive method was selected for a more accurate, non-simulated estimation of LAI for shrubs growing in limited rooftop areas.

In order to delve into the investigation of LAI for the present study, it is first necessary to obtain the mean values of certain other parameters that are useful for the calculation of LAI, primarily mean canopy density (CD) and mean leaf area (A_L). Following the harvesting of all plants at the end of the study, the leaves of each individual belonging to the monospecific population of every species were removed from their woody stems, counted and used determine canopy density (CD), leaf biomass (B_L) and leaf area (A_L), amongst other parameters. CD is intended as the average total number of leaves per plant, B_L as the dry weight of a leaf and A_L as the one-sided projected area of a green and mature leaf (A_L). Table 14 below lists the mean CD per species and the mean B_L and A_L per species (further subdivided into B_L and A_L per plant and per leaf) of the leafy aboveground biomass removed, analysed and dried after harvesting at the end of the study. Table 15a instead lists the total mean B_L and A_L of the leaves sampled during each summer over the entire study. Tables 15b and 15c show the mean values of B_L and A_L, respectively, for Years 1, 2 and 3 of the study separately, with respective *p*-values of the difference tested for each species between the different years, in order to assess any changes in these parameters over time. The notable difference between mean values of both B_L and A_L per leaf between those measured in the post-harvest study (Table 14) and in the yearly sampling (Tables 15a, b and c) is most likely due to the fact that only sun leaves (i.e. the most external leaves of the canopy, usually with the highest leaf density and thickness) were sampled during the yearly summer sampling (for the calculation of mean LMA, i.e. B_L/A_L; See Section 3.1.1.3), whereas all leaves (sun and shade) belonging to a single plant were used for the measurements of leaf biomass after the harvesting, which will have reduced the average dry weight and area per leaf, as it included leaves of all sizes and thicknesses.

Table 14. Species foliage density and above-ground biomass measured post-harvest. For every plant, the mean number of leaves (canopy density, CD), leaf dry weight (B_L) and leaf area (A_L) per species. For every leaf, the mean leaf dry weight (B_L) and leaf area (A_L) per species. This data is based on biomass measurements obtained after the harvesting of all plants at the end of the study.

	Per plant			**Per leaf**	
Species	**CD (*n*)**	**B_L (kg)**	**A_L (m^2)**	**B_L (mg)**	**A_L (cm^2)**
Viburnum tinus	**1,650.8**±132.5	**0.091**±0.008	**0.619**±0.044	**55.15**±1.97	**3.91**±0.16
Cistus × hybridus	**873.8**±120.2	**0.021**±0.003	**0.162**±0.023	**25.37**±2.20	**1.95**±0.17
Elaeagnus angustifolia	**910.2**±128.5	**0.024**±0.003	**0.403**±0.047	**32.01**±3.79	**4.89**±0.41
Ceanothus thyrsiflorus	**1,561.2**±115.5	**0.033**±0.003	**0.293**±0.024	**20.86**±0.82	**1.89**±0.10
Buddleja davidii	**397.9**±21.9	**0.013**±0.001	**0.218**±0.013	**32.45**±1.42	**5.47**±0.11
Cotinus coggygria	**910.0**±124.8	**0.042**±0.006	**0.595**±0.073	**49.52**±5.10	**7.03**±0.57

Table 15a. Mean leaf biomass and area measured throughout the study. Mean leaf dry weight (B_L) and leaf area (A_L) per species. Data is based on the analysis of sun leaves as sampled throughout all three years of the study.

Species	**B_L (mg)**	**A_L (cm^2)**
Viburnum tinus	**147.97**±2.71	**9.96**±0.15
Cistus × hybridus	**48.97**±1.18	**4.12**±0.08
Elaeagnus angustifolia	**66.51**±1.52	**10.01**±0.23
Ceanothus thyrsiflorus	**32.93**±0.76	**3.22**±0.09
Buddleja davidii	**135.64**±3.09	**12.89**±0.33
Cotinus coggygria	**231.87**±6.04	**26.04**±0.59

Table 15b. Changes in leaf biomass over time. Mean leaf dry weight (B_L) per species of sun leaves sampled each year of the study, and *p*-values of the difference tested between values of B_L through the years.

	Year 1	**Year 2**	**Year 3**	
Species	**B_L (mg)**	**B_L (mg)**	**B_L (mg)**	***P*-values**
Viburnum tinus	**144.34**±3.93	**149.86**±5.50	**151.63**±5.08	0.474
Cistus × hybridus	**46.04**±1.53	**56.86**±2.27	**47.59**±2.22	**<0.001**
Elaeagnus angustifolia	**66.16**±2.34	**67.86**±3.21	**66.07**±2.59	0.894
Ceanothus thyrsiflorus	**28.84**±0.90	**37.29**±1.36	**35.54**±1.40	**<0.001**
Buddleja davidii	**119.77**±4.40	**142.89**±4.90	**152.37**±5.11	**<0.001**
Cotinus coggygria	**228.21**±8.13	**259.50**±12.67	**218.00**±11.32	**0.036**

Table 15c. Changes in leaf area over time. Mean leaf area (A_L) per species of sun leaves sampled each year of the study, and *p*-values of the difference tested between values of A_L through the years.

	Year 1	**Year 2**	**Year 3**	
Species	**A_L (cm^2)**	**A_L (cm^2)**	**A_L (cm^2)**	***P*-value**
Viburnum tinus	**10.12**±0.23	**10.08**±0.29	**9.65**±0.26	0.361
Cistus × hybridus	**4.12**±0.11	**4.13**±0.11	**4.13**±0.20	0.998
Elaeagnus angustifolia	**11.40**±0.31	**8.81**±0.39	**8.93**±0.39	**<0.001**
Ceanothus thyrsiflorus	**2.39**±0.07	**3.31**±0.13	**4.31**±0.12	**<0.001**
Buddleja davidii	**11.54**±0.40	**10.67**±0.34	**16.25**±0.47	**<0.001**
Cotinus coggygria	**26.93**±0.90	**26.27**±0.88	**24.68**±1.17	0.254

In terms of mean CD, the data in Table 14 displays a noteworthy trend – the species rank as follows, from highest to lowest CD: *Viburnum* > *Ceanothus* > *Elaeagnus* > *Cotinus* > *Cistus* > *Buddleja,* or simply: Evergreen > Deciduous > Semi-deciduous. In other words, the evergreen shrubs have the densest foliage, the deciduous shrubs have intermediate foliage density while surprisingly the semi-deciduous have the least amount of foliage per plant. While the evergreen shrubs *Viburnum* (~1651 leaves) and *Ceanothus* (~1561 leaves) and the deciduous *Elaeagnus* and *Cotinus* (both ~910 leaves) have approximately the same number of leaves within their functional groups (no significant difference within them), the semi-deciduous *Cistus* (~874 leaves) and *Buddleja* (~398 leaves) have statistically different CDs ($P<0.001$). *Viburnum* and *Ceanothus* have about 4 times the amount of leaves compared to *Buddleja* and even *Cistus* has about twice the amount. Testing the correlation between CD and other plant parameters studied could help in understanding this difference between the two semi-deciduous shrubs, however the only parameter with which CD was significantly correlated was branch length ($P=0.034$ and $R=–0.846$, See Table A in Appendix B). This negative correlation signifies that, as branch length increases, CD decreases. Branch length was effectively the highest in *Buddleja* and one of the lowest in *Cistus* (See the previous Section 3.1.2.1), which could in part explain their contrasting CDs.

In fact, shrub height may be an influencing factor in both foliage density and mean leaf area. While mean B_L and A_L per *plant* (post-harvest) in Table 14 were highest in *Viburnum* and *Cotinus* and again lowest in the semideciduous shrubs (*Cistus* and *Buddleja*), the same trend was not found for mean B_L and A_L per *leaf* (post-harvest). Here, mean A_L per leaf (post-harvest) showed a 'short vs tall shrub' polarity – it was highest in the 'tall shrubs' (*Cotinus*, *Buddleja* and *Elaeagnus*) and lowest in the 'short shrubs' (*Viburnum*, *Cistus* and *Ceanothus*); the difference between the mean A_L for tall (2.58 ± 0.66 cm^2) and short shrubs (5.80 ± 0.64 cm^2) was in fact found to be significant ($P=0.025$). Interestingly, the same (but reversed) trend was found in LMA_B (See Section 3.1.1.3), which was highest in the short shrubs (12.93 ± 0.87 mg cm^{-2}) and lowest in the tall shrubs (6.41 ± 0.27 mg cm^{-2}), and this difference was found to be significant ($P=0.002$). Mean B_L per leaf, on the other hand, ranked as follows (from highest to lowest): *Viburnum* > *Cotinus* > *Buddleja* > *Elaeagnus* > *Cistus* > *Ceanothus* – clearly, *Viburnum* could be considered an outlier, as otherwise there may have been a short vs tall polarisation in this case as well (N.B. *Viburnum* was an 'outlier' in more than one occasion in this study, presenting an extraordinary survival rate, fitness and ability to buffer extreme temperatures, as will be described further in this chapter).

Although neither A_L or B_L were found to be correlated with branch length (See Table A in Appendix B), branch length and/or plant height may well be factors influencing biomass allocation – the short shrubs, producing shorter branches, may choose to allocate that carbon not spent in height growth to producing more leaves (i.e. higher CD) and to making them more resistant (i.e. higher LMA_B, especially the evergreen shrubs), whereas taller shrubs allocate a large quantity of carbon in producing longer branches and may therefore have less carbon to allocate to leaves, thereby producing a comparatively lower number of leaves that are nevertheless bigger (i.e. higher A_L) but less mechanically resistant. Two of the taller shrubs were deciduous – as deciduous species have higher photosynthetic capacity and leaf maintenance costs, they generally apportion a larger amount of carbon to stem and leaf growth (including large amounts of non-photosynthetic tissue) compared to evergreens; however, deciduous species also have a shorter growing season, shorter leaf lifespan and undergo dormancy and complete foliage loss at the end of the growing season (Monk 1966, Hollinger 1992, Aerts 1995, Givnish 2002). In order to understand why the other tall shrub – *Buddleja* – had one of the lowest mean A_L per plant (0.22 m^2, in Table 14) despite clearly allocating much of its carbon gain to plant height, it is necessary to remember that, like *Cistus*, *Buddleja* is what is known as a 'seasonally dimorphic' shrub, one that can replace its winter habit of larger, mesomorphic leaves with a summer habit of relatively smaller, xeromorphic leaves at the beginning of the arid season, without ever completely shedding their foliage (Harley et al. 1987). Unlike both the evergreens, which had a single cohort of leaves to maintain year-round, and the deciduous shrubs, which had only one cohort of leaves to maintain for a brief growing season and then shed, the semi-deciduous had to produce *two* cohorts of leaves every year. Thereby, the yearly carbon expenditure of the semi-deciduous shrubs may well have been double or more that of the other functional groups, an assumption that may also explain why these shrubs also had the lowest CD amongst the shrubs. Having to essentially regrow two complete sets of leaves every year will most likely have reduced the carbon budget allocated to producing foliage in the semi-deciduous shrubs. *Cistus*, despite having the second-lowest CD, had double the number of leaves as *Buddleja* and this may be because it most likely allocated less carbon to branch growth than it did to leaf biomass compared to *Buddleja*.

The 'tall vs short shrub' trend observed previously with mean A_L per leaf measured after the harvesting of the shrubs (See Table 14) is repeated in the values of mean A_L per leaf as sampled yearly during the summer months of the study – the species rank as follows, from highest to lowest overall mean A_L (See Table 15a): *Cotinus* > *Buddleja* > *Elaeagnus* > *Viburnum* > *Cistus* > *Ceanothus*, or tall shrubs > short shrubs, with mean values of A_L for tall shrubs (5.77±2.11 cm^2) and short shrubs (16.31±2.22 cm^2) significantly different (P=0.026). The same ranking can be observed in Table 15c for the separate values of mean A_L for each year of sampling, especially in Year 1. However, only *Elaeagnus*, *Ceanothus* and *Buddleja* saw a significant change in values of mean A_L going from Year 1 to year 3, with *Ceanothus* progressively increasing in A_L whereas both *Elaeagnus* and especially *Buddleja* saw a dip in A_L in Year 2 followed by an increase in Year 3. The 'tall vs short shrub' trend does not apply as strongly to values of mean B_L as it does to A_L, however, almost all species saw a significant change in mean B_L going from Year 1 to Year 3 (Table 15b), with *B*L steadily increasing throughout in *Buddleja* while increasing in Year 2 but decreasing in Year 3 in *Cistus*, *Ceanothus* and especially *Cotinus*. However, both A_L and B_L remained highest in *Cotinus* and lowest in *Ceanothus* throughout the study.

After an exhaustive analysis of CD, B_L and A_L, the investigation of each study species' leaf area index can now proceed. According to Sparkes (2003), the two factors that affect the interception of incident radiation by a plant canopy are the canopy light extinction coefficient (*k*) and the leaf area index (LAI). The concept of *k* will be discussed towards the end of this section; it can be disregarded for now, as it is not needed to estimate LAI.

LAI, or leaf area per unit ground area, can be calculated as follows:

$$\mathbf{LAI} = \boldsymbol{N_p} \times \boldsymbol{N_1} \times \boldsymbol{A_1}$$

where N_p is the number of plants per unit area, N_1 is the number of leaves per plant and A_1 is the mean area per leaf (Sparkes 2003).

LAI can therefore be easily estimated based on the biomass data acquired post-harvest – N_1 is equivalent to mean CD, A_1 is equivalent to mean A_L per leaf (converted from cm^2 to m^2; See Table 14) and $N_p = 3$, in that the number of plants per unit area (i.e. 1 container of 0.44 m in diameter or 0.15 m^2 in area) was 3 in the present study. The estimated values of LAI for each of the shrub species are presented below in Table 16.

Table 16. Leaf area index. Leaf area index (LAI) for each species, calculated by multiplying N_p (number of plants per unit) by N_1 (mean number of leaves per plant) and A_1 (mean area per leaf, in m^2).

Species	**N_p (*n*)**	**N_1 (*n*)**	**A_1 (m^2)**	**LAI**
Viburnum tinus	3	1650.8	0.000391	**1.94**
Cistus × hybridus	3	873.8	0.000195	**0.51**
Elaeagnus angustifolia	3	910.2	0.000489	**1.33**
Ceanothus thyrsiflorus	3	1561.2	0.000189	**0.88**
Buddleja davidii	3	397.9	0.000547	**0.65**
Cotinus coggygria	3	910.0	0.000703	**1.92**

The different study species can therefore be ranked as follows, from highest to lowest LAI:

Viburnum > *Cotinus* > *Elaeagnus* > *Ceanothus* > *Buddleja* > *Cistus*

Unsurprisingly, *Viburnum* was found to have the highest value of LAI, with 1.94 (closely followed by *Cotinus*, with 1.92), while the semi-deciduous shrubs *Buddleja* and *Cistus* were found to have the lowest values of LAI, with 0.65 and 0.51, respectively. Despite having the second highest CD, the LAI of *Ceanothus* was estimated to be lower than some of the other shrubs (0.88), owing to its characteristically small leaves.

In analysing the relationship between LAI and the other parameters in this study, it was obvious that LAI would be highly and positively significantly correlated with mean A_L per plant ($P<0.001$, $R=0.998$) – the greater the overall leaf area of a canopy, the greater the LAI. This significance indicates that mean A_L per plant could be used as a relatively accurate proxy for the determination of species-specific LAI, which could enormously aid the process for the selection of suitable shrubs or other plants for green roofs. Using a LAI meter or plant canopy analyser, for example, would certainly be less time consuming and destructive, but it would also entail equipment costs and be less accurate, as LAI may vary slightly in different conditions of sunlight and therefore would may make the true representation or estimation of LAI (i.e. in field conditions) more difficult. Insofar as the author is aware, LAI meters and other equipment for identifying LAI directly on specific shrub species for green roof studies have not been utilised. Some studies may give a rough estimate of LAI of the species used in performance simulations of green roof energy models (e.g. only an LMA of either 0.5 or 1.0 was attributed to the 4 herbaceous species in the study by Gomes et al. 2019), but most studies will simply input an assumed LAI in the form of a range, e.g. 0.1 to 5.0 (e.g. Olivieri et al. 2013, Silva et al. 2016, Pianella et al. 2017) – a range that is likely unrealistic at the top end – rather than input a LAI based on actual direct measurements on the study species. On the other hand, finding the mean total leaf area of a plant canopy for each species, as was done in the present study, is also very time consuming, and even the estimation of one via random sampling for other parameters (e.g. leaf mass per area, specific leaf area) can take some time and effort. The study that came the closest to directly analysing shrub foliage density in relation to a green roof's thermal performance was that of Karachaliou, Santamouris and Pangalou (2016), which made the effort of measuring the plant height and the foliage surface temperature, via thermal imaging camera, of 14 Mediterranean sub-shrub species growing on an intensive green roof. However, the foliage density of each species was not measured, it was only assumed and broadly characterised (e.g. high vs low density), thereby forgoing the possibility of finding direct correlations between foliage density and temperature.

What is perhaps more remarkable in terms of proxies is that LAI in the present study was significantly and negatively correlated with maximum quantum yield, or QY ($P=0.031$, $R=–0.853$), a parameter that will be discussed in more detail subsequently in Section 3.2.1.1. This correlation signifies that, at least based on the shrub species in this study, LAI increases as QY decreases, as visualised in Fig. 12 below.

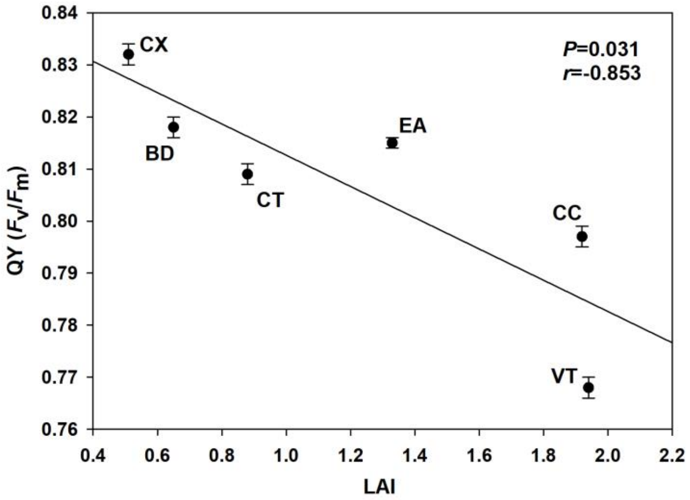


Figure 12. As leaf area index increases, photosynthetic efficiency decreases. Scatter plot with regression for the correlation between LAI and QY, for each species (VT=*Viburnum*, CX=*Cistus*, EA=*Elaeagnus*, CT=*Ceanothus*, BD=*Buddleja*, CC=*Cotinus*).

The measurement of QY is a much easier and quicker process compared to any direct method of estimating LAI (See Section 2.5.4 in Methods), and potentially even compared to using LAI meters and plant canopy analysers. Granted that the regression of the correlation between LAI and QY was not very strong (R=–0.853), the use of QY as a proxy for the evaluation of LAI for potential green roof shrubs, in combination with other simple plant parameters (e.g. branch length), could be the key to quicker species suitability assessments, at least for broadleaf shrubs. Further investigation into this aspect could prove to be a worthwhile future study.

The final part of this section on canopy morphology will be dedicated to results obtained from a small experiment on *Buddleja davidii* carried out at the end of the study, to investigate canopy interception of irradiance. As mentioned previously, two important factors affecting the level of light interception by a plant canopy are LAI and the canopy light extinction coefficient, k (Sparkes 2003). k describes the efficiency or rate by which the canopy intercepts or extinguishes incident solar radiation and is determined by the inclination of the leaf and the angle of solar zenith, although other properties of leaves can also affect it (e.g. size, shape, thickness, presence of trichomes). A canopy with a high k indicates that it can intercept a great amount of the incident radiation and therefore only a small amount of it makes it through to the understory (Zhang et al. 2014). Plants with large flat leaves will have higher values of k while plants with erect leaves (e.g. grasses) will have lower values (Sparkes 2003).

After various investigations through the years, it is now known that *Buddleja* in this study had the following characteristics or behaviours:

- Individual plants experienced zero mortality and had no replacements – all individuals survived the study;
- Growth and level of branching was intermediate compared to the other species, but relative growth rate was one of the lowest in the last 21 months of the study;
- Compared to the other study species, it had the lowest LMA_B, foliage density (i.e. average of only about 398 leaves) and leaf biomass per plant and one of the lowest leaf areas per plant;
- It had the second lowest value of LAI, after *Cistus*;
- It had the highest mean plant height and the second highest woody biomass per plant and leaf biomass and area per sun leaf;
- It had the second highest photosynthetic efficiency (QY), after *Cistus*;
- It had the overall highest assimilation rate (A), or photosynthetic rate (i.e. carbon gain), and the second highest transpiration rate (E) and photosynthetic water-use efficiency (WUE_P);
- It was one of the species with the lowest leaf relative water content (RWC_L);
- It reached the most negative values of leaf water potential (Ψ_L) after *Elaeagnus*, another tall shrub with similar leaf characteristics.
- It was one of the worst performing species in terms of cooling/insulating.

Buddleja was therefore an intriguing species on which to carry out an experiment investigating canopy interception of irradiance. *Buddleja*'s tall, erect and compact vertical canopy also helped with discerning the effect of varying foliage density and leaf to branch biomass ratio (L/B) going from the top of the crown to the bottom of the plant. Table 17 shows the mean leaf to branch biomass ratio for each species.

Table 17. Leaf-to-branch biomass ratio. The ratio of leaf to branch biomass (L/B) for each species.

Species	**L (kg)**	**B (kg)**	**L/B**
Viburnum tinus	**0.101**±0.009	**0.149**±0.007	**0.598**±0.037
Cistus × hybridus	**0.021**±0.003	**0.142**±0.016	**0.150**±0.018
Elaeagnus angustifolia	**0.025**±0.003	**0.124**±0.012	**0.205**±0.019
Ceanothus thyrsiflorus	**0.033**±0.003	**0.070**±0.004	**0.455**±0.021
Buddleja davidii	**0.013**±0.001	**0.131**±0.004	**0.101**±0.008
Cotinus coggygria	**0.042**±0.006	**0.103**±0.009	**0.393**±0.036

The following ranks the species from highest to lowest L/B: *Viburnum* > *Ceanothus* > *Cotinus* > *Elaeagnus* > *Cistus* > *Buddleja*, or better Evergreen > Deciduous > Semi-deciduous. Here is yet another example of ranking of the species by functional type, a recurring theme in this study. Therefore *Buddleja* was the species with lowest leaf to branch biomass ratio. This means that, despite having a relatively high branch dry weight (i.e. woody biomass), the number of leaves and their dry weight per plant (i.e. leaf biomass) are low in comparison to its branching characteristics (i.e. high plant height, branch length and ramification). In plainer terms, *Buddleja* may have a higher ratio of exposed woody biomass compared to leaf biomass and therefore light may penetrate more into the canopy compared to the other study species. As will be discussed in Section 3.3 further on, leaf to branch ratio and other leaf and branching characteristics of this species may have contributed to *Buddleja*'s inefficacy to shade from high irradiance throughout the study, resulting in a much poorer performance in terms of buffering extreme temperatures on a rooftop compared to the other shrub species**.**

The experiment as described in Section 2.5.1.4 of the previous 'Methods' chapter resulted in following findings: the average amount of light that passed through *Buddleja*'s canopy was 19.79 W m^{-2}, with the middle section of the canopy permitting the least amount of light to pass through (13.99 W m^{-2}), while the top section allowed the most light to pass through (25.55 W m^{-2}). Surprisingly, the bottom section had an intermediate effect on the incident light (19.81 W m^{-2}). The three sections of the canopy were found to have significantly different values of irradiance post-interception by the canopy ($P<0.001$). As the strobe light used in the experiment flashed a light of 1500 W from a rectangular lamp (0.1 m^2 in area), it may be assumed that the actual amount of incident light before passing through the canopy was in reality just 150 W m^{-2} (i.e. 1500 W × 0.1 m^2). However, as the lamp was placed at a fixed distance of 0.5 m away from the surface of the canopy, it may be assumed that the amount of incident light may have been approximately half of 150 W m^{-2} and therefore more like 75 W m^{-2}. If this were true, then *Buddleja*'s canopy on average extinguished about 74% or about three-fourths of the incident light, with up to 81% for what is assumed to be the leafier middle part of the canopy. Although not strictly a light extinction coefficient, this percentage of light reduction through the canopy could give an indication of the level of light reduction that can occur through a shrub canopy; as *Buddleja* had the lowest foliage density and one of the lowest values of LAI, it is likely that the other shrubs had the capacity to extinguish more than 74% of incident light through their canopies.

A.4.2 The effects of plant density, population size and species mixture on the physiology and fitness of six woody shrubs

A.4.2.1 Effects of stress on photosynthetic performance and water use efficiency

A.4.2.1.1 Maximum quantum yield (QY)

Photosystem II (PII) is the first protein complex in the chain of light-dependent reactions that occur in photosynthesis. The reaction centre of this protein contains a chlorophyll molecule that, upon absorbing photons (light energy), releases an energised electron into a downward chain of reactions that ultimately prompts chlorophyll to extract electrons from water, causing water molecules to break down into hydrogen ions (used to power the production of ATP and NADPH that in turn power the production of carbohydrates) and oxygen gas (Barber 2003, Ferreira et al. 2004). What was presently described is only one of the three pathways that photons can take after being absorbed by chlorophyll – they can also either be re-emitted as chlorophyll fluorescence or be dissipated as heat (Baker 2008). As it happens, the amount of energy re-emitted as variable chlorophyll fluorescence (F_v) can give an indication of how well PII is working within the leaf and if the plant is undergoing any stress. An easy and common way of measuring F_v in the field is with a portable chlorophyll fluorometer, which measures the photosynthetic efficiency of PII in a dark-adapted state by allowing the maximum number of photons to take the fluorescence pathway (Baker and Rosenqvist 2004). What the chlorophyll fluorometer does is compare the values of minimal fluorescence (F_0), measured when an area of a leaf has been adapted to darkness, to those of maximal fluorescence (F_m), when that same leaf area is exposed to a flash of saturating light that reduces the maximum number of reaction centres available for photon capture; the fluorometer will then divide this difference (F_v) by F_m. The ratio F_v/F_m, generally referred to as the maximum quantum yield, will become progressively lower as less reaction centres are left available for light absorption and as the plant undergoes higher degrees of stress. For guidance, a value of F_v/F_m in the range of 0.790 to 0.840 signifies optimal photosynthetic efficiency; anything less may indicate plant stress (Maxwell and Johnson 2000).

Maximum quantum yield (F_v/F_m) is therefore a parameter that can characterise the photosynthetic performance of the different shrub species and ascertain the levels of stress they may have experienced during the study. For each species, Table 18 below presents: 1) the mean values of F_v/F_m as measured separately in the three years of the study (QY_1, QY_2 and QY_3), to evaluate possible increases or decreases in performance over time; 2) the *p*-values associated to the One-Way ANOVA applied to test the differences in F_v/F_m between the three years and 3) total mean F_v/F_m (QY).

Table 18. Change in photosynthetic efficiency over time. Mean values of maximum quantum yield (F_v/F_m) for each year of the study (QY_1, QY_2 and QY_3), the *p*-values associated to the differences tested and total mean F_v/F_m (QY).

Species	QY_1	QY_2	QY_3	***P*-value**	**QY**
Viburnum tinus	**0.776**±0.003	**0.762**±0.004	**0.763**±0.005	**0.009**	**0.768**±0.002
Cistus × hybridus	**0.828**±0.003	**0.842**±0.002	**0.828**±0.004	**<0.001**	**0.832**±0.002
Elaeagnus angustifolia	**0.816**±0.002	**0.823**±0.002	**0.803**±0.004	**0.001**	**0.815**±0.001
Ceanothus thyrsiflorus	**0.809**±0.002	**0.829**±0.002	**0.788**±0.007	**<0.001**	**0.809**±0.002
Buddleja davidii	**0.827**±0.002	**0.840**±0.001	**0.781**±0.005	**<0.001**	**0.818**±0.002
Cotinus coggygria	**0.806**±0.003	**0.788**±0.003	**0.795**±0.003	**<0.001**	**0.797**±0.002

Table 18 shows that total mean F_v/F_m (QY) was significantly different ($P<0.001$) amongst the different species. If one solely looks at QY, what stands out is the fact that *Cistus* had the highest QY (0.832), whereas *Viburnum* had the lowest QY (0.768), in this order: *Cistus* > *Buddleja* > *Elaeagnus* > *Ceanothus* > *Cotinus* > *Viburnum*. Thereby, one can say that on average *Cistus* was constantly working close to the upper limit of the optimal performance range throughout the study period, whereas *Viburnum* was constantly working below it. Again, we have a situation where the semi-deciduous (*Cistus* and *Buddleja*) and the evergreen shrubs (*Ceanothus* too, but especially *Viburnum*) are physiologically polarised. This is not surprising, as a key feature of woody plants with evergreen habits is low photosynthetic capacity (usually coupled with low nutrient requirement) as a result of lower investment in enzyme content (Baldocchi et al. 2010). In fact, QY was significantly and negatively correlated with both B_L ($P=0.005$, $R=-0.945$) and A_L ($P=0.021$, $R=-0.880$) per plant (See previous Section 3.1.2.2 and Table A in Appendix B), as can be observed in the scatter plots in Fig. 13. This translates to: "as photosynthetic performance increases, both the total leaf biomass and leaf canopy area per plant decreases," which could mean that the study species that had a lower total leaf biomass and area per plant may have compensated for their reduced aboveground canopies by allocating more enzymes in their photosystems and thereby ensuring higher photosynthetic capacity within each leaf. Although CD was not significantly correlated with QY ($P=0.166$, See Section 3.1.2.2 and Table A in Appendix B), the trend may still point towards a relationship between reduced foliage density and a greater concentration of photosynthetic apparatus per leaf as an adaptive strategy in seasonally dimorphic shrubs like *Cistus* and *Buddleja* – in their case, a reduced habit in terms of both number of leaves and leaf area may be necessary to compensate for the seasonal shed and regrowth of entire cohorts of leaves every year (as mentioned in the previous Section 3.1.2.2), while still maintaining an equivalent (if not superior) photosynthetic capacity to other functional groups.

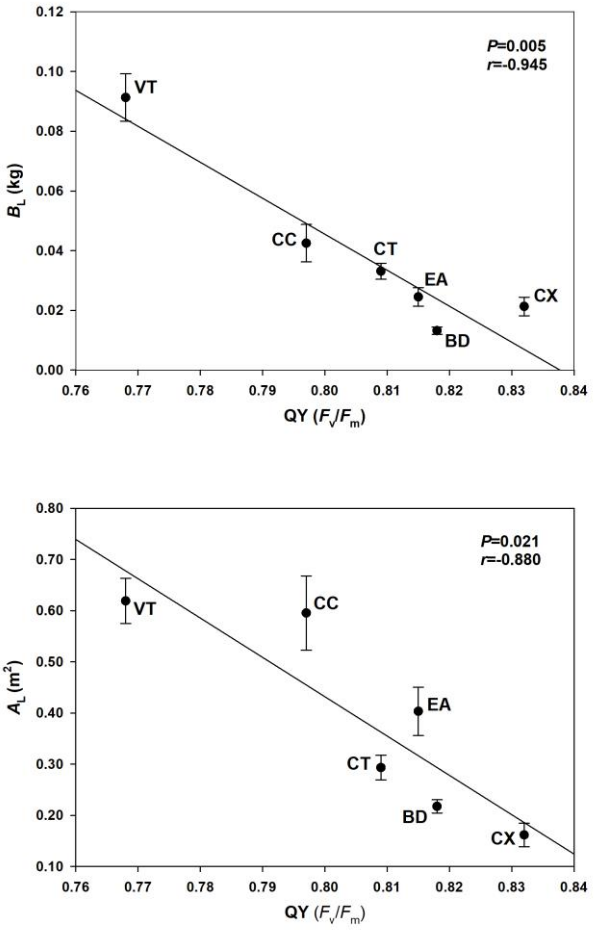


Figure 13. As photosynthetic efficiency increases, leaf biomass and area decrease. Scatter plot with regression for the correlations between QY and B_L per plant (above) and QY and A_L per plant (below), for each species (VT=*Viburnum*, CX=*Cistus*, EA=*Elaeagnus*, CT=*Ceanothus*, BD=*Buddleja*, CC=*Cotinus*).

What can also be evinced from Table 18 is that, over time, all species demonstrated a significant increase in photosynthetic performance going from Year 1 (QY_1) to Year 2 (QY_2) of the study, with the exception of *Viburnum* and *Cotinus* which presented slight dips in F_v/F_m. However, going from Year 2 (QY_2) to Year 3 (QY_3), all species had a significant reduction in photosynthetic performance (most notably *Buddleja* and *Ceanothus*), with the exception of *Viburnum*, which maintained a stable mean F_v/F_m, and *Cotinus*, which even showed a slight increase in F_v/F_m in the last year of the study. However, QY_3 in *Cotinus* was ultimately lower than the initial QY_1.

A logic explanation for this behaviour could be that most shrubs "geared up" going from Year 1 to Year 2 of the study, allowing their photosystems to work at higher levels when initially finding a fairly hospitable environment (e.g. individuals not yet grown to full capacity of containers and still in relatively full health, constant high levels of irradiance), but going forward the photosystems of most shrubs were probably not able to stabilise at such high "revs" and had to adapt to working more efficiently at lower levels. While QY did not significantly influence M (P=0.273), it did have a significant effect on both G and RGR (P=0.017): in testing the correlation between the two parameters, G and RGR were negatively correlated with QY (R= –0.892), meaning that G and RGR increased as QY decreased (See Table A in Appendix B). The regression in this case is not particularly strong (ideally it would need to be at least 0.98), nevertheless the significance of the correlation might indicate that shrubs with photosystems that constantly work at high performance levels (i.e. are inefficient) without substantially adapting to lower levels in the long-term could cause a drastic reduction in woody biomass (in the hopes of saving energy?) that could even threaten vitality. This could explain the drastic reduction in G and RGR in *Cistus* between the first 12 months and the latter period of the study, as previously described in Section 3.1.1 – *Cistus* simply could not adjust its photosynthetic efficiency for long-term survival mode. This high photosynthetic performance could be related to the fact that *Cistus* leaves have a lower chlorophyll content in spring leaves compared to the autumn ones (See Appendix A) and therefore might need to maximise photosynthesis in the fewer chlorophyll molecules in the summer. In nature, *Cistus* is a xeric shrub with impressive adaptive strategies to both drought and heat stress, but it is also a pioneering component of degraded scrubland prone to seasonal fires. Ecologically speaking, *Cistus* is a fairly transient shrub that needs to tolerate extreme conditions and colonise post-fire environments rather quickly and may not be designed for long-term survival and adaptation, as is the case for many other ruderals. Like most sclerophylls, *Viburnum* may instead choose to sacrifice photosynthetic performance and other physiological activities in order to walk the fine line of maintaining both leaf longevity and constant biomass growth.

During the first year of the study, all six shrub species were arranged into monospecific (MP) populations, but each species was divided into sparse (SP) and dense (DP) populations, to evaluate the effect of plant density on various plant parameters. The year after, the shrubs were rearranged into four polyspecific populations (PP) that were further arranged into one of the following combinations: a) SP 3×3; b) SP 4×4; c) DP 3×3 or d) DP 4×4 (See Section 2.2.3.2 for more details). For each study species, Table 19 below wants to highlight the differences between mean values of F_v/F_m in terms of MP and PP and therefore has these values divided into study year. Year 3 was dedicated to directly compare (i.e. same year, same exact conditions) the effects of species mixture on F_v/F_m and other plant parameters.

Table 19. The effect of species mixture on photosynthetic efficiency over time. Comparison of mean F_v/F_m between populations of MP (QY_{MP}) and PP (QY_{PP}) shrubs, divided by species and year of study (Year 1, 2 & 3). *P* is the *p*-value of the test (within each species) between QY_{MP} in Year 1 and QY_{PP} in Year 2, and the test between QY_{MP} and QY_{PP} in Year 3.

	Year 1	**Year 2**		**Year 3**		
Species	**QY_{MP}**	**QY_{PP}**	***P***	**QY_{MP}**	**QY_{PP}**	***P***
Viburnum tinus	**0.776**±0.003	**0.762**±0.004	**0.003**	**0.770**±0.010	**0.760**±0.005	0.310
Cistus × hybridus	**0.828**±0.003	**0.842**±0.002	**<0.001**	**0.831**±0.003	**0.827**±0.002	0.298
E. angustifolia	**0.816**±0.002	**0.823**±0.002	**0.014**	**0.804**±0.011	**0.803**±0.003	0.880
C. thyrsiflorus	**0.809**±0.002	**0.829**±0.002	**<0.001**	**0.786**±0.011	**0.789**±0.004	0.748
Buddleja davidii	**0.827**±0.002	**0.840**±0.001	**<0.001**	**0.791**±0.009	**0.777**±0.003	0.071
Cotinus coggygria	**0.806**±0.003	**0.788**±0.003	**<0.001**	**0.802**±0.005	**0.792**±0.002	**0.029**

The importance of having direct comparisons for different categories can easily be observed in Table 19 – while the difference between the effects of species mixture (MP vs PP) on photosynthetic performance is significant in all the shrubs when comparing data from Year 1 (MP) against data from Year 2 (PP), the same cannot be said when directly comparing the same categories in Year 3, where only *Cotinus* showed significantly higher F_v/F_m (P=0.029) in MP (0.802) compared to PP (0.792). However, it is also true that Year 3 had a smaller cohort of plants to dedicate to each category compared to Years 1 and 2 and therefore may have contributed to the reduced significance of the results. Despite the fact that the study plants had already been growing on the rooftops for over a year by Year 2 of the study, and therefore had already undergone more than a year of potential stress, all shrubs (with the exception of *Viburnum*) presented significantly higher values of F_v/F_m in the PP category (QY_{PP}) compared to the MP category (QY_{MP}) in Year 1. These results could either mean that, as explained in the previous paragraphs, the plants had adapted to rooftop environment and were all still in sufficient health to maintain high levels of photosynthesis into Year 2, or that effectively the rearrangement of shrubs into a mixed population of different shrub species (PP) had a significantly positive effect on the majority of the species' photosynthetic efficiency. It could also mean that the majority of the species were experiencing such levels of stress by Year 3 of the study that, unlike Year 1 and 2, species mixture did not affect their photosynthetic fitness in a significant way.

What is not ambiguous is whether plant density and population size affected shrub photosynthetic performance. The best way to observe the effects of plant density and population size is to present the data in a series of tables, with relative *p*-values for the tests applied to identify the differences between categories. Below are: 1) Table 20 , presenting the values of mean F_v/F_m per species as divided into sparse (QY_{SP}) and dense (QY_{DP}) population within Years 1 and 2 of the study; 2) Table 21, presenting the values of mean F_v/F_m per species in Year 2 as divided into both population size 3×3 ($QY_{3\times3}$) and 4×4 ($QY_{4\times4}$) and into plant density sparse (QY_{SP}) and dense (QY_{DP}), and finally 3)

Tables 22a and 22b, presenting results and *p*-values, respectively, for mean F_v/F_m per species in Year 2 as divided into the various different combinations of categories (QY_{SP+3x3}, QY_{DP+3x3}, QY_{SP+4x4} and QY_{DP+4x4}).

Table 20. The effect of plant density on the photosynthetic efficiency of populations with different species mixtures. Comparison of mean F_v/F_m per species between sparse (QY_{SP}) and dense (QY_{DP}) populations. Data divided by: Year 1 (shrubs in MP & 3×3 size) and Year 2 (shrubs in PP & only in 3×3 size). *P* is the *p*-value of the test between QY_{SP} and QY_{DP} in Year 1 and in Year 2 of the study.

	Year 1 (MP, 3×3)			**Year 2 (PP, 3×3)**		
Species	$\mathbf{QY_{SP}}$	$\mathbf{QY_{DP}}$	***P***	$\mathbf{QY_{SP}}$	$\mathbf{QY_{DP}}$	***P***
Viburnum tinus	**0.768**±0.005	**0.784**±0.004	**0.017**	**0.738**±0.008	**0.798**±0.005	**<0.001**
Cistus × hybridus	**0.830**±0.005	**0.826**±0.005	0.602	**0.845**±0.003	**0.836**±0.006	0.178
Elaeagnus angustifolia	**0.816**±0.003	**0.816**±0.004	0.889	**0.828**±0.003	**0.831**±0.002	0.378
Ceanothus thyrsiflorus	**0.805**±0.003	**0.812**±0.003	0.097	**0.818**±0.003	**0.835**±0.003	**<0.001**
Buddleja davidii	**0.822**±0.003	**0.831**±0.003	**0.048**	**0.842**±0.001	**0.843**±0.002	0.565
Cotinus coggygria	**0.806**±0.002	**0.805**±0.005	0.795	**0.789**±0.005	**0.789**±0.005	0.978

Table 21. The effect of increasing population size and plant density on the photosynthetic efficiency of shrubs in polyspecific populations. Comparison of mean F_v/F_m per species in Year 2 (comprised of only PP), between: 1) small population size ($QY_{3\times3}$) and big population size ($QY_{4\times4}$), and 2) low (QY_{SP}) and high (QY_{DP}) plant density. *P* is the *p*-value per species of the test between $QY_{3\times3}$ and $QY_{4\times4}$ and between QY_{SP} and QY_{DP}.

	Year 2 (PP)					
Species	$\mathbf{QY_{3\times3}}$	$\mathbf{QY_{4\times4}}$	***P***	$\mathbf{QY_{SP}}$	$\mathbf{QY_{DP}}$	***P***
Viburnum tinus	**0.768**±0.007	**0.757**±0.005	0.190	**0.736**±0.005	**0.788**±0.004	**<0.001**
Cistus × hybridus	**0.840**±0.003	**0.844**±0.002	0.292	**0.845**±0.002	**0.840**±0.003	0.155
Elaeagnus angustifolia	**0.829**±0.002	**0.819**±0.003	**0.002**	**0.821**±0.003	**0.825**±0.002	0.270
Ceanothus thyrsiflorus	**0.827**±0.002	**0.831**±0.002	0.253	**0.820**±0.002	**0.837**±0.002	**<0.001**
Buddleja davidii	**0.842**±0.001	**0.838**±0.001	**0.021**	**0.838**±0.001	**0.841**±0.001	0.063
Cotinus coggygria	**0.789**±0.004	**0.787**±0.005	0.752	**0.781**±0.005	**0.795**±0.004	**0.021**

Table 22a. The combined effect of population size and plant density on photosynthetic efficiency. Mean values of F_v/F_m as combinations of the different categories tested in Year 2 ($QY_{SP+3\times3}$, $QY_{DP+3\times3}$, $QY_{SP+4\times4}$, and $QY_{DP+4\times4}$).

Species	$\mathbf{QY_{SP+3\times3}}$	$\mathbf{QY_{DP+3\times3}}$	$\mathbf{QY_{SP+4\times4}}$	$\mathbf{QY_{DP+4\times4}}$
Viburnum tinus	**0.738**±0.008	**0.798**±0.005	**0.734**±0.007	**0.780**±0.005
Cistus × hybridus	**0.845**±0.003	**0.836**±0.006	**0.845**±0.004	**0.843**±0.003
Elaeagnus angustifolia	**0.828**±0.003	**0.831**±0.002	**0.817**±0.004	**0.821**±0.003
Ceanothus thyrsiflorus	**0.818**±0.003	**0.835**±0.003	**0.822**±0.003	**0.839**±0.003
Buddleja davidii	**0.842**±0.001	**0.843**±0.002	**0.835**±0.002	**0.840**±0.002
Cotinus coggygria	**0.789**±0.005	**0.789**±0.005	**0.774**±0.008	**0.800**±0.005

Table 22b. Results of statistical tests comparing the effects of plant density and population size on photosynthetic efficiency. *P*-values of the tests between categories of mean F_v/F_m in Year 2, in terms of: 1) the effect of plant density within each population size, 3×3 ($QY_{SP+3\times3}$ vs $QY_{DP+3\times3}$) & 4×4 ($QY_{SP+4\times4}$ vs $QY_{DP+4\times4}$); and 2) the effect of population size within each type of plant density, SP ($QY_{SP+3\times3}$ vs $QY_{SP+4\times4}$) & DP ($QY_{DP+3\times3}$ vs $QY_{DP+4\times4}$).

	Plant density		**Population size**	
Species	$QY_{SP+3\times3}$ **vs** $QY_{DP+3\times3}$	$QY_{SP+4\times4}$ **vs** $QY_{DP+4\times4}$	$QY_{SP+3\times3}$ **vs** $QY_{SP+4\times4}$	$QY_{DP+3\times3}$ **vs** $QY_{DP+4\times4}$
Viburnum tinus	**<0.001**	**<0.001**	0.645	**0.021**
Cistus × hybridus	0.178	0.550	0.880	0.252
Elaeagnus angustifolia	0.378	0.386	**0.026**	**0.026**
Ceanothus thyrsiflorus	**<0.001**	**<0.001**	0.311	0.359
Buddleja davidii	0.632	**0.045**	**0.012**	0.390
Cotinus coggygria	0.979	**0.008**	0.158	0.142

What can be observed from the four tables above is that all shrubs except for *Cistus* were significantly affected by either plant density, population size or both at some point in the study. The species most significantly affected by plant density was *Viburnum*, which also presented a significant decrease (*P*=0.021) in mean F_v/F_m going from a small (0.798) to a slightly bigger (0.780) DP population. However, in all other circumstances, *Viburnum* had significantly higher mean F_v/F_m when placed in a DP than when in an SP. Therefore, high plant density had a positive effect on *Viburnum*'s photosynthetic performance until the population size of that DP increased, potentially causing self-shading in the canopy that may have reduced photosynthetic capacity. *Ceanothus*, another evergreen shrub, also was significantly affected by plant density, with mean values of F_v/F_m all significantly higher in DP than in SP, independent of population size. *Elaeagnus* was the species least affected by plant density and the most affected by population size, showing a significant reduction in mean F_v/F_m going from a small to a slightly bigger population, independent of plant density. *Buddleja* was the other species significantly affected by population size, also presenting lower values of F_v/F_m in the 4×4 compared to the 3×3 population. As *Elaeagnus* and *Buddleja* were the tallest shrubs in the study, an increase in population size might have caused greater exposure of their canopies to wind and irradiance, for example, as their plants were distributed within PP and therefore within populations of plants with heterogeneous canopy heights.

Irrespective of significance, all shrubs generally showed higher mean F_v/F_m when placed in DP compared to when they were placed in SP, with *Cistus* being the notable exception and exhibiting the opposite trend.

A.4.2.1.2 Gas exchange: Transpiration rate (*E*), stomatal conductance (g_S), assimilation (*A*), leaf temperature (T_L) and photosynthetic water use efficiency (WUE_P)

In the previous section, the analysis of QY was used as a comparative tool to differentiate the study species' photosynthetic efficiencies at energy and particle level. In this section, photosynthetic performance of the different shrub species was analysed as well, only at molecular and cellular level, by evaluating gas exchange processes. Photosynthesis is always a derived parameter, in other words it can only be calculated from measurements of other parameters (Field, Ball and Berry 2000), and in this case photosynthesis was derived from gas exchange parameters measured *in vivo* through a particular gas exchange system called a portable infrared gas analyser, or IRGA (detailed in Section 2.5.3 and Table 2 in Chapter 2).

The evaluation of gas exchange parameters is best carried out with an appreciation of what stomata do and how they function. Stomata are pores in the epidermis of green plant organs (most commonly in leaves), which are surrounded by two specialised guard cells that control the size of stomatal aperture and therefore regulate gas exchange (Fricker and Willmer 1996, Kirkham 2014). Their precise role in plant physiology is complex and not completely understood, but it is generally accepted that stomata have evolved to undertake three (not mutually exclusive) main functions: 1) to control transpiration rate (*E*), in other words to minimise evaporative water loss via regulated stomatal conductance (g_S), while still allowing CO_2 uptake for photosynthetic assimilation, *A* (i.e. rate of carbon gain); 2) to prevent deficits in xylem water potential (Ψ) that could damage xylem vessels through cavitation and embolism, and 3) to maintain optimal leaf temperature, T_L (Jones 1998). The stomata therefore determine photosynthetic capacity of leaves through their regulation of mesophyll conductance of CO_2 between the air surrounding the leaf in substomatal cavities and the chloroplasts where net carbon fixation occurs (Flexas et al. 2012). IRGAs exploit the CO_2 molecules' ability to absorb infrared light to estimate CO_2 concentration in proportion to the quantum decrease in infrared light – the time it takes for CO_2 concentration to decrease by a predetermined amount is inversely proportional to the photosynthetic rate of the leaf, *A* (Espinosa-Calderon et al. 2011).

With the exception of xylem water potential, all of the parameters mentioned above (*E*, g_S, T_L), including CO_2 and H_2O concentrations in the air entering and exiting the system, were measured with an IRGA, which used these parameters to calculate the rate of carbon gain, or photosynthetic rate of assimilation (*A*), per unit leaf area. In addition to the analysis of photosynthetic performance, the same gas exchange parameters were also used to extrapolate instantaneous photosynthetic water-use efficiency (WUE_P) of the different shrub species (Section 3.2.1.2), by dividing the carbon gain in photosynthesis (*A*) by the water lost through transpiration (*E*), in units of mmol mol^{-1}. So, WUE_P is the evaluation of how much water is used by a unit of leaf area in the fixation of CO_2 during photosynthesis (Lambers, Chapin and Pons 2008, Medrano et al. 2012, Soh et al. 2019), therefore another important parameter to analyse in close association with photosynthetic performance. WUE_P can in fact increase at mild conditions of water stress as perceived by a species, however, it can falter as mesophyll cells progressively dehydrate and lose the ability to efficiently utilise available CO_2 as water stress continues, thus causing the inhibition of photosynthesis and a reduction in stomatal conductance (Ashraf and Harris 2013). According to Lambers, Chapin and Pons (2008), the study species in the present study were expected to have mean values of WUE_P ranging between 2 and 11 mmol mol^{-1}, according to the category they fall under (woody C_3 plants).

On the summer days of each year in which the gas exchange measurements were carried out, the microclimatic conditions between the experimental sites were very similar (Table 23a); only air temperature ($P<0.001$) and soil moisture content ($P=0.022$) in Year 2 and wind speed in both years ($P<0.001$) were significantly different between the two study sites (Lower Hicks roof and Hadfield roof garden). In particular, the mean values of vapour pressure deficit in the air (VPD_{air}) were not significantly different between the two experimental sites and fell within an optimal range (Lambers, Chapin and Pons 2008; Shamshiri et al. 2018). VPD_{air} is one of the main drivers of evapotranspiration and is the difference between the pressure of water vapour in the air at saturation, SVP, and the actual pressure at a specific temperature, AVP (Yuan et al. 2019). There is usually a close relationship between mean values of VPD_{air} and plant transpiration rate (E) and stomatal conductance (g_S) and correlations were found to be significant between mean values of VPD_{air} and these plant parameters in almost all species, especially in the semi-deciduous species (*Cistus* and *Buddleja*).

Table 23a. Microclimate and soil moisture conditions on the experimental sites during gas exchange measurements. Comparison of the microclimate parameters at each study site (Hicks roof and Hadfield roof) at the time of gas exchange measurements for Year 1 and Year 2 – photosynthetically active radiation, PAR (µmol m^{-2} s^{-1}), air temperature (°C), wind speed (m s^{-1}), relative humidity (%), air vapour pressure deficit, VPD_{air} (kPA) and soil moisture content, SMC (m^3 m^{-3}). VPD_{air} was calculated from the formula in Yuan et al. 2019 (i.e. SVP – AVP = VPD; SVP and AVP were calculated using the National Weather Service 2020).

	Year 1		**Year 2**	
Species	**Hicks roof**	**Hadfield roof**	**Hicks roof**	**Hadfield roof**
PAR (µmol m^{-2} s^{-1})	**894.98**±81.85	**888.88**±53.54	**1364.23**±36.63	**1330.98**±39.95
Air temperature (°C)	**20.87**±0.15	**21.25**±0.44	**21.04**±0.38	**19.09**±0.22
Wind speed (m s^{-1})	**4.69**±0.23	**1.14**±0.08	**4.26**±0.29	**1.17**±0.09
Relative humidity (%)	**58.37**±0.70	**57.10**±0.53	**55.98**±1.04	**53.16**±0.92
VPD_{air} (kPA)	**1.03**±0.02	**1.09**±0.04	**1.12**±0.05	**1.04**±0.03
SMC (m^3 m^{-3})	**0.201**±0.027	**0.194**±0.004	**0.066**±0.007	**0.127**±0.015

There were, however, significant differences in the mean values of soil moisture content (SMC) measured for each species in both Year 1 and 2, with noticeably lower values of SMC in Year 2 compared to Year 1 despite similar experimental conditions. In Year 1, the highest mean values were found for *Viburnum* (0.255±0.019 $m^3 m^{-3}$) and the lowest were found in *Cistus* (0.170±0.009 $m^3 m^{-3}$), whereas *Buddleja* had the highest values in Year 2 (0.154±0.010 $m^3 m^{-3}$) and *Cistus* again had the lowest (0.053±0.010 $m^3 m^{-3}$). There were also significant differences in SMC in relation to plant density, but only in Year 1 (Table 23b) – SMC was significantly higher in *Viburnum* (P<0.001) when placed in a sparse population (SMC_{SP}) compared to when it was placed in a dense one (SMC_{DP}), whereas the opposite was true for *Cotinus* (P=0.006). In Year 2, however, neither plant density nor population size had any effect on the water use of the different species, perhaps due to the 'homogenising' effect of placing all shrubs in polyspecific populations. In fact, measurements of SMC carried out in Year 3 alongside measurements of physiological parameters indeed revealed a distinct effect of species mixture on the mean values of SMC in the different study species – SMC was significantly higher in the polyspecific rather than in the monospecific population (MP) of *Ceanothus* (P=0.004), while values were *lower* in the polyspecific (PP) rather than in the MP of the semi-deciduous *Cistus* (P=0.079) and *Buddleja* (P=0.093), though not significantly so in their case. All other species showed no significant difference between MP and PP. A higher mean SMC in units containing *Ceanothus* (a short shrub) when placed in a mixed species population (i.e. PP) compared to populations composed of only *Ceanothus* (i.e. MP) indicate a positive shading effect on mean SMC for that species and a differentiated water-use strategy compared to the semi-deciduous species, for example.

Table 23b. The effect of plant density on soil moisture content in populations with different species mixtures. Mean values of soil moisture content (SMC, $m^3 m^{-3}$) per unit (i.e. container with 3 shrubs), as measured on the same days as gas exchange measurements, for each study species growing in either a sparse (SMC_{SP}) or a dense population (SMC_{DP}), as measured in Year 1 (i.e. all monospecific populations) and in Year 2 (i.e. all polyspecific populations). P is the p-value of tests between SMC_{SP} and SMC_{DP} for each study year, in order to determine the effect of plant density on SMC.

Species	**Year 1 (monospecific)**			**Year 2 (polyspecific)**		
	SMC_{SP} ($m^3 m^{-3}$)	**SMC_{DP} ($m^3 m^{-3}$)**	***P***	**SMC_{SP} ($m^3 m^{-3}$)**	**SMC_{DP} ($m^3 m^{-3}$)**	***P***
V. tinus	**0.338**±0.031	**0.214**±0.013	**<0.001**	**0.083**±0.012	**0.070**±0.010	0.383
C. × hybridus	**0.149**±0.012	**0.180**±0.012	0.125	**0.057**±0.013	**0.045**±0.007	0.488
E. angustifolia	**0.200**±0.028	**0.165**±0.013	0.206	**0.078**±0.015	**0.051**±0.001	0.252
C. thyrsiflorus	**0.193**±0.013	**0.191**±0.011	0.919	**0.127**±0.015	**0.124**±0.014	0.909
B. davidii	**0.183**±0.006	**0.194**±0.009	0.303	**0.150**±0.011	**0.157**±0.010	0.642
C. coggygria	**0.180**±0.008	**0.223**±0.013	**0.006**	**0.100**±0.027	**0.102**±0.026	0.968

Unsurprisingly then, the study species demonstrated significantly different ($P<0.001$) total mean values of all gas exchange parameters (E, g_S, A, T_L and WUE$_P$) carried out in the first two years of the study (Table 24). More interestingly, there were only two cases in which plant functional groups demonstrated a statistically significant relationship with the gas exchange parameters – 1) the semi-deciduous shrubs (*Buddleja* and *Cistus*), which did not show a difference in mean values of g_S ($P=0.484$), and 2) the evergreen (*Viburnum* and *Ceanothus*) and deciduous shrubs (*Elaeagnus* and *Cotinus*), which did not show a significant difference in mean values of WUE$_P$ ($P=0.250$ and $P=0.667$, respectively). Otherwise, there were no correlations between plant functional group and total mean values of gas exchange parameters. Plant height may have played an important role in influencing other parameters, such as leaf mass per area, LMA (Sect. 3.1.1.3), woody biomass, B_W (Sect. 3.1.2.1) and leaf area, A_L (3.1.2.2). Therefore, the potential relationship between gas exchange parameters and plant height was assessed by testing the mean value of each parameter within the 'short' shrubs (*Viburnum*, *Cistus* and *Ceanothus*) against the mean value of each parameter within the 'tall' shrubs (*Elaeagnus*, *Buddleja* and *Cotinus*). All tests of this type resulted not significant except for WUE$_P$ ($P=0.006$), which was statistically higher in the 'tall' shrubs (5.20±0.08 mmol m^{-1}) than in the 'short' shrubs (3.85±0.24 mmol m^{-1}).

Table 24. Total mean values of gas exchange parameters per species. Total mean values of gas exchange measurements, carried out in Year 1 and Year 2, for each study species – leaf temperature (T_L, °C), stomatal conductance (g_S, mmol m^{-2} s^{-1}), rate of assimilation (A, µmol m^{-2} s^{-1}) and transpiration rate (E, mmol m^{-2} s^{-1}) per unit leaf area. The mean value of WUE$_P$ (photosynthetic water use efficiency) was extrapolated as the ratio A/E, also calculated per study species.

Species	**Total**				
	T_L (°C)	**g_S (mmol m^{-2} s^{-1})**	**A (µmol m^{-2} s^{-1})**	**E (mmol m^{-2} s^{-1})**	**WUE$_P$ (mmol m^{-1})**
Viburnum tinus	**26.15**±0.32	**69.54**±9.66	**3.32**±0.24	**0.95**±0.04	**3.83**±0.30
Cistus × hybridus	**26.55**±0.42	**183.71**±32.38	**5.13**±0.53	**1.51**±0.07	**3.45**±0.20
Elaeagnus angustifolia	**25.89**±0.22	**72.31**±4.34	**4.78**±0.37	**1.08**±0.05	**5.11**±0.35
Ceanothus thyrsiflorus	**23.75**±0.13	**150.15**±9.95	**7.17**±0.44	**1.78**±0.08	**4.28**±0.21
Buddleja davidii	**23.79**±0.14	**161.68**±8.62	**8.93**±0.38	**1.80**±0.06	**5.11**±0.16
Cotinus coggygria	**23.26**±0.19	**195.28**±17.43	**8.71**±0.45	**2.00**±0.08	**5.36**±0.47

However, despite what seemed like relatively small differences in microclimate on the separate experimental rooftops (Table 23), the strongest relationship with the total mean values of gas exchange parameters was the rooftop on which the study species were grown: *Viburnum*, *Cistus* and *Elaeagnus* on the Lower Hicks building rooftop and *Ceanothus*, *Buddleja* and *Cotinus* on the Hadfield building roof garden. In fact, the parameters E, A and T_L showed a significant relationship with microclimate when subdividing the data by rooftop and testing it against each parameter, with even g_S (P=0.205) and WUE_P (P=0.261) presenting a potential trend. In particular, the shrubs growing on the Lower Hicks rooftop had significantly lower mean values of E (1.18±0.17 mmol m^{-2} s^{-1}) and A (4.41±0.56 µmol m^{-2} s^{-1}) and significantly higher mean values of T_L (26.20±0.19 °C) compared to those growing on the Hadfield roof garden (E=1.86±0.07, P=0.020; A=8.27±0.55, P=0.008; and T_L=23.60±0.17, P<0.001, respectively). These findings demonstrate the importance in field work of having all experimental plants growing on the same experimental site, or on at least two experimental sites with very similar growing conditions. This difference in microclimate conditions between the two experimental sites has revealed to be one of the most important limitations of the present study.

When observing the change in mean values of gas exchange parameters between Year 1 (Table 25a) and Year 2 (Table 25b) of the study, it is clear that all parameters were negatively affected and the fitness of almost all shrub species decreased by the passage of time (stress), by the change of plant species distribution from populations composed of a single species (monospecific, MP) in Year 1 to populations of mixed species (polyspecific, PP) in Year 2, or by a combination of both. The parameters that showed the highest sensitivity to stress and/or species mixture were *g*S and E (Table 25c), followed by A and WUE_P, with T_L showing a significant increase from Year 1 to Year 2 in only *Cistus* and *Viburnum*. *Viburnum* was the species that showed the most significant differences between Year 1 and Year 2 in gas exchange parameters, followed closely by the semi-deciduous species (*Cistus* and *Buddleja*), whereas the deciduous species *Cotinus* and *Elaeagnus* showed the least difference. In these species, all parameters showed a decrease in E, g_S, A and WUE_P and an increase in T_L going from Year 1 to Year 2. In contrast, *Ceanothus* showed a significant increase in mean values of A, E and WUE_P going from Year 1 to Year 2, with even g_S increasing despite the lack of significance (P=0.200). A possible explanation to *Ceanothus*' contrasting behaviour compared to the other species could be that, as the shortest species, the change in species mixture from MP to PP may have given *Ceanothus* a disproportionate advantage due to the sudden increase in shading procured by the surrounding taller shrubs (*Buddleja* and *Cotinus*, both 'tall' shrubs). Finally, it can be observed that the semi-deciduous species showed the highest dip in mean values of E and gS going from Year 1 to Year 2, whereas WUE_P was not affected in these species (Tables 25a and b).

Table 25a. Mean values of gas exchange parameters per species in monospecific populations. Mean values of gas exchange measurements carried out in Year 1, for each study species – leaf temperature (T_L, °C), stomatal conductance (g_S, mmol m^{-2} s^{-1}), rate of assimilation (A, µmol m^{-2} s^{-1}) and transpiration rate (E, mmol m^{-2} s^{-1}) per unit leaf area. The mean value of WUE$_P$ (photosynthetic water use efficiency) was extrapolated as the ratio A/E, also calculated per study species.

	Year 1 (Monospecific)				
Species	**T_L (°C)**	**g_S (mmol m^{-2} s^{-1})**	**A (µmol m^{-2} s^{-1})**	**E (mmol m^{-2} s^{-1})**	**WUE$_P$ (mmol m^{-1})**
Viburnum tinus	**24.36**±0.32	**148.41**±52.98	**6.79**±0.84	**0.96**±0.14	**9.81**±1.02
Cistus × hybridus	**23.29**±0.23	**469.69**±69.70	**10.97**±1.98	**2.04**±0.23	**4.14**±0.73
Elaeagnus angustifolia	**25.07**±0.45	**118.00**±14.80	**5.16**±1.46	**1.19**±0.15	**5.92**±0.69
Ceanothus thyrsiflorus	**23.78**±0.20	**134.53**±20.48	**3.43**±0.53	**1.41**±0.12	**3.64**±0.49
Buddleja davidii	**23.47**±0.21	**262.47**±14.10	**11.60**±0.82	**2.33**±0.12	**5.28**±0.44
Cotinus coggygria	**23.11**±0.25	**177.92**±35.57	**8.23**±0.80	**1.80**±0.14	**6.34**±1.02

Table 25b. Mean values of gas exchange parameters per species in polyspecific populations. Mean values of gas exchange measurements carried out in Year 2 – leaf temperature (T_L, °C), stomatal conductance (g_S, mmol m^{-2} s^{-1}), rate of assimilation (A, µmol m^{-2} s^{-1}) and transpiration rate (E, mmol m^{-2} s^{-1}) per unit leaf area. The mean value of WUE$_P$ (photosynthetic water use efficiency) was extrapolated as the ratio A/E, also calculated per study species.

	Year 2 (Polyspecific)				
Species	**T_L (°C)**	**g_S (mmol m^{-2} s^{-1})**	**A (µmol m^{-2} s^{-1})**	**E (mmol m^{-2} s^{-1})**	**WUE$_P$ (mmol m^{-1})**
Viburnum tinus	**26.26**±0.27	**53.55**±2.60	**2.61**±0.17	**0.95**±0.04	**2.70**±0.15
Cistus × hybridus	**27.55**±0.52	**74.49**±4.45	**4.95**±0.36	**1.37**±0.05	**3.35**±0.19
Elaeagnus angustifolia	**26.05**±0.25	**62.87**±3.50	**4.75**±0.31	**1.07**±0.05	**4.60**±0.26
Ceanothus thyrsiflorus	**23.72**±0.16	**160.63**±9.29	**9.69**±0.43	**2.03**±0.09	**4.93**±0.14
Buddleja davidii	**23.46**±0.18	**122.87**±3.83	**7.73**±0.23	**1.57**±0.03	**5.09**±0.11
Cotinus coggygria	**23.54**±0.29	**187.15**±11.31	**9.50**±0.47	**2.17**±0.10	**4.55**±0.14

Table 25c. Results of statistical tests comparing the effects of species mixture on gas exchange parameters. P-values of the tests comparing Year 1 (shrubs grown in monospecific populations, MP) and Year 2 (shrubs grown in polyspecific populations, PP) within each of the gas exchange categories (for each species): 1) leaf temperature (T_L, °C), 2) stomatal conductance (g_S, mmol m^{-2} s^{-1}), 3) rate of assimilation (A, µmol m^{-2} s^{-1}), 4) transpiration rate (E, mmol m^{-2} s^{-1}) and 5) photosynthetic water use efficiency (WUE$_P$), per unit leaf area and for both years of measurements.

	Year 1 (MP) vs Year 2 (PP)				
Species	**T_L (°C)**	**g_S (mmol m^{-2} s^{-1})**	**A (µmol m^{-2} s^{-1})**	**E (mmol m^{-2} s^{-1})**	**WUE$_P$ (mmol m^{-1})**
Viburnum tinus	**0.002**	**<0.001**	**<0.001**	0.902	**<0.001**
Cistus × hybridus	**<0.001**	**<0.001**	0.339	**<0.001**	0.139
Elaeagnus angustifolia	0.079	**<0.001**	0.665	0.313	**<0.001**
Ceanothus thyrsiflorus	0.822	0.200	**<0.001**	**<0.001**	**0.002**
Buddleja davidii	0.976	**<0.001**	**<0.001**	**<0.001**	0.562
Cotinus coggygria	0.273	0.799	0.168	**0.032**	0.059

The effects of low (i.e. sparse populations, SP) and high (i.e. dense populations, DP) plant density on the different gas exchange parameters were heterogeneous (Tables 26a–c), when taking into account data from both Year 1 and Year 2 of the study. g_S was significantly higher in dense populations of *Viburnum*, *Elaeagnus* and *Ceanothus* compared to sparse populations of the same species, and both *A* and *E* were significantly higher in dense populations of evergreen shrubs (*Viburnum* and *Ceanothus*) compared to the sparse populations of evergreens. The parameters T_L and WUE_P were not significantly affected by plant density, however the mean values of WUE_P within the dense populations can be ranked as following (from highest to lowest): *Elaeagnus* > *Buddleja* > *Cotinus* > *Ceanothus* > *Viburnum* > *Cistus*, or tall shrubs > short shrubs. This is another example of how WUE_P appears to be correlated to plant height.

Table 26a. The effect of low plant density on gas exchange parameters. Mean values of gas exchange measurements carried out in Year 1 and 2 on shrubs growing in sparse populations (SP), or populations of low plant density – leaf temperature (T_L, °C), stomatal conductance (g_S, mmol m^{-2} s^{-1}), rate of assimilation (*A*, µmol m^{-2} s^{-1}) and transpiration rate (*E*, mmol m^{-2} s^{-1}) per unit leaf area. The mean value of WUE_P (photosynthetic water use efficiency) was extrapolated as the ratio *A*/*E*, also calculated per study species grown in sparse populations.

Species	**Low plant density (SP)**				
	T_L (°C)	**g_S (mmol m^{-2} s^{-1})**	**A (µmol m^{-2} s^{-1})**	**E (mmol m^{-2} s^{-1})**	**WUE_P (mmol m^{-1})**
Viburnum tinus	**25.86**±0.35	**51.86**±4.07	**2.84**±0.28	**0.77**±0.04	**3.45**±0.39
Cistus × hybridus	**26.30**±0.43	**112.03**±18.03	**6.09**±0.65	**1.45**±0.08	**3.79**±0.29
Elaeagnus angustifolia	**25.95**±0.27	**62.97**±4.58	**4.83**±0.40	**1.01**±0.06	**4.98**±0.46
Ceanothus thyrsiflorus	**23.88**±0.18	**117.63**±10.67	**6.52**±0.45	**1.55**±0.11	**4.56**±0.33
Buddleja davidii	**23.53**±0.22	**164.95**±12.32	**9.57**±0.47	**1.74**±0.08	**5.40**±0.24
Cotinus coggygria	**23.34**±0.25	**182.55**±13.74	**9.16**±0.69	**2.12**±0.15	**4.35**±0.39

Table 26b. The effect of high plant density on gas exchange parameters. Mean values of gas exchange measurements carried out in Year 1 and 2 on shrubs growing in dense populations (DP), or populations of high plant density – leaf temperature (T_L, °C), stomatal conductance (g_S, mmol m^{-2} s^{-1}), rate of assimilation (*A*, µmol m^{-2} s^{-1}) and transpiration rate (*E*, mmol m^{-2} s^{-1}) per unit leaf area. The mean value of WUE_P (photosynthetic water use efficiency) was extrapolated as the ratio *A*/*E*, also calculated per study species grown in dense populations.

Species	**High plant density (DP)**				
	T_L (°C)	**g_S (mmol m^{-2} s^{-1})**	**A (µmol m^{-2} s^{-1})**	**E (mmol m^{-2} s^{-1})**	**WUE_P (mmol m^{-1})**
Viburnum tinus	**25.99**±0.33	**67.94**±3.84	**4.23**±0.36	**1.09**±0.06	**4.10**±0.43
Cistus × hybridus	**26.81**±0.74	**146.16**±23.17	**6.16**±0.75	**1.57**±0.12	**3.28**±0.26
Elaeagnus angustifolia	**25.77**±0.37	**85.65**±7.59	**5.92**±0.57	**1.19**±0.07	**5.20**±0.54
Ceanothus thyrsiflorus	**23.64**±0.18	**165.02**±10.28	**8.68**±0.63	**1.97**±0.10	**4.40**±0.26
Buddleja davidii	**24.02**±0.16	**164.79**±12.07	**9.17**±0.47	**1.88**±0.08	**5.01**±0.20
Cotinus coggygria	**23.20**±0.28	**183.28**±11.61	**8.95**±0.54	**1.92**±0.10	**4.80**±0.22

Table 26c. Results of statistical tests comparing the effect of low vs high plant density on gas exchange parameters. *P*-values of the tests comparing the sparse and dense populations within each of the gas exchange categories (for each study species): 1) leaf temperature (T_L, °C), 2) stomatal conductance (g_S, mmol m^{-2} s^{-1}), 3) rate of assimilation (A, µmol m^{-2} s^{-1}), 4) transpiration rate (E, mmol m^{-2} s^{-1}) and 5) photosynthetic water use efficiency (WUE$_P$), per unit leaf area and for both years of measurements.

Species	**T_L (°C)**	**g_S (mmol m^{-2} s^{-1})**	**A (µmol m^{-2} s^{-1})**	**E (mmol m^{-2} s^{-1})**	**WUE$_P$ (mmol m^{-1})**
Viburnum tinus	0.784	**0.005**	**0.004**	**<0.001**	0.276
Cistus × hybridus	0.543	0.248	0.939	0.408	0.210
Elaeagnus angustifolia	0.688	**0.009**	0.111	0.051	0.748
Ceanothus thyrsiflorus	0.349	**0.002**	**0.011**	**0.005**	0.704
Buddleja davidii	0.066	0.992	0.550	0.195	0.220
Cotinus coggygria	0.716	0.968	0.816	0.240	0.278

When looking at the effect of plant density on the gas exchange parameters in Year 1 compared to the effect it had on the same parameters in Year 2 (Tables 27a – e), it is clear that E, g_S and A were significantly more affected by plant density in shrubs placed in polyspecific populations (Year 2) compared to those placed in monospecific populations (Year 1) (Tables 27a–c). In fact, within the polyspecific populations, E, g_S and A were significantly higher for *Viburnum* and *Ceanothus* (both evergreen shrubs) when placed in dense populations, whereas E was significantly lower in *Cotinus* (Table 27a) and A was significantly lower in *Buddleja* (Table 27c) when placed in dense populations. In contrast, it would seem that T_L was most affected by plant density when shrubs were arranged in monospecific populations (Year 1) rather than in polyspecific populations (Year 2) (Table 27d), with again the evergreen species (*Viburnum* and *Ceanothus*) showing significantly higher T_L in the dense population compared to the sparse one. However, *Ceanothus* showed significantly lower T_L within the dense population when placed in a polyspecific population (Year 2), perhaps due to higher shading compared to monospecific populations of *Ceanothus*. WUE$_P$, on the other hand, was only affected by plant density within the semi-deciduous species, which presented significantly higher WUE$_P$ within the sparse populations: *Cistus* within the monospecific population in Year 1 and *Buddleja* within the polyspecific population in Year 2 (Table 27e).

Table 27a. The effect of increasing plant density on transpiration rate in monospecific vs polyspecific populations. Mean values of transpiration rate (*E*, mmol m^{-2} s^{-1}) per unit leaf area of shrubs growing in either a sparse (E_{SP}) or a dense population (E_{DP}), as measured in Year 1 (i.e. all monospecific populations) and in Year 2 (i.e. all polyspecific populations). *P* is the p-value of tests between E_{SP} and E_{DP} for each study year, in order to determine the effect of plant density on *E* and the potential differences in *E* going from Year 1 to Year 2 of the study for each species.

Species	**Year 1 (monospecific)**			**Year 2 (polyspecific)**		
	E_{SP} **(mmol m^{-2} s^{-1})**	E_{DP} **(mmol m^{-2} s^{-1})**	***P***	E_{SP} **(mmol m^{-2} s^{-1})**	E_{DP} **(mmol m^{-2} s^{-1})**	***P***
V. tinus	**0.74**±0.08	**1.07**±0.21	0.286	**0.78**±0.04	**1.09**±0.05	**<0.001**
C. × hybridus	**2.25**±0.29	**1.94**±0.31	0.526	**1.32**±0.06	**1.40**±0.09	0.428
E. angustifolia	**1.02**±0.17	**1.27**±0.20	0.436	**1.01**±0.07	**1.16**±0.06	0.106
C. thyrsiflorus	**1.47**±0.20	**1.33**±0.11	0.589	**1.62**±0.08	**2.28**±0.12	**<0.001**
B. davidii	**2.07**±0.19	**2.58**±0.15	**0.036**	**1.56**±0.05	**1.55**±0.05	0.978
C. coggygria	**1.73**±0.20	**1.87**±0.12	0.554	**2.43**±0.08	**2.02**±0.13	**0.044**

Table 27b. The effect of increasing plant density on stomatal conductance in monospecific vs polyspecific populations. Mean values of stomatal conductance (g_S, mmol m^{-2} s^{-1}) per unit leaf area of shrubs growing in either a sparse (g_{SP}) or a dense population (g_{DP}), as measured in Year 1 (i.e. all monospecific populations) and in Year 2 (i.e. all polyspecific populations). *P* is the p-value of tests between g_{SP} and g_{DP} for each study year, in order to determine the effect of plant density on g_S and the potential differences in g_S going from Year 1 to Year 2 of the study for each species.

Species	**Year 1 (monospecific)**			**Year 2 (polyspecific)**		
	g_{SP} **(mmol m^{-2} s^{-1})**	g_{DP} **(mmol m^{-2} s^{-1})**	***P***	g_{SP} **(mmol m^{-2} s^{-1})**	g_{DP} **(mmol m^{-2} s^{-1})**	***P***
V. tinus	**115.56**±12.36	**85.71**±10.25	0.087	**42.46**±2.73	**63.50**±3.92	**<0.001**
C. × hybridus	**587.75**±116.60	**417.22**±85.47	0.267	**73.96**±5.29	**74.22**±7.53	0.977
E. angustifolia	**92.56**±16.69	**130.72**±20.20	0.231	**59.12**±4.54	**68.38**±5.45	0.195
C. thyrsiflorus	**155.35**±35.71	**108.76**±11.22	0.263	**109.89**±6.45	**192.49**±12.33	**<0.001**
B. davidii	**244.83**±25.75	**279.38**±22.64	0.318	**115.53**±6.09	**110.86**±4.94	0.548
C. coggygria	**160.88**±20.05	**194.96**±20.14	0.237	**211.44**±15.85	**175.50**±14.03	0.121

Table 27c. The effect of increasing plant density on assimilation rate in monospecific vs polyspecific populations. Mean values of assimilation rate (A, μmol m^{-2} s^{-1}) per unit leaf area of shrubs growing in either a sparse (A_{SP}) or a dense population (A_{DP}), as measured in Year 1 (i.e. all monospecific populations) and in Year 2 (i.e. all polyspecific populations). P is the p-value of tests between A_{SP} and A_{DP} for each study year, in order to determine the effect of plant density on A and the potential differences in A going from Year 1 to Year 2 of the study for each species.

Species	**Year 1 (monospecific)**			**Year 2 (polyspecific)**		
	$\boldsymbol{A_{\mathrm{SP}}}$ **(μmol m^{-2} s^{-1})**	$\boldsymbol{A_{\mathrm{DP}}}$ **(μmol m^{-2} s^{-1})**	$\boldsymbol{P}$	$\boldsymbol{A_{\mathrm{SP}}}$ **(μmol m^{-2} s^{-1})**	$\boldsymbol{A_{\mathrm{DP}}}$ **(μmol m^{-2} s^{-1})**	$\boldsymbol{P}$
V. tinus	**6.86**±0.49	**7.75**±0.46	0.252	**2.35**±0.25	**3.08**±0.23	**0.031**
C. × hybridus	**16.89**±1.66	**8.57**±2.90	**0.043**	**4.80**±0.44	**4.99**±0.55	0.793
E. angustifolia	**5.79**±1.26	**9.25**±1.77	0.179	**4.58**±0.42	**5.00**±0.46	0.514
C. thyrsiflorus	**3.06**±0.60	**3.76**±0.65	0.432	**8.16**±0.36	**10.64**±0.62	**0.004**
B. davidii	**11.25**±1.16	**12.55**±1.03	0.403	**8.46**±0.35	**7.54**±0.30	**0.046**
C. coggygria	**8.09**±1.08	**9.27**±1.08	0.445	**10.46**±0.71	**9.03**±0.57	0.138

Table 27d. The effect of increasing plant density on leaf temperature in monospecific vs polyspecific populations. Mean values of leaf temperature (T_{L}, °C) per unit leaf area of shrubs growing in a sparse (T_{SP}) or a dense population (T_{DP}), as measured in Year 1 (i.e. all monospecific populations) and in Year 2 (i.e. all polyspecific populations). P is the p-value of tests between T_{SP} and T_{DP} for each study year, to determine the effect of plant density on T_{L} and potential differences in T_{L} going from Year 1 to Year 2 in each species.

Species	**Year 1 (monospecific)**			**Year 2 (polyspecific)**		
	$\boldsymbol{T_{\mathrm{SP}}}$ **(°C)**	$\boldsymbol{T_{\mathrm{DP}}}$ **(°C)**	$\boldsymbol{P}$	$\boldsymbol{T_{\mathrm{SP}}}$ **(°C)**	$\boldsymbol{T_{\mathrm{DP}}}$ **(°C)**	$\boldsymbol{P}$
V. tinus	**22.57**±0.29	**25.26**±0.27	**<0.001**	**26.34**±0.36	**26.68**±0.64	0.662
C. × hybridus	**23.08**±0.34	**23.39**±0.31	0.534	**26.83**±0.46	**28.31**±0.97	0.142
E. angustifolia	**25.57**±0.66	**24.82**±0.59	0.444	**26.00**±0.29	**26.13**±0.44	0.787
C. thyrsiflorus	**23.26**±0.20	**24.43**±0.33	**0.003**	**24.47**±0.25	**23.25**±0.19	**<0.001**
B. davidii	**23.06**±0.32	**23.87**±0.26	0.055	**23.79**±0.28	**24.09**±0.22	0.389
C. coggygria	**23.03**±0.35	**23.20**±0.38	0.741	**23.86**±0.32	**23.21**±0.39	0.289

Table 27e. The effect of increasing plant density on photosynthetic water-use efficiency in monospecific vs polyspecific populations. Mean values of photosynthetic water-use efficiency ($\mathrm{WUE_P}$, mmol m^{-1}) per unit leaf area of shrubs growing in either a sparse ($\mathrm{WUE_{SP}}$) or a dense population ($\mathrm{WUE_{DP}}$), as measured in Year 1 (i.e. all monospecific populations) and in Year 2 (i.e. all polyspecific populations). P is the p-value of tests between $\mathrm{WUE_{SP}}$ and $\mathrm{WUE_{DP}}$ for each study year, in order to determine the effect of plant density on $\mathrm{WUE_P}$ and the potential differences in $\mathrm{WUE_P}$ going from Year 1 to Year 2 in each species.

Species	**Year 1 (monospecific)**			**Year 2 (polyspecific)**		
	$\mathbf{WUE_{SP}}$ **(mmol m^{-1})**	$\mathbf{WUE_{DP}}$ **(mmol m^{-1})**	$\boldsymbol{P}$	$\mathbf{WUE_{SP}}$ **(mmol m^{-1})**	$\mathbf{WUE_{DP}}$ **(mmol m^{-1})**	$\boldsymbol{P}$
V. tinus	**9.06**±1.67	**10.21**±1.31	0.602	**2.72**±0.26	**2.67**±0.16	0.859
C. × hybridus	**5.91**±1.06	**2.55**±0.95	**0.033**	**3.43**±0.27	**3.24**±0.27	0.615
E. angustifolia	**4.90**±0.87	**6.51**±0.95	0.270	**4.76**±0.36	**4.37**±0.38	0.472
C. thyrsiflorus	**2.88**±0.64	**3.65**±0.70	0.415	**5.22**±0.20	**4.75**±0.19	0.109
B. davidii	**5.27**±0.70	**5.29**±0.56	0.984	**5.34**±0.16	**4.87**±0.14	**0.028**
C. coggygria	**5.23**±1.06	**4.98**±0.51	0.827	**4.27**±0.21	**4.69**±0.18	0.157

The effects of a small (i.e. 3×3 populations) compared to a relatively larger (i.e. 4×4 populations) population of shrubs on the different gas exchange parameters were also varied (Tables 28a–c). The parameter that was most influenced by population size was g_S (Table 28a), with the evergreen *Viburnum* and the deciduous *Elaeagnus* and *Cotinus* showing significantly higher mean values of g_S in the larger (4×4) population compared to the smaller (3×3) one, with the other three species also presenting intruiging but not significant differences in g_S between two population sizes (i.e. *P*-values between 0.111 and 0.190). Although not significant, it is also very interesting that the semi-deciduous shrubs (*Buddleja* and *Cistus*) were the only species to show a decrease in both mean g_S and *E* when placed in the larger rather than the smaller population (Table 28a). The mean values of *A* and $\mathrm{WUE_P}$ were also affected by population size in the same way again in *Buddleja* (Tables 28b and 28c), with mean values of these parameters significantly decreasing going from a small to a larger population of shrubs. The only species to be significantly affected by population size in terms of T_L was *Cotinus*, which presented significantly lower T_L when placed in a larger population (Table 28b).

Table 28a. The effect of increasing population size on transpiration rate and stomatal conductance. Mean values of transpiration rate (*E*, mmol m^{-2} s^{-1}) and stomatal conductance (g_S, mmol m^{-2} s^{-1}) per unit leaf area of shrubs growing in either a relatively small ($E_{3×3}$ and $g_{3×3}$) or a large population ($E_{4×4}$ and $g_{4×4}$), as measured in Year 2 (i.e. all polyspecific populations). *P* is the p-value of tests between both $E_{3×3}$ and $E_{4×4}$ and $g_{3×3}$ and $g_{4×4}$, to determine the effect of shrub population size on *E* and g_S for each species.

Species	**Transpiration rate, *E***			**Stomatal conductance, g_S**		
	$E_{3×3}$ **(mmol m^{-2} s^{-1})**	$E_{4×4}$ **(mmol m^{-2} s^{-1})**	***P***	$g_{3×3}$ **(mmol m^{-2} s^{-1})**	$g_{4×4}$ **(mmol m^{-2} s^{-1})**	***P***
V. tinus	**0.88**±0.06	**0.99**±0.04	0.114	**47.56**±4.18	**57.87**±3.24	**0.050**
C. × hybridus	**1.42**±0.09	**1.29**±0.05	0.208	**81.17**±7.53	**67.13**±4.50	0.111
E. angustifolia	**0.97**±0.06	**1.13**±0.07	0.111	**53.62**±3.82	**68.73**±5.08	**0.035**
C. thyrsiflorus	**1.85**±0.16	**2.13**±0.10	0.117	**145.19**±15.41	**170.33**±11.52	0.190
B. davidii	**1.62**±0.06	**1.51**±0.04	0.127	**119.67**±7.02	**108.27**±4.25	0.146
C. coggygria	**2.00**±0.12	**2.24**±0.15	0.212	**163.68**±14.80	**208.00**±15.00	**0.042**

Table 28b. The effect of increasing population size on assimilation rate and leaf temperature. Mean values of assimilation rate (*A*, µmol m^{-2} s^{-1}) and leaf temperature (T_L, °C) per unit leaf area of shrubs growing in either a relatively small ($A_{3×3}$ and $T_{3×3}$) or a large population ($A_{4×4}$ and $T_{4×4}$), as measured in Year 2 (i.e. all polyspecific populations). *P* is the p-value of tests between both $A_{3×3}$ and $A_{4×4}$ and $T_{3×3}$ and $T_{4×4}$, in order to determine the effect of shrub population size on *A* and T_L for each species.

Species	**Assimilation rate, *A***			**Leaf temperature, T_L**		
	$A_{3×3}$ **(µmol m^{-2} s^{-1})**	$A_{4×4}$ **(µmol m^{-2} s^{-1})**	***P***	$T_{3×3}$ **(°C)**	$T_{4×4}$ **(°C)**	***P***
V. tinus	**3.03**±0.29	**2.55**±0.21	0.178	**26.93**±0.44	**26.23**±0.56	0.364
C. × hybridus	**4.66**±0.49	**5.10**±0.49	0.525	**27.53**±0.86	**27.41**±0.52	0.905
E. angustifolia	**4.01**±0.39	**5.37**±0.44	**0.033**	**26.21**±0.31	**25.95**±0.35	0.612
C. thyrsiflorus	**9.30**±0.70	**9.93**±0.55	0.481	**23.96**±0.19	**23.58**±0.24	0.269
B. davidii	**8.97**±0.29	**7.26**±0.30	**<0.001**	**23.94**±0.31	**23.96**±0.20	0.967
C. coggygria	**8.84**±0.62	**10.08**±0.64	0.173	**24.12**±0.26	**22.80**±0.47	**0.021**

Table 28c. The effect of increasing population size on photosynthetic water-use efficiency. Mean values of photosynthetic water-use efficiency (WUE_P, mmol m^{-1}) per unit leaf area of shrubs growing in either a relatively small ($WUE_{3×3}$) or a large population ($WUE_{4×4}$), as calculated from the ratio of two gas exchange parameters (i.e. *A*/*E*), as measured in Year 2 (i.e. all polyspecific populations). *P* is the p-value of tests between $WUE_{3×3}$ and $WUE_{4×4}$, in order to determine the effect of shrub population size on WUE_P for each species.

Species	**Water-use efficiency, WUE_P**		
	$WUE_{3×3}$ (mmol m^{-1})	**$WUE_{4×4}$ (mmol m^{-1})**	***P***
Viburnum tinus	**3.15**±0.28	**2.40**±0.15	**0.012**
Cistus × hybridus	**3.02**±0.22	**3.67**±0.31	0.091
Elaeagnus angustifolia	**4.24**±0.43	**4.85**±0.33	0.261
Ceanothus thyrsiflorus	**5.20**±0.20	**4.76**±0.19	0.129
Buddleja davidii	**5.55**±0.16	**4.76**±0.12	**<0.001**
Cotinus coggygria	**4.36**±0.17	**4.73**±0.21	0.189

Finally, mean values of gas exchange parameters as measured in Year 2 within the categories of plant density (sparse and dense populations) and population size (3×3 and 4×4 populations) were also analysed in relation to the following four combinations: ʻsparse & 3×3’; ʻdense & 3×3’; ʻsparse & 4×4’, and ʻdense & 4×4’. This was done to extricate any possible influence of population size on plant density when examining the effects of plant density on the shrubs’ gas exchange and photosynthetic performance, and vice versa when wanting to examine the effects of population size on the same aspects. The main findings from the analysis of these combinations of data (Tables 29–33) is that: 1) both plant density and population size influenced the mean values of gas exchange parameters in the different species; 2) generally, plant density had a more significant effect on *E*, g_S and *A* while population size had a more significant effect on T_L and WUE_P; 3) going from a low to a high plant density and from a small to a larger population generally caused a positive effect on *E*, *A* and gS, while the effect on T_L and WUE_P was mixed, and 4) the effects of plant density and population size on the gas exchange parameters were species-specific and not related to either their functional group (i.e. leaf longevity, plant height) or the experimental site they grew on. With regards to the last point, *Ceanothus* was the study species that was most affected by both plant density and population size. Following closely behind were *Viburnum* and *Buddleja*, with *Viburnum* equally affected by both plant density and population size but *Buddleja* mostly affected by population size. The species least affected by either plant density or population size was *Cistus*.

Therefore, in terms of how affected the gas exchange parameters were by both plant density and population size within each species, the shrubs can be ranked as follows (from highest to lowest): *Ceanothus* > *Viburnum* = *Buddleja* > *Cotinus* > *Elaeagnus* > *Cistus*. What comes to mind when looking at this ranking is the mortality rate of the different species – the most affected species (*Ceanothus*, *Viburnum*, *Buddleja*) were also the species with the lowest mortality rates, and the least affected species (*Cistus*, *Elaeagnus*, *Cotinus*) were also the ones with the highest mortality rates, especially *Cistus*. Unfortunately, none of the gas exchange parameters correlated with mortality rate, *M* (Table C in Appendix B). However, the level of response or 'sensitivity' of a species' physiological activities – especially those closely related to a species fitness such as photosynthetic performance – to combinations of factors that can dictate shading, temperature, humidity, levels of irradiance, etc., like plant density and population size, could potentially be effective predictors of not only plant fitness but also of the ability of a species to survive long-term on a green roof. In conclusion, woody shrub species that are physiologically highly responsive to the spatial arrangements of individuals on a rooftop could also denote greater levels of long-term vigour, adaptability and survival and therefore greater suitability as green roof plants.

Table 29a. The combined effect of population size and plant density on transpiration rate. Mean values of transpiration rate (E, mmol m^{-2} s^{-1}) as combinations of the different categories tested in Year 2 ($E_{\mathrm{SP+3\times3}}$, $E_{\mathrm{DP+3\times3}}$, $E_{\mathrm{SP+4\times4}}$, and $E_{\mathrm{DP+4\times4}}$).

Species	$E_{\mathrm{SP+3\times3}}$	$E_{\mathrm{DP+3\times3}}$	$E_{\mathrm{SP+4\times4}}$	$E_{\mathrm{DP+4\times4}}$
Viburnum tinus	**0.65**±0.05	**1.10**±0.10	**0.88**±0.05	**1.09**±0.06
Cistus × hybridus	**1.40**±0.11	**1.44**±0.14	**1.25**±0.07	**1.35**±0.09
Elaeagnus angustifolia	**0.96**±0.08	**1.08**±0.10	**1.04**±0.10	**1.24**±0.07
Ceanothus thyrsiflorus	**1.31**±0.10	**2.45**±0.21	**1.96**±0.05	**2.21**±0.14
Buddleja davidii	**1.59**±0.08	**1.65**±0.09	**1.52**±0.07	**1.50**±0.05
Cotinus coggygria	**2.48**±0.11	**1.58**±0.11	**2.32**±0.09	**2.15**±0.20

Table 29b. Results of statistical tests comparing the effects of plant density and population size on transpiration rate. *P*-values of the tests between categories of mean transpiration rate (E, mmol m^{-2} s^{-1}) in Year 2, in terms of: 1) the effect of plant density within each population size, 3×3 ($E_{\mathrm{SP+3\times3}}$ vs $E_{\mathrm{DP+3\times3}}$) & 4×4 ($E_{\mathrm{SP+4\times4}}$ vs $E_{\mathrm{DP+4\times4}}$); and 2) the effect of population size within each type of plant density, SP ($E_{\mathrm{SP+3\times3}}$ vs $E_{\mathrm{SP+4\times4}}$) & DP ($E_{\mathrm{DP+3\times3}}$ vs $E_{\mathrm{DP+4\times4}}$).

	Plant density		**Population size**	
Species	$E_{\mathrm{SP+3\times3}}$ **vs** $E_{\mathrm{DP+3\times3}}$	$E_{\mathrm{SP+4\times4}}$ **vs** $E_{\mathrm{DP+4\times4}}$	$E_{\mathrm{SP+3\times3}}$ **vs** $E_{\mathrm{SP+4\times4}}$	$E_{\mathrm{DP+3\times3}}$ **vs** $E_{\mathrm{DP+4\times4}}$
Viburnum tinus	**<0.001**	**0.013**	**0.004**	0.884
Cistus × hybridus	0.806	0.390	0.249	0.601
Elaeagnus angustifolia	0.348	0.137	0.546	0.204
Ceanothus thyrsiflorus	**<0.001**	0.256	**<0.001**	0.349
Buddleja davidii	0.674	0.853	0.484	0.150
Cotinus coggygria	**<0.001**	0.684	0.326	**0.045**

Table 30a. The combined effect of population size and plant density on stomatal conductance. Mean values of stomatal conductance (g_{S}, mmol m^{-2} s^{-1}) as combinations of the different categories tested in Year 2 ($g_{\mathrm{SP+3\times3}}$, $g_{\mathrm{DP+3\times3}}$, $g_{\mathrm{SP+4\times4}}$, and $g_{\mathrm{DP+4\times4}}$).

Species	$g_{\mathrm{SP+3\times3}}$	$g_{\mathrm{DP+3\times3}}$	$g_{\mathrm{SP+4\times4}}$	$g_{\mathrm{DP+4\times4}}$
V. tinus	**35.63**±3.57	**59.48**±6.89	**47.88**±3.78	**66.15**±4.68
C. × hybridus	**77.42**±9.17	**88.86**±12.15	**71.20**±6.17	**60.33**±6.06
E. angustifolia	**51.86**±4.81	**74.83**±11.01	**64.38**±6.96	**74.35**±7.41
C. thyrsiflorus	**90.43**±7.89	**204.15**±20.91	**130.85**±6.63	**187.43**±15.30
B. davidii	**119.04**±9.77	**110.11**±9.75	**103.77**±6.54	**111.27**±5.60
C. coggygria	**214.58**±21.78	**111.86**±8.55	**205.17**±21.55	**201.29**±19.00

Table 30b. Results of statistical tests comparing the effects of plant density and population size on stomatal conductance. *P*-values of the tests between categories of mean stomatal conductance (g_{S}, mmol m^{-2} s^{-1}) in Year 2, in terms of: 1) the effect of plant density within each population size, 3×3 ($g_{\mathrm{SP+3\times3}}$ vs $g_{\mathrm{DP+3\times3}}$) & 4×4 ($g_{\mathrm{SP+4\times4}}$ vs $g_{\mathrm{DP+4\times4}}$); and 2) the effect of population size within each type of plant density, SP ($g_{\mathrm{SP+3\times3}}$ vs $g_{\mathrm{SP+4\times4}}$) & DP ($g_{\mathrm{DP+3\times3}}$ vs $g_{\mathrm{DP+4\times4}}$).

	Plant density		**Population size**	
Species	$g_{\mathrm{SP+3\times3}}$ **vs** $g_{\mathrm{DP+3\times3}}$	$g_{\mathrm{SP+4\times4}}$ **vs** $g_{\mathrm{DP+4\times4}}$	$g_{\mathrm{SP+3\times3}}$ **vs** $g_{\mathrm{SP+4\times4}}$	$g_{\mathrm{DP+3\times3}}$ **vs** $g_{\mathrm{DP+4\times4}}$
Viburnum tinus	**0.003**	**0.004**	**0.024**	0.409
Cistus × hybridus	0.452	0.246	0.564	0.057
Elaeagnus angustifolia	**0.032**	0.334	0.176	0.971
Ceanothus thyrsiflorus	**<0.001**	**0.022**	**<0.001**	0.540
Buddleja davidii	0.523	0.392	0.194	0.912
Cotinus coggygria	**<0.001**	0.923	0.789	**0.001**

Table 31a. The combined effect of population size and plant density on assimilation rate. Mean values of assimilation rate (A, µmol m^{-2} s^{-1}) as combinations of the different categories tested in Year 2 ($A_{\mathrm{SP+3\times3}}$, $A_{\mathrm{DP+3\times3}}$, $A_{\mathrm{SP+4\times4}}$, and $A_{\mathrm{DP+4\times4}}$).

Species	$A_{\mathrm{SP+3\times3}}$	$A_{\mathrm{DP+3\times3}}$	$A_{\mathrm{SP+4\times4}}$	$A_{\mathrm{DP+4\times4}}$
Viburnum tinus	**2.58**±0.42	**3.34**±0.39	**2.18**±0.30	**2.85**±0.29
Cistus × hybridus	**4.06**±0.56	**5.30**±0.80	**5.42**±0.65	**4.59**±0.75
Elaeagnus angustifolia	**3.83**±0.46	**5.96**±0.82	**5.26**±0.64	**5.34**±0.60
Ceanothus thyrsiflorus	**7.40**±0.49	**11.35**±1.13	**8.98**±0.46	**10.34**±0.75
Buddleja davidii	**9.10**±0.38	**8.32**±0.39	**7.50**±0.49	**7.10**±0.39
Cotinus coggygria	**10.67**±0.94	**6.91**±0.50	**10.05**±1.09	**9.83**±0.78

Table 31b. Results of statistical tests comparing the effects of plant density and population size on assimilation rate. P-values of the tests between categories of mean assimilation rate (A, μmol m^{-2} s^{-1}) in Year 2, in terms of: 1) the effect of plant density within each population size, 3×3 ($A_{\mathrm{SP+3\times3}}$ vs $A_{\mathrm{DP+3\times3}}$) & 4×4 ($A_{\mathrm{SP+4\times4}}$ vs $A_{\mathrm{DP+4\times4}}$); and 2) the effect of population size within each type of plant density, SP ($A_{\mathrm{SP+3\times3}}$ vs $A_{\mathrm{SP+4\times4}}$) & DP ($A_{\mathrm{DP+3\times3}}$ vs $A_{\mathrm{DP+4\times4}}$).

	Plant density		**Population size**	
Species	$A_{\mathrm{SP+3\times3}}$ **vs** $A_{\mathrm{DP+3\times3}}$	$A_{\mathrm{SP+4\times4}}$ **vs** $A_{\mathrm{DP+4\times4}}$	$A_{\mathrm{SP+3\times3}}$ **vs** $A_{\mathrm{SP+4\times4}}$	$A_{\mathrm{DP+3\times3}}$ **vs** $A_{\mathrm{DP+4\times4}}$
Viburnum tinus	0.197	0.109	0.422	0.318
Cistus × hybridus	0.207	0.419	0.126	0.535
Elaeagnus angustifolia	**0.019**	0.927	0.097	0.548
Ceanothus thyrsiflorus	**0.003**	0.261	**0.026**	0.465
Buddleja davidii	0.163	0.524	**0.015**	**0.046**
Cotinus coggygria	**0.001**	0.896	0.695	**0.012**

Table 32a. The combined effect of population size and plant density on leaf temperature. Mean values of leaf temperature (T_{L}, °C) as combinations of the different categories tested in Year 2 ($T_{\mathrm{SP+3\times3}}$, $T_{\mathrm{DP+3\times3}}$, $T_{\mathrm{SP+4\times4}}$, and $T_{\mathrm{DP+4\times4}}$).

Species	$T_{\mathrm{SP+3\times3}}$	$T_{\mathrm{DP+3\times3}}$	$T_{\mathrm{SP+4\times4}}$	$T_{\mathrm{DP+4\times4}}$
Viburnum tinus	**26.36**±0.54	**27.49**±0.69	**26.33**±0.48	**26.15**±0.94
Cistus × hybridus	**26.98**±0.56	**26.55**±0.63	**26.72**±0.71	**28.57**±0.67
Elaeagnus angustifolia	**26.38**±0.32	**24.62**±0.62	**25.72**±0.44	**26.25**±0.59
Ceanothus thyrsiflorus	**24.07**±0.28	**23.83**±0.25	**24.91**±0.39	**23.00**±0.23
Buddleja davidii	**23.19**±0.44	**24.82**±0.33	**24.36**±0.30	**23.69**±0.26
Cotinus coggygria	**23.93**±0.36	**24.28**±0.37	**23.70**±0.70	**22.58**±0.54

Table 32b. Results of statistical tests comparing the effects of plant density and population size on leaf temperature. P-values of the tests between categories of mean leaf temperature (T_{L}, °C) in Year 2, in terms of: 1) the effect of plant density within each population size, 3×3 ($T_{\mathrm{SP+3\times3}}$ vs $T_{\mathrm{DP+3\times3}}$) & 4×4 ($T_{\mathrm{SP+4\times4}}$ vs $T_{\mathrm{DP+4\times4}}$); and 2) the effect of population size within each type of plant density, SP ($T_{\mathrm{SP+3\times3}}$ vs $T_{\mathrm{SP+4\times4}}$) & DP ($T_{\mathrm{DP+3\times3}}$ vs $T_{\mathrm{DP+4\times4}}$).

	Plant density		**Population size**	
Species	$T_{\mathrm{SP+3\times3}}$ **vs** $T_{\mathrm{DP+3\times3}}$	$T_{\mathrm{SP+4\times4}}$ **vs** $T_{\mathrm{DP+4\times4}}$	$T_{\mathrm{SP+3\times3}}$ **vs** $T_{\mathrm{SP+4\times4}}$	$T_{\mathrm{DP+3\times3}}$ **vs** $T_{\mathrm{DP+4\times4}}$
Viburnum tinus	0.205	0.876	0.963	0.308
Cistus × hybridus	0.613	0.084	0.780	**0.036**
Elaeagnus angustifolia	**0.008**	0.456	0.257	0.087
Ceanothus thyrsiflorus	0.527	**<0.001**	0.090	**0.041**
Buddleja davidii	**0.007**	0.105	**0.034**	**0.012**
Cotinus coggygria	0.512	0.336	0.745	**0.033**

Table 33a. The combined effect of population size and plant density on photosynthetic water-use efficiency. Mean values of photosynthetic water-use efficiency (WUE$_{P}$, mmol m^{-1}) as combinations of the different categories tested in Year 2 (WUE$_{SP+3\times3}$, WUE$_{DP+3\times3}$, WUE$_{SP+4\times4}$, and WUE$_{DP+4\times4}$).

Species	**WUE$_{SP+3\times3}$**	**WUE$_{DP+3\times3}$**	**WUE$_{SP+4\times4}$**	**WUE$_{DP+4\times4}$**
Viburnum tinus	**3.32**±0.47	**2.97**±0.30	**2.26**±0.26	**2.76**±0.21
Cistus × hybridus	**2.72**±0.24	**3.36**±0.36	**4.02**±0.42	**3.09**±0.42
Elaeagnus angustifolia	**4.26**±0.57	**4.20**±0.64	**5.16**±0.46	**4.46**±0.48
Ceanothus thyrsiflorus	**5.77**±0.23	**4.59**±0.25	**4.62**±0.26	**4.82**±0.25
Buddleja davidii	**5.88**±0.20	**5.19**±0.24	**4.85**±0.19	**4.70**±0.17
Cotinus coggygria	**4.25**±0.27	**4.45**±0.22	**4.30**±0.38	**4.83**±0.25

Table 33b. Results of statistical tests comparing the effects of plant density and population size on photosynthetic water-use efficiency. *P*-values of the tests between categories of mean photosynthetic water-use efficiency (WUE$_{P}$, mmol m^{-1}) in Year 2, in terms of: 1) the effect of plant density within each population size, 3×3 (WUE$_{SP+3\times3}$ vs WUE$_{DP+3\times3}$) & 4×4 (WUE$_{SP+4\times4}$ vs WUE$_{DP+4\times4}$); and 2) the effect of population size within each type of plant density, SP (WUE$_{SP+3\times3}$ vs WUE$_{SP+4\times4}$) & DP (WUE$_{DP+3\times3}$ vs WUE$_{DP+4\times4}$).

	Plant density		**Population size**	
Species	**WUE$_{SP+3\times3}$ vs WUE$_{DP+3\times3}$**	**WUE$_{SP+4\times4}$ vs WUE$_{DP+4\times4}$**	**WUE$_{SP+3\times3}$ vs WUE$_{SP+4\times4}$**	**WUE$_{DP+3\times3}$ vs WUE$_{DP+4\times4}$**
Viburnum tinus	0.538	0.127	**0.041**	0.567
Cistus × hybridus	0.140	0.143	**0.013**	0.634
Elaeagnus angustifolia	0.949	0.301	0.220	0.747
Ceanothus thyrsiflorus	**0.002**	0.625	**0.003**	0.572
Buddleja davidii	**0.031**	0.551	**<0.001**	0.094
Cotinus coggygria	0.575	0.321	0.923	0.297

A.4.2.2 Effects of stress on plant water status

Leaf water status is a reflection of soil water status (i.e. at field capacity vs water deficit) and is regulated by stomatal closure and lower conductance of water and CO_2 as a result of species-specific drought resistance or avoidance strategies (Jones 2007). Drought stress can lead to progressively lower gas exchange and CO_2 assimilation rates, which in turn can cause metabolic impairment and in the longer term a reduction in root and shoot growth, leaf size, water use efficiency (WUE) and productivity (Medrano et al. 2002, Anjum et al. 2011). In particular, progressively negative leaf water potentials (Ψ_L) in response to drought can induce a greater transport of assimilates to roots rather than to leaves, thereby reducing leaf growth, in the attempt to reduce the ratio of evapotranspirative surfaces (Lambers, Chapin and Pons 2008).

There are many ways of measuring leaf water status, depending on the experimental objectives. In the present study, several physiological parameters (RWC_L, Ψ_L, SMC and ET), discussed in subsequent sections, were investigated to understand the effects of rooftop environment on leaf water content and how potential changes in these interconnected aspects of plant fitness may have affected the study species' overall survival, growth and physiology, thereby identifying the breadth of adaptive strategies to stress and drought in the different shrubs. Correlations between these and other parameters investigated throughout the study may also indicate possible relationships linking physiological and morphological characteristics of the shrubs. Any significant associations of this type can facilitate their best use as proxies in the selection process for green roof shrubs.

A.4.2.2.1 Leaf relative water content (RWC_L)

Leaf relative water content (RWC) estimates the water content of leaf tissue at the time of sampling relative to maximum water content at full turgidity (Tanentzap, Stempel and Ryser 2015). In the present study, leaves were sampled and measured throughout the three years of the study (Section 2.5.2.1) and RWC was determined using the original formula by Barrs and Weatherley (1962). Depending on species, values of RWC can range between 98% or more in fully turgid and transpiring leaves to about 30-40% in extremely dry and dying leaves. However, the reduction of RWC to just 75% can significantly reduce rates of photosynthetic assimilation (A), stomatal conductance (g_S), cell functioning and even cause cell death (Lawlor and Cornic 2002). Even a small reduction in RWC can therefore signal a decline in fitness.

Mean RWC for the entire study (RWC_L) was significantly different ($P<0.001$) amongst the study species, with *Viburnum* showing the highest mean values of RWC_L and *Elaeagnus* the lowest (Table

34). With the exception of *Ceanothus*, all shrubs saw a significant change in RWC through the years going from Year 1 (RWC$_{1}$) to Year 3 (RWC$_{3}$). All species save for *Ceanothus* experienced a significant dip in RWC going from Year 1 to Year 2 (Table 35) and, although all species saw an increase in RWC in the last year of the study (RWC$_{3}$), only *Elaeagnus* (*P*=0.010) and *Cotinus* (*P*=0.048) saw a significant recovery.

Table 34. Change in leaf relative water content over time. For each species, the mean values of leaf relative water content for each year of the study (RWC$_{1}$, RWC$_{2}$ and RWC$_{3}$), the *p*-values associated to the differences tested between the mean values for each study year and total relative leaf water content (RWC$_{L}$).

Species	**RWC$_{1}$ (%)**	**RWC$_{2}$ (%)**	**RWC$_{3}$ (%)**	***P*-value**	**RWC$_{L}$ (%)**
Viburnum tinus	**95.56**±0.19	**89.22**±1.18	**91.27**±0.43	**<0.001**	**92.38**±0.42
Cistus × hybridus	**89.38**±0.35	**76.91**±1.73	**76.94**±1.18	**<0.001**	**81.64**±0.85
Elaeagnus angustifolia	**82.28**±1.08	**71.19**±1.84	**76.41**±1.02	**<0.001**	**77.31**±0.83
Ceanothus thyrsiflorus	**89.74**±0.49	**90.47**±0.69	**89.60**±0.38	0.483	**89.87**±0.29
Buddleja davidii	**87.21**±0.62	**81.54**±0.70	**81.74**±0.51	**<0.001**	**83.76**±0.43
Cotinus coggygria	**94.33**±0.37	**88.92**±0.89	**91.03**±0.62	**<0.001**	**91.75**±0.40

Despite a significant difference between mean values of RWC between shrubs grown in monospecific populations (RWC$_{MP}$) in Year 1 and those in polyspecific populations (RWC$_{PP}$) in Year 2 of the study (Table 35), the direct comparison of the effects of species mixture on mean values of RWC in Year 3 did not result in any significant differences between the two categories in any of the species. Therefore, species mixture did not have a significant effect on the RWC$_{L}$ of the shrubs.

Table 35. The effect of species mixture on leaf relative water content over time. Comparison of mean leaf relative water content between populations of MP (RWC$_{MP}$) and PP (RWC$_{PP}$) shrubs, divided by species and year of study (Year 1, 2 & 3). *P* is the *p*-value of the test (within each species) between RWC$_{MP}$ in Year 1 and RWC$_{PP}$ in Year 2, and the test between RWC$_{MP}$ and RWC$_{PP}$ in Year 3.

	Year 1	**Year 2**		**Year 3**		
Species	**RWC$_{MP}$**	**RWC$_{PP}$**	***P***	**RWC$_{MP}$**	**RWC$_{PP}$**	***P***
Viburnum tinus	**95.56**±0.19	**89.22**±1.18	**<0.001**	**90.72**±0.69	**91.56**±0.55	0.362
Cistus × hybridus	**89.38**±0.35	**76.91**±1.73	**<0.001**	**76.87**±2.09	**76.97**±1.46	0.966
E. angustifolia	**82.28**±1.08	**71.19**±1.84	**<0.001**	**77.41**±2.10	**75.89**±1.12	0.484
C. thyrsiflorus	**89.74**±0.49	**90.47**±0.69	0.379	**89.52**±0.81	**89.64**±0.42	0.879
Buddleja davidii	**87.21**±0.62	**81.54**±0.70	**<0.001**	**82.08**±0.90	**81.57**±0.62	0.644
Cotinus coggygria	**94.33**±0.37	**88.92**±0.89	**<0.001**	**91.07**±0.76	**91.02**±0.87	0.968

When comparing the effect of plant density on the species' RWC in equivalent-sized populations (i.e. 27 individuals in units of 3×3), the only species to be significantly affected was *Buddleja* in Year

1 growing in a monospecific population, whereas no other species including *Buddleja* was affected by species density in the polyspecific population (Table 36). The same can be said when comparing the effect of plant density in shrubs placed in all sizes of polyspecific populations (i.e. both 3×3 and 4×4) (Table 37) and all combinations of population size and plant density (i.e. $RWC_{SP+3\times3}$, $RWC_{DP+3\times3}$, $RWC_{SP+4\times4}$ and $RWC_{DP+4\times4}$) in Year 2 (Tables 38a and 38b). While plant density may not have affected RWC significantly, population size seemed to have affected *Cotinus*, which showed a significant increase in RWC (*P*=0.032) going from a smaller population ($RWC_{3\times3}$) to a larger population ($RWC_{4\times4}$), while a larger population size had the reverse effect on *Buddleja* (*P*=0.003) (Table 37). Again, only *Buddleja* seemed to be affected by population size within the various combinations in Year 2, showing a significant decrease (*P*=0.013) in mean RWC only within the combination 'larger population with sparse plant density' ($RWC_{SP+4\times4}$) compared to the combination 'smaller population with sparse plant density ($RWC_{SP+3\times3}$) (Tables 38a and 38b). Due to the contradictory nature of the results in this section, it may be wiser to conclude that neither species mixure, plant density nor population size of the shrubs had any effect on mean values of RWC throughout the study.

Table 36. The effect of increasing plant density on leaf relative water content in monospecific vs polyspecific populations. Comparison of mean leaf relative water content per species between sparse (RWC_{SP}) and dense (RWC_{DP}) populations. Data divided by: Year 1 (shrubs in MP & 3×3 size) and Year 2 (shrubs in PP & only in 3×3 size). *P* is the *p*-value of the test between RWC_{SP} and RWC_{DP} in Year 1 and in Year 2 of the study.

	Year 1 (MP, 3×3)			**Year 2 (PP, 3×3)**		
Species	**RWC_{SP}**	**RWC_{DP}**	***P***	**RWC_{SP}**	**RWC_{DP}**	***P***
Viburnum tinus	**95.39**±0.29	**95.73**±0.24	0.365	**90.86**±2.36	**91.35**±1.54	0.865
Cistus × hybridus	**89.18**±0.56	**89.59**±0.49	0.570	**80.68**±3.33	**77.29**±3.05	0.469
Elaeagnus angustifolia	**80.80**±1.41	**83.76**±1.60	0.173	**74.81**±3.35	**71.97**±3.43	0.567
Ceanothus thyrsiflorus	**89.18**±0.70	**90.30**±0.67	0.257	**89.64**±1.54	**88.74**±1.43	0.677
Buddleja davidii	**85.28**±0.63	**89.15**±0.89	**<0.001**	**84.29**±1.45	**83.27**±0.81	0.554
Cotinus coggygria	**93.95**±0.38	**94.72**±0.62	0.294	**89.33**±1.17	**84.17**±2.91	0.131

Table 37. The effect of increasing population size and plant density on leaf relative water content in polyspecific populations. Comparison of mean leaf relative water content per species in Year 2 (comprised of only PP), between: 1) small population size (RWC$_{3\times3}$) and big population size (RWC$_{4\times4}$), and 2) low (RWC$_{SP}$) and high (RWC$_{DP}$) plant density. *P* is the *p*-value per species of the test between RWC$_{3\times3}$ and RWC$_{4\times4}$ and between RWC$_{SP}$ and RWC$_{DP}$.

	Year 2 (PP)					
Species	**RWC$_{3\times3}$**	**RWC$_{4\times4}$**	***P***	**RWC$_{SP}$**	**RWC$_{DP}$**	***P***
Viburnum tinus	**91.10**±1.34	**87.80**±1.75	0.170	**89.38**±1.62	**89.05**±1.77	0.892
Cistus × hybridus	**78.98**±2.21	**75.35**±2.52	0.309	**80.15**±1.47	**73.67**±2.94	0.060
Elaeagnus angustifolia	**73.39**±2.33	**69.54**±2.70	0.309	**71.21**±2.40	**71.16**±2.88	0.990
Ceanothus thyrsiflorus	**89.19**±1.01	**91.42**±0.90	0.112	**90.59**±0.99	**90.34**±1.01	0.857
Buddleja davidii	**83.78**±0.81	**79.86**±0.86	**0.003**	**81.57**±1.02	**81.51**±0.99	0.968
Cotinus coggygria	**86.75**±1.69	**90.55**±0.72	**0.032**	**90.40**±0.77	**87.44**±1.54	0.097

Table 38a. The combined effect of population size and plant density on leaf relative water content. Mean values of leaf relative water content as combinations of the different categories tested in Year 2 (RWC$_{SP+3\times3}$, RWC$_{DP+3\times3}$, RWC$_{SP+4\times4}$, and RWC$_{DP+4\times4}$).

Species	**RWC$_{SP+3\times3}$**	**RWC$_{DP+3\times3}$**	**RWC$_{SP+4\times4}$**	**RWC$_{DP+4\times4}$**
Viburnum tinus	**90.86**±2.36	**91.35**±1.54	**88.28**±2.26	**87.33**±2.82
Cistus × hybridus	**80.68**±3.33	**77.29**±3.05	**79.75**±1.00	**70.96**±4.55
Elaeagnus angustifolia	**74.81**±3.35	**71.97**±3.43	**68.51**±3.21	**70.56**±4.54
Ceanothus thyrsiflorus	**89.64**±1.54	**88.74**±1.43	**91.31**±1.31	**91.53**±1.31
Buddleja davidii	**84.29**±1.45	**83.27**±0.81	**79.53**±0.92	**80.19**±1.50
Cotinus coggygria	**89.33**±1.17	**84.17**±2.91	**91.20**±0.98	**89.90**±1.05

Table 38b. Results of statistical tests comparing the effects of plant density and population size on leaf relative water content. *P*-values of the tests between categories of mean leaf relative water content in Year 2, in terms of: 1) the effect of plant density within each population size, 3×3 (RWC$_{SP+3\times3}$ vs RWC$_{DP+3\times3}$) & 4×4 (RWC$_{SP+4\times4}$ vs RWC$_{DP+4\times4}$); and 2) the effect of population size within each type of plant density, SP (RWC$_{SP+3\times3}$ vs RWC$_{SP+4\times4}$) & DP (RWC$_{DP+3\times3}$ vs RWC$_{DP+4\times4}$).

	Plant density		**Population size**	
Species	**RWC$_{SP+3\times3}$ vs RWC$_{DP+3\times3}$**	**RWC$_{SP+4\times4}$ vs RWC$_{DP+4\times4}$**	**RWC$_{SP+3\times3}$ vs RWC$_{SP+4\times4}$**	**RWC$_{DP+3\times3}$ vs RWC$_{DP+4\times4}$**
Viburnum tinus	0.865	0.798	0.452	0.279
Cistus × hybridus	0.469	0.080	0.766	0.305
Elaeagnus angustifolia	0.567	0.719	0.206	0.819
Ceanothus thyrsiflorus	0.677	0.905	0.426	0.179
Buddleja davidii	0.554	0.713	**0.013**	0.129
Cotinus coggygria	0.131	0.383	0.244	0.061

A.4.2.2.2 Bulk leaf water potential (Ψ_L)

A common technique used for measuring plant water status is that of obtaining the bulk water potential of a leaf (Ψ_L), defined as the negative hydrostatic pressure at which the xylem in the leaf was under at the time of sampling (Lambers, Chapin and Pons 2008). Water in the xylem is constantly under tension in transpiring plants (Saliendra, Sperry and Comstock 1995). The water potential difference across a leaf (i.e. between stomata and leaf petiole/veins) is in fact the impetus behind water transport (Sack and Holbrook 2006), a process driven by the negative suction tension caused by capillary forces between water molecules in the xylem during plant transpiration (Lambers, Chapin and Pons 2008). Moreover, low water availability as signalled by plant hormones in the roots can cause water potentials in leaves to drop further, thereby inducing stomatal closure (Sperry 2000, Medrano et al. 2002) and preventing the plant from reaching critically low water potentials that could compromise fitness (Saliendra, Sperry and Comstock 1995). Nevertheless, the precise water potential at which stomatal closure is triggered is species-specific and depends on the stress history and the environmental and growing conditions (e.g. rooftop, size of container) of the individual plant (Medrano et al. 2002). Ψ_L can thereby indicate the physiological drought experienced by a species and its drought tolerance, especially when measured in the dry season and at peak stomatal conductance at mid-morning to midday (Brodribb and Cochard 2009).

For these reasons, the mean values of Ψ_L for each species were measured using a pressure chamber during the first year of the study, in which all shrubs were placed in monospecific populations (see Section 2.5.2.2 for details on methods). Results from this data collection can be viewed in Table 39. The soil moisture content (SMC) of each plant from which leaves were sampled (Table 40) and the maximum quantum yield (QY) of each sampled leaf (Table 41) were also measured before every sampling session (morning, midday and late afternoon), in order to relate the Ψ_L measurements to assess fitness at the time of sampling and any possible water stress experienced by the shrubs. The days chosen for sampling (10 & 11 August 2016) were ideal for undertaking Ψ_L measurements, because the weather had been very warm and dry for weeks. Despite the dry weather and no irrigation, values of mean SMC were still found to be significantly different between the various shrub species ($P<0.001$), indicating species-specific water use (Fig. 14). In particular, the evergreen shrubs (*Viburnum* and *Ceanothus*) had the highest mean values of SMC (0.255 $m^3 m^{-3}$ and 0.190 $m^3 m^{-3}$, respectively), reflecting the predisposition of evergreen woody species, especially sclerophylls like *Viburnum*, to be the most water-efficient (McCarthy, Pataki and Jenerette 2011). In fact, *Viburnum* had the highest photosynthetic water-use efficiency (WUE_P) in the first year of the study. However, *Viburnum*'s WUE_P declined drastically after that (Section 3.2.1.2), possibly as a result of being rearranged into polyspecific populations (i.e. higher shading) or as an effect of intensified growth (Section 3.1.1.2), where water use may have had to increase in order to supplement higher biomass gain for greater mechanical support and additional foliage density in response to the increasingly harsh rooftop conditions (e.g. exposure to wind, intense solar radiation).

Unsurprisingly then, the mean values of both Ψ_L and QY were also significantly different between the study species ($P<0.001$, Fig. 15 and Fig. 16). However, what *was* surprising was the fact that Ψ_L was not significantly correlated to the mean values of SMC as measured on the day of data collection ($P=0.659$), and even less so to the mean values of SMC as measured in the summer months of Year 1 ($P=0.900$). Ψ_L was also not significantly correlated to the mean values of QY as measured in the summer months of Year 1 ($P=0.775$), however the correlation with mean values of QY as measured on the day of data collection ($P=0.224$), though not significant, may be a better indicator of how stress may have been influencing the Ψ_L of the different species. Moreover, the following parameters had marginally better correlations with Ψ_L and may therefore have had a greater influence over it, despite again not being significant: 1) the mean values of leaf temperature, (T_L, $P=0.065$), leaf relative water content (RWC_L, $P=0.107$) and leaf mass per area (LMA_T, $P=0.171$) as measured in Year 1, as well as 2) the mean values of stomatal conductance (g_S, $P=0.162$), transpiration rate (E, $P=0.170$) and branch length ($P=0.228$) as measured throughout the entire study (Tables B and C in Appendix B). According to these correlations, Ψ_L became more negative as T_L and branch length increased and as RWC_L, g_S, E and LMA_T decreased – for the tall shrubs *Elaeagnus* and *Buddleja* (i.e. long branches), which had thinner leaves (i.e. low LMA_T) with lower succulence (i.e. low RWC_L) and thus prone to overheating when under water stress (i.e. high T_L), this may be the case; in fact, their leaves reached the most negative values of Ψ_L out of the study species. However, the correlations were not strong enough to confirm these associations.

With regard to the effect of plant density on mean values of Ψ_L (Table 39), *Buddleja* was the only species to have significantly less negative values of Ψ_L ($P=0.018$) when placed in a dense population of shrubs (–0.729 MPa) compared to when it was placed in a sparse one (–0.858 MPa). In other words, the *Buddleja* plants were significantly less stressed when placed in a denser population of shrubs. Though not significant differences, *Viburnum* ($P=0.067$) and *Cotinus* ($P=0.092$) also had less negative values of Ψ_L in the denser population, while *Elaeagnus* ($P=0.169$) and *Cistus* ($P=0.247$) were the only species to show the opposite trend of having more negative values of Ψ_L in the denser populations rather than in the sparse ones. In fact, *Elaeagnus* and *Cistus* were also the only species to have significantly lower mean values of QY in the dense populations compared to the sparse ones (Table 41), as well as the lowest values of SMC amongst the species (Table 40). It may be that in these species, being placed in a denser population may have had a negative rather than a positive effect on both their photosynthetic efficiency (QY) and their water use (SMC), ultimately caused by increased xylem tension (i.e. more negative Ψ_L). In fact, *Elaeagnus* and *Cistus* also had the lowest mean values of relative leaf water content, RWC_L (Table 34, in Section 3.2.2.1), especially when placed in a small and dense population and increasingly so when placed in a large and dense population (Table 38a). *Elaeagnus* and *Cistus'* mean values of stomatal conductance (g_S) and consequently transpiration rate (E) also increased going from low to high plant density (Tables 26a and 26b, Section 3.2.1.2), though not significantly in *Cistus* (Table 26c), thereby potentially explaining the more negative values of Ψ_L in these species when placed in populations with higher plant density.

Table 39. Total mean values of bulk leaf water potentials and the effect of plant density on the same parameter. Bulk leaf water potential (Ψ_L, –MPa) for each species as measured on the days of data collection (10 & 11 August 2016) and expressed as the total mean, the mean for shrubs growing in the sparse population and the mean for shrubs growing in the dense population. The *p*-values are the results of the analysis testing the differences between the mean values of Ψ_L for the shrubs growing in the sparse population and the mean values of Ψ_L for those growing in the dense population, within each species.

	Ψ_L (–MPa)			
Species	**Total**	**Sparse**	**Dense**	***P*-value**
Viburnum tinus	**0.775**±0.027	**0.825**±0.028	**0.725**±0.045	0.067
Cistus × hybridus	**0.749**±0.030	**0.714**±0.035	**0.783**±0.047	0.247
Elaeagnus angustifolia	**1.071**±0.049	**1.003**±0.064	**1.139**±0.073	0.169
Ceanothus thyrsiflorus	**0.628**±0.015	**0.643**±0.023	**0.612**±0.020	0.327
Buddleja davidii	**0.794**±0.028	**0.858**±0.029	**0.729**±0.043	**0.018**
Cotinus coggygria	**0.678**±0.023	**0.718**±0.037	**0.639**±0.027	0.092

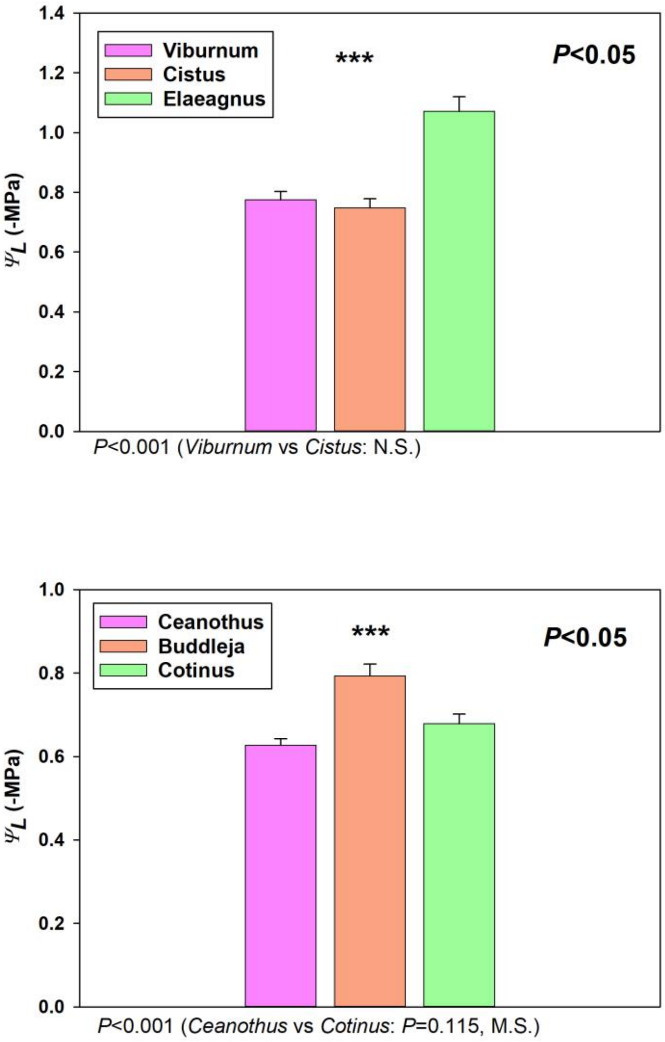
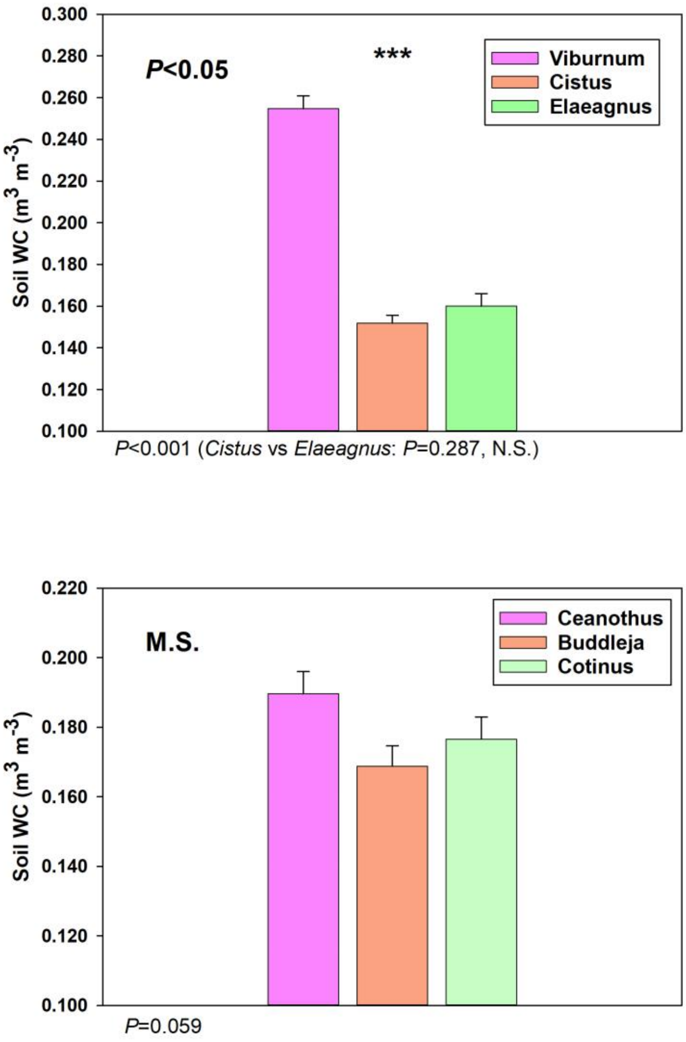


Figure 14. The taller shrubs (*Elaeagnus* and *Buddleja*) reached significantly more negative values of bulk leaf water potential. Vertical bar graphs with error bars comparing the total mean values of bulk leaf water potential (Ψ_L, –MPa) for each species growing on the Lower Hicks roof (above) and on the Hadfield roof garden (below), as measured during the first summer of the study.

Table 40. Total mean values of volumetric soil moisture content and the effect of plant density on the same parameter. Soil moisture content (SMC, $m^3\ m^{-3}$) for each species as measured on the days of data collection (10 & 11 August 2016) and expressed as the total mean, the mean for shrubs growing in the sparse population and the mean for shrubs growing in the dense population. The *p*-values are the results of the analysis testing the differences between the mean values of SMC for the shrubs growing in the sparse population and the mean values of SMC for those growing in the dense population, within each species.

	SMC ($m^3\ m^{-3}$)			
Species	**Total**	**Sparse**	**Dense**	***P*-value**
Viburnum tinus	**0.255**±0.006	**0.280**±0.007	**0.230**±0.008	**<0.001**
Cistus × hybridus	**0.152**±0.004	**0.150**±0.006	**0.154**±0005	0.600
Elaeagnus angustifolia	**0.160**±0.006	**0.149**±0.007	**0.171**±0.010	0.076
Ceanothus thyrsiflorus	**0.190**±0.006	**0.181**±0.009	**0.198**±0.009	0.167
Buddleja davidii	**0.169**±0.006	**0.169**±0.009	**0.169**±0.007	0.987
Cotinus coggygria	**0.177**±0.006	**0.173**±0.009	**0.181**±0.009	0.541



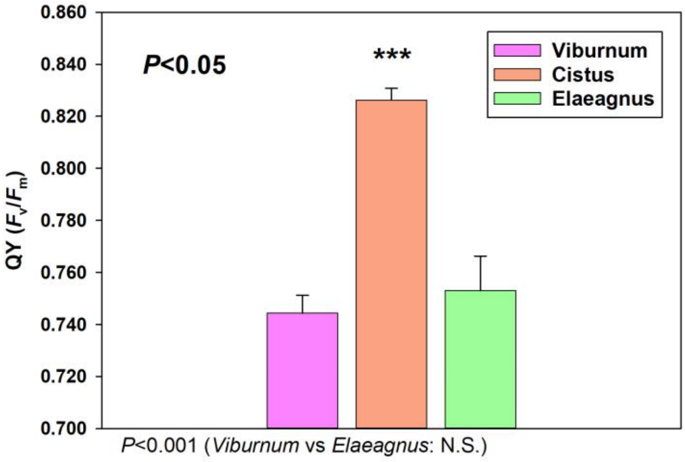
P<0.001 (*Cistus* vs *Elaeagnus*: *P*=0.287, N.S.)

P=0.059

Figure 15. The evergreen shrubs (*Viburnum* and *Ceanothus*) tended to maintain greater soil moisture content. Vertical bar graphs with error bars comparing the total mean values of soil moisture content (SMC, m^3 m^{-3}) for each species growing on the Lower Hicks roof (above) and on the Hadfield roof garden (below), as measured during the sampling of leaves for leaf water potential measurements.

Table 41. Total mean values of photosynthetic efficiency and the effect of plant density on the same parameter. Maximum quantum yield (QY, F_v/F_m) for each species as measured on the days of data collection (10 & 11 August 2016) and expressed as the total mean, the mean for shrubs growing in the sparse population and the mean for shrubs growing in the dense population. The *p*-values are the results of the analysis testing the differences between the mean values of QY for the shrubs growing in the sparse population and the mean values of QY for those growing in the dense population, within each species.

	QY (F_v/F_m)			
Species	**Total**	**Sparse**	**Dense**	***P*-value**
Viburnum tinus	**0.744**±0.007	**0.752**±0.010	**0.737**±0.009	0.275
Cistus × hybridus	**0.826**±0.004	**0.835**±0.007	**0.818**±0.001	**0.037**
Elaeagnus angustifolia	**0.753**±0.013	**0.785**±0.008	**0.721**±0.017	**0.007**
Ceanothus thyrsiflorus	**0.814**±0.005	**0.816**±0.009	**0.813**±0.006	0.787
Buddleja davidii	**0.832**±0.003	**0.829**±0.003	**0.836**±0.004	0.192
Cotinus coggygria	**0.814**±0.006	**0.808**±0.006	**0.819**±0.010	0.368



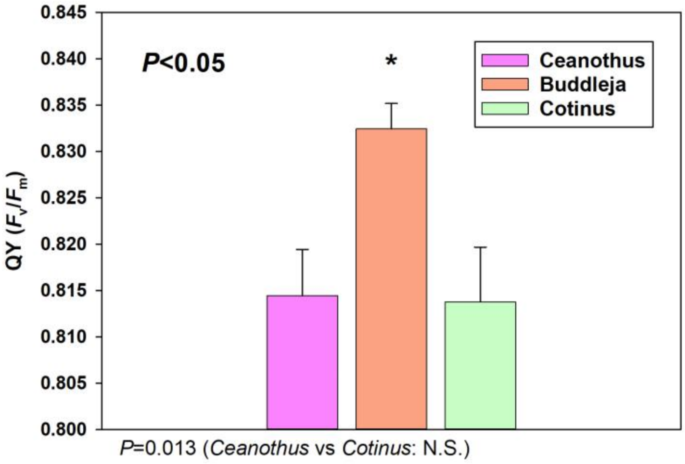


Figure 16. The semi-deciduous shrubs (*Cistus* and *Buddleja*) had significantly higher photosynthetic efficiency. Vertical bar graphs with error bars comparing the total mean values of maximum quantum yield (QY, F_v/F_m) for each species growing on the Lower Hicks roof (above) and on the Hadfield roof garden (below), as measured during the sampling of leaves for leaf water potential measurements.

A.5 Discussion

Study 'A' of the research project was a 3-year study that had the aim of evaluating shrub morphological and physiological performance, or the ability of six woody shrubs to survive, grow, respond and adapt to rooftop environment in the summer. A total of 324 individual shrubs were used, belonging to six different species, two of which were evergreen (*Viburnum tinus* and *Ceanothus thyrsiflorus*), two were semi-deciduous (*Cistus* × *hybridus* and *Buddleja davidii*) and two were deciduous (*Elaeagnus angustifolia* and *Cotinus coggygria*). The species were selected for their known resilience to harsh environments, their ruderal nature and for their range of drought-tolerant characteristics thought to facilitate their survival in rooftop environment. An evergreen, a semi-deciduous and a deciduous species were placed on each of the two research sites, two nearby but separate building rooftops each provided with a weather station for the monitoring of rooftop conditions. The shrubs were placed in experimental shrub populations and their spatial arrangement changed each year to assess the effects of species-specific characteristics, plant density, population size and species mixture on the morphological and physiological responses of the shrubs. Shrub morphological and physiological performance was quantified through the monitoring of a range of plant traits, which was carried out through sampling and the use of specific field and lab equipment to collect data on these traits from experimental shrub populations. The morphological plant traits measured were mortality rate, growth rate, leaf area and leaf mass per area, branching architecture and above-ground biomass; the physiological plant traits measured were leaf relative water content, bulk leaf water potential, gas exchange, photosynthetic performance and photosynthetic water-use efficiency. The analysis of morphological and physiological responses by the different species of shrubs and by the different experimental categories tested the differences amongst species, between high and low plant density, between small and large shrub population size and between single-species and mixed-species shrub populations, to evince their influence on shrub morphological and physiological performance. The analysis also included a reflection on the ability of the shrub canopy to intercept irradiance, which closely related to the second part of the research project (Study 'B').

The purpose of the research project was in fact of finding the relationship between shrub canopy traits (i.e. Study 'A', the study of shrub physiological and morphological performance in rooftop environment) and shrub canopy microclimate (i.e. Study 'B', the study of shrub thermal performance in rooftop environment) to determine combinations of plant traits and spatial arrangements that can potentially enhance green roof thermal performance when using woody shrubs as green roof vegetation. The findings from this research project therefore hope to shed light on how the plant selection process for green roof and/or green infrastructure vegetation can be improved to enhance functionality in terms of both thermal performance and long-term plant survival, especially when using woody shrub vegetation. The selection of suitable green roof shrubs should be a holistic endeavor that takes into account local climate, building height and position and the type of green roof implemented. Amongst other influencing factors is the budget for plants and their expected replacements due to **mortality** or **declining fitness** over time. Ranking the six shrub species used in this study based on their mortality rates across the entire growth period in and of itself cannot provide a complete picture in terms of the overall research aim – to identify the plant traits (and their combinations) inherent to woody shrubs that maximise morphological, physiological and thermal performance in rooftop environment. However, mortality rate is a parameter that can give a good indication of the different species' ability to survive transplant from an optimal or nursery setting to the highly exposed conditions on green infrastructure, to adapt to harsh and nutrient-poor rooftop environment and to survive long-term, all of which may have important economic and practical implications. Inasmuch as the replacement and maintenance of green roof plants can present a significant economic burden on administrators, as well as a potential loss in energy savings due to underperformance of the green roof, a simple yet rigorous, standardised system for the selection of appropriate green roof plants could allow for the use of a wider spectrum of plants, including woody shrubs, and ultimately a more widespread implementation of green roofs globally, an ambition that is still sought after today. This system needs to effectively anticipate mortality rate and predict long-term survival on rooftop environment after initial transplant of certain typologies of plants that, through their idiosyncratic functional plant traits, are potentially best equiped for the job.

Average shrub mortality in this study was about 26%, or 2.5 plants dying per month. Therefore, about 1 in 4 shrubs died during the study, with a progressive increase in mortality from about 7% in the first 12 months to about 19% in the last 21 months. However, about 70% of total mortality was associated to the species with the highest mean mortality rate: *Cistus* × *hybridus*. On the whole, half of the species demonstrated high mortality rates while the other half were mostly unaffected. With time, the lowest performing half of the species either saw a drastic decline in fitness (*Cistus*) or an increase in mortality rate towards the end of the study (the deciduous species *Elaeagnus angustifolia* and *Cotinus coggygria*). On the contrary, the high performing half were in relatively good health without showing signs of stress and saw either only two shrubs die (*Viburnum tinus*) or 100% survival rate (*Buddleja davidii* and *Ceanothus thyrsiflorus*). **Predicting mortality rates in species of woody shrubs is therefore fundamental in plant selection for improving green roof functionality, as choosing unsuitable species could result in very high mortality and consequently in performance and economic loss.**

Growth can be another good indicator of fitness and the ability of a species to adapt. If applied in real rooftop scenarios, as was done in this study, comparing the relative growth rates of different species could be one of the simplest and foolproof ways of predicting long-term survival on green roofs. Unsurprisingly, the six shrub species presented significantly different relative growth rates and

Viburnum had the highest growth rate, followed by *Cotinus* and *Ceanothus*. Relative growth rate slowed significantly for all shrubs in the last 21 months of the study, with the exception of the two evergreen shrubs (*Viburnum* and *Ceanothus*), and *Buddleja* and especially *Cistus*' growth rates decreased most of all during this period. This analysis also revealed that *Ceanothus* made the highest growth increase from the beginning to the end of the study, going from least growing species to just behind *Viburnum*, whereas *Cistus* had the highest decline in growth. *Cistus* was clearly struggling to grow and even survive, especially in the last 21 months of the study. All this could indicate that the evergreen shrubs might have had a slightly greater ability to adapt to rooftop environment in the long-term. Although species mixture (i.e. whether shrubs grew in single- or mixed-species populations) did not significantly affect growth, plant density certainly did. **Growth was significantly lower in high-density shrub populations compared to low-density ones for all species. A potential explanation for this could be that high plant density may have created more self-shading by the canopies that may have impacted on the shrubs' photosynthesis and thereby their growth.**

In confirmation of the 'self-shading' theory, **leaf thickness** (leaf mass per area) of the different shrub species was also not affected by species mixture or population size but definitely was by plant density. Leaf mass per area is not a performance indicator but it is significantly influenced by light and temperature levels and therefore would affected by plant density. In fact, leaf thickness was significantly higher in low-density populations (i.e. no or minimal self-shading) compared to high-density ones (i.e. high self-shading) for the evergreen shrubs (*Viburnum* and *Ceanothus*) and for *Buddleja* but not for the deciduous species (*Elaeagnus* and *Cotinus*) and *Cistus*. Interestingly, the first group of shrubs (*Viburnum*, *Ceanothus* and *Buddleja*) was also the one that had the lowest mortality rates. **Choosing species that are highly responsive to changes in plant density in terms of increasing leaf thickness in conditions of low-plant density, where shrubs would be more exposed to light and other environmental factors, could represent an advantage to plants growing on green roofs. Therefore, leaf mass per area could be another parameter capable of predicting shrub mortality and suitability of a species to rooftop environment.**

Predictably, leaf thickness was also significantly different amongst the species, with highest thickness in the evergreens, intermediate thickness in the semi-deciduous species (*Buddleja* and *Cistus*) and lowest thickness in the deciduous shrubs. **All shrubs increased leaf thickness during the course of the study, most likely as an adaptation to protect the canopy from constant exposure to environmental stresses, such as high irradiance, heat, frost and wind.** While *Viburnum* showed the highest increase in leaf thickness, *Ceanothus* presented a conspicuous decrease during the last year of the study. Furthermore, leaf mass per area as analysed from biomass measurements post-harvest was found to significantly and negatively correlate with **branch length**

– leaf thickness increasing with decreasing branch length. In fact, shrubs with the shortest branches (*Viburnum*, *Ceanothus* and *Cistus*) also presented the highest leaf thickness, potentially caused by a preferential allocation of carbon to leaves rather than to branch growth in the short shrubs; the shrubs with the longest branches and also the lowest leaf thickness (*Buddleja*, *Elaeagnus* and *Cotinus*) would therefore have distributed more biomass into branch growth and therefore into canopy height rather than into leaf thickness.

Branch length was in fact part of the measurements for determining the apical dominance index (i.e. level of ramification), which essentially describes the **branching architecture** of a woody species. This plant trait will be used to evaluate whether it affected shrub thermal performance (in Study 'B') in terms of how levels of branching may have contributed to temperature mitigation through the interception of light by the canopy. In order to understand light interception and extreme temperature abatement by the woody shrubs, it is essential to keep in mind the plant height and the habits of the different species. The **plant height** of the 'tall shrubs' (*Buddleja, Elaeagnus* and *Cotinus*) ranged between 0.80 and 1.20 m, whereas the plant height of the 'short shrubs' (*Ceanothus*, *Cistus* and *Viburnum*) was between 0.50 and 0.70 m. Their habits varied widely: *Buddleja* had the tallest and narrowest canopy with slender, rigid branches; *Elaeagnus* was also tall and slightly more oval with stiff, heavy branches; *Cotinus* was tall and rounded canopy with brittle branches; *Viburnum* was short and fan-shaped with thick, sturdy branches; *Cistus* was shorter and more rounded with supple branches and finally *Ceanothus* was the shortest shrub with a prostrate habit with bendy branches. As a consequence of their differing heights and habits, the six shrub species presented significantly different mean values of above-ground biomass and area, ramification, branch length and apical dominance index. *Ceanothus* had the most ramified canopy but also had the lowest **woody biomass area and weight** – in other words, *Ceanothus* had a highly branching but also very small and lightweight canopy. By contrast, the *Cotinus* canopy was the least ramified, with half the level of ramification compared to *Ceanothus*. The *Cistus* canopy had the highest biomass area and the second highest level of ramification despite having one of the shortest branch lengths, while *Buddleja* had the second lowest biomass area but the highest branch length with similar levels of ramification to *Viburnum*. **Therefore, the woody species showed a truly diverse spectrum of physical characteristics that will undoubtedly have influence light interception.**

Both plant height and **leaf area index** (LAI) influenced canopy microclimate in terms of shading and light interception. The evergreen shrubs had the highest **canopy density** (or foliage density) while the semi-deciduous shrubs had the lowest foliage density. *Buddleja* in particular had 4 times less leaves than the evergreen shrubs. Foliage density was in fact negatively correlated with branch length, meaning that the longer the branches the less dense the foliage. Similarly, **leaf area** was also significantly affected by plant height – on average, the tallest shrubs had the biggest leaves and the shortest shrubs had smallest leaves. Although neither leaf area nor **leaf biomass** were correlated with branch length, both branch length and plant height will most likely have affected the species' biomass allocation. The short shrubs, producing shorter branches, may have chosen to allocate the carbon not spent in growing in height to producing more leaves (i.e. higher foliage density) and to making them more resistant (i.e. higher leaf mass per area), whereas taller shrubs may have chosen to allocate a large quantity of carbon in producing longer branches and may therefore have allocated less carbon to producing leaves (i.e. lower foliage density) that are nevertheless bigger (i.e. higher leaf area) but less mechanically resistant (i.e. lower leaf mass per area). Leaf area index was calculated based on foliage density and leaf area and was found to be highest in *Viburnum* and *Cotinus*, which had 3 to 4 times higher values of LAI compared to the semi-deciduous shrubs (*Buddleja* and *Cistus*) who had the lowest values. Despite having the lowest foliage density and one of the lowest values of LAI, *Buddleja* was still able to **intercept** about 74% of incident light during an ad hoc experiment, which is a high percentage in spite of having the lowest **leaf to branch biomass ratio** (i.e. a higher ratio of exposed woody biomass compared to leaf biomass) and therefore a greater predisposition to allow light to pass through the canopy. **As leaf area index was highly and positively correlated with leaf area, the measurement of leaf area could be used as a simpler method to predict a species' LAI, which could speed up the process for selecting shrubs with the best characteristics for light interception.**

The capturing of a species' LAI as a key parameter to determine plant suitability could be further accelerated with the measurement of **maximum quantum yield** (QY), or photosynthetic performance, as proxy. That is because the two parameters were found to be significantly and negatively correlated – in other words, the photosynthetic performance of the woody shrubs decreased as LAI increased. Logically, a shrub with a denser foliage (e.g. *Viburnum*) would need to photosynthesise less per leaf than a shrub with a canopy consisting of fewer leaves (e.g. *Buddleja*, *Cistus*), therefore the latter would have to maximise photosynthesis per leaf in order to maintain vital functions. This is exactly what happened in the study – *Cistus* and *Buddleja* had the highest photosynthetic performance while *Viburnum* had the lowest. What this probably means is that *Cistus* was constantly working close to the upper limit of photosynthetic performance throughout the study, while *Viburnum* was constantly working below it. This is not surprising, because evergreen woody plants tend to have low photosynthetic capacity as a result of lower investment in enzyme content. To further prove the point, QY was significantly and negatively correlated with both leaf biomas and leaf area, which roughly means that, as both total leaf biomass and leaf canopy area per plant decrease, photosynthetic performance increases – *Cistus*, which had a lower total leaf biomass and area per plant may have compensated for its reduced aboveground canopies by allocating more enzymes in its photosystems, thereby ensuring higher photosynthetic capacity within each leaf.

In general, all species had significant increases in photosynthetic performances in the first year of the study but then saw declines in the final year. As QY is also used to assess the levels of stress experienced by a plant, it was clear that the shrubs were under significant stress by the end of the study and that they adapted to lower levels of photosynthesis in order to maintain vital functions. QY was not found to significantly influence mortality rates but it did significantly correlate with growth rate, with growth rates decreasing with increasing photosynthetic performance. **This correlation suggests that shrubs with photosystems that constantly work at high performance levels without substantially adapting to lower levels in the long-term (i.e. are inefficient) could cause a drastic reduction in woody biomass to save energy and even threaten vitality**, which sounds like the case of *Cistus*. The reason why *Cistus* may have had such inefficient photosystems may have be related to the fact that it is a dimorphic species (i.e. has seasonal changes in habit), which allows it to quickly adapt to highly stressful environments. *Cistus* is a pioneering shrub that is tolerant of extreme conditions in order to colonise rapidly during the initial successional stages of post-fire environments, therefore it may not be a species that is designed for long-term survival. On the contrary, *Viburnum*, like most sclerophylls, may instead have chosen to sacrifice photosynthetic performance and other physiological activities in order to maintain both leaf longevity and constant biomass growth.

Lastly, plant density and population size also had a significant effect on the photosynthetic performance of all species, except for *Cistus*. *Viburnum* was affected by both plant density and population size, with photosynthetic performance significantly lower in larger and low-density shrub populations. *Ceanothus*, the other evergreen shrub, also had lower photosynthetic performance in low-density populations, independent of population size. *Elaeagnus* and *Buddleja* were the least affected by plant density and the most affected by population size, showing a significant reduction in photosynthetic performance in bigger populations, independent of plant density. As *Elaeagnus* and *Buddleja* were the tallest shrubs and in this case were placed in polyspecific populations (i.e. within populations of mixed species and therefore of heterogeneous plant heights), an increase in population size might have caused greater exposure of their canopies to wind and irradiance, thereby affecting their photosynthetic performance.

Differential exposure to environmental conditions potentially caused by plant density, population size and type of species mixture is thought to also have affected the **soil moisture content** of certain shrub species. **The shrub species presented significantly different mean values of soil moisture content, with *Viburnum* and *Buddleja* maintaining the highest and *Cistus* the lowest values, but over time there was a general decline in soil moisture content in all species, potentially reflecting increasing levels of stress experienced during the study.** Plant density was found to significantly affect soil moisture content in two species: *Viburnum*, with higher values in low-density populations, and *Cotinus*, with higher values in high-density populations. *Ceanothus* was the only species to have been significantly affected by species mixture, presenting significantly higher values of soil moisture content in polyspecific ('mixed') populations, which may have represented greater shading conditions for this species due to greater height differences in these populations. Population size, however, did not have a significant effect on the soil moisture content of any of the shrubs, potentially as a result of the 'homogenising' effect of placing all shrubs in polyspecific populations in Year 2.

In terms of leaf water status and potential levels of drought stress experienced by the woody shrubs, **relative leaf water content** (RWC_L) was significantly different among the shrub species but was not affected by either plant density, population size or species mixture. Plant density also had limited influence on the species' **bulk leaf water potentials** (Ψ_L), with only one species (*Buddleja*) showing significantly less negative potentials (i.e. were less stressed) in high-density populations. *Buddleja* was also the species that reached the most negative potentials after *Elaeagnus*, while the evergreens (*Ceanothus* and *Viburnum*) maintained the least negative potentials. **Therefore, the evergreen shrubs were the least affected by water stress.** This perfectly aligned with the RWC_L of the different species – *Viburnum* and *Ceanothus* had the highest RWC_L and *Elaeagnus* and *Buddleja* had the lowest. The correlation between Ψ_L and RWC_L was not significant (P=0.076), however it is difficult to dismiss the fact that the two parameters have both highlighted that **certain species were probably more stressed or had a lower water-use efficiency (*Elaeagnus* and *Buddleja*) than the others (the evergreen shrubs), which may have impacted other physiological activities.** For example, the measurements of **soil moisture content** taken during the leaf sampling for Ψ_L indicated that the evergreen shrubs had the highest soil water content and therefore most likely had the best water-use efficiency. Supporting this hypothesis was the fact that *Viburnum* also had the highest photosyntethic water-use efficiency (WUE_P).

Differing plant height amongst the species was not found to significantly influence **gas exchange parameters**, with the exception of the extrapolated parameter **photosynthetic water-use efficiency** (WUE_P). WUE_P was significantly higher in the 'tall shrubs' (*Buddleja*, *Elaeagnus* and *Cotinus*) than in the 'short shrubs' (*Ceanothus*, *Cistus* and *Viburnum*), suggesting **a relationship between greater plant height and higher water-use efficiency in photosynthetic processes**. In fact, despite not being significantly affected by plant density, WUE_P was generally higher in tall shrubs than in short shrubs when these were placed in high-density populations. However, tall shrubs also had the highest mean leaf areas, a more plausible reason for this difference compared to purely plant height (N.B.: the correlation between WUE_P and A_L* was marginally significant, P=0.110; see Appendix B). Additionally, mean values of WUE_P were not significantly different between the evergreens (*Viburnum* and *Ceanothus*) and between the deciduous shrubs (*Elaeagnus* and *Cotinus*), **indicating**

a strong association betwen photosynthetic water-use efficiency and shrub lifeform (or leaf longevity). In general, however, plant density and population size affected other gas exchange parameters (**evapotranspiration rate**, **assimilation** and **stomatal conductance**) significantly more than they did WUE_P, with significantly higher values associated with the combination 'large high-density population'.

As previously mentioned, evapotranspiration rate, assimilation and stomatal conductance were not affected by either plant height or shrub form. However, plant density had a significantly greater effect on these same parameters when the shrubs were placed in polyspecific rather than in monospecific populations, thereby suggesting that **a more heterogeneous plant height in shrub populations may have significantly affected the way shrubs photosynthesised**. Photosynthesis instead differed unsurprisingly on the basis of *species*. In fact, the effects of both plant density and population size on evapotranspiration rate, assimilation and stomatal conductance were most significant in *Ceanothus*, followed by *Viburnum* and *Buddleja*, whereas the parameters were least affected by plant density and population size in *Cistus*, followed by the deciduous shrubs (*Elaeagnus* and *Cotinus*). This last observation curiously resembles the way mortality affected the different species – *Buddleja*, *Ceanothus* and *Viburnum* had the lowest mortality rates and *Cistus* with the highest mortality rate, followed by the deciduous shrubs. **Although mortality did not correlate with any of the gas exchange parameters, it is clear that there is an unmistakeable connection between the level of photosynthetic response or 'sensitivity' of a species to changes in shading conditions (i.e. caused by variations in plant density, population size and species mixture) and species fitness and vitality. A species' photosynthetic response to change could therefore be an effective predictor of fitness and long-term survival. The implication of this finding within the context of the study is then that <u>woody shrub species that are physiologically highly responsive to changes in plant density, population size and species mixture could potentially indicate greater levels of adaptability and long-term vigour and therefore greater suitability as green roof vegetation</u>.**

Finally, the analysis of gas exchange parameters highlighted the greatest limitation to Study 'A' – the comparability between measurements carried out on shrubs growing on two separate sites. Despite relatively small differences in microclimate on the two rooftops, there was a significant relationship between the rooftop microclimates and the responses of some gas exchange parameters (evapotranspiration rate, assimilation and leaf temperature) in the species growing on the respective rooftops (i.e. *Viburnum*, *Cistus* and *Elaeagnus* on the Lower Hicks rooftop; *Ceanothus*, *Buddleja* and *Cotinus* on the Hadfield roof garden). For example, *Viburnum*, *Cistus* and *Elaeagnus* (Lower Hicks rooftop) had significantly lower evapotranspiration and assimilation rates and significantly higher **leaf temperatures** compared to *Ceanothus*, *Buddleja* and *Cotinus* (Hadfield roof garden). This fact highlighted the importance of a basic scientific dogma: **comparability**. Out of necessity, the practicality of separating the species between two different experimental sites was deemed more important than guaranteeing strict comparability, but this was eventually reflected in the species' gas exchange values. **Ensuring comparability in experimentation is therefore of the highest importance in field and laboratory work, because it will influence and put in jeopardy the significance of the results.**

STUDY ‘B’

The effect of species traits, plant density, population size and species mixture on the thermal performance of six woody shrubs growing on rooftops

B.1 Overview and aims of the study

Study ‘B’ of the research project was dedicated to assessing the thermal performance of six distinct species of woody shrubs placed in populations of varying plant density, population size and type of species mixture during the coldest hours of the day in the winter and the warmest hours of the day in the summertime. This study was carried out during the winter and summer months of three consecutive years (2016–2018). The aim was to shed light on the ability of woody shrubs to improve rooftop temperatures during the warmest and coldest months of the year, potentially translating to increased building thermal performance for buildings with green roofs composed primarily of shrub vegetation. Temperature profile analysis was the method used to identify differences between species and to quantify the effect that plant density, population size and species mixture had on the shrubs’ ability to abate extreme rooftop temperatures. The monitoring of plant canopy microclimate was essential for the creation of temperature profiles, which were used to evaluate the ability of the study species to cool the rooftop (i.e. reduce temperatures) in the summer and to insulate the rooftop (i.e. increase temperatures) in the winter. The interaction between species-specific canopy characteristics (e.g. transpiration rates, foliage density) and environmental factors (e.g. air temperature, irradiance, rain, wind) will have influenced the type of microclimate created underneath the plant canopy of each shrub species, as well as the immediate surroundings above the canopy.

The sections that follow describe:

1) the equipment and experimental design used for monitoring plant canopy microclimate of the six woody shrub species through the three years of the study (Section B.2.1),
2) the calculation of ΔT to create the temperature profiles of the shrubs and of the different experimental categories within each year, in order to quantify the effects of plant density, population size and species mixture on shrub thermal performance (Section B.2.2), and
3) the statistical analysis (‘Results’) of the effects of plant density, population size and species mixture on shrub thermal performance (Section B.3), including the overall effects on shrub thermal performance in winter vs summer as three-year averages (Section B.3.4).

A discussion of the results for Study ‘B’ concludes this second part of the thesis (Section B.4).

B.2 Material and Methods

As described previously (Chapter 4), the experiments for Study ‘B’ were the same as those used for Study ‘A’, therefore placed on the same two research sites (Lower Hicks rooftop and Hadfield roof garden, Section 4.1) and the two studies were carried out simultaneously over the same period. However, while the morphological and physiological plant parameters measured in Study ‘A’ were carried out primarily in the summer months, the monitoring of plant microclimate in Study ‘B’ was carried out during both the winter *and* summer months.

B.2.1 The monitoring of shrub canopy microclimate

Shrub canopy microclimate was monitored during the winter and summer months of three consecutive years. In the experiments, shrubs were planted and arranged on rooftops according to the experimental design common to both Study ‘A’ and Study ‘B’ (Section 4.1). The experimental design is described in more detail in this section for Year 1 (Section B.2.1.1), Year 2 (Section B.2.1.2) and Year 3 (Section B.2.1.3) of the study. TGP-4505 Tinytag Plus 2 temperature sensors (Gemini Data Loggers, Ltd., Chichester, UK) were used to log temperature (*T*, °C) and create the temperature profiles of the different species of shrubs and experimental categories, to evaluate the potential effects of plant density, population size and species mixture on shrub thermal performance. These rugged temperature sensors were placed on the substrate surface of the central-most unit of each species and of each experimental category observed during Year 1 (Section B.2.1.1), Year 2 (Section B.2.1.2) and Year 3 (Section B.2.1.3) of the study, including of the Control unit, or bare substrate (Fig. 2). The sensors logged one record of temperature data per minute for the entirety of the winter and summer months during each year of the study.

In most cases, the monitoring of plant canopy ‘microclimate’ refers to the collection and analysis of temperature data as recorded *below* the plant canopy, at substrate level. However, in Year 3 of the study, temperature data was also recorded *above* the shrub canopy, with sensors placed c. 150 mm above the shrub canopy surface. Above-canopy temperature data was collected to evaluate the microclimate immediately surrounding the plant canopy and how it could be impacted by species choice, plant density, population size and species mixture, as well as to assess if it could be significantly different from both Control and the air temperature logged by the weather stations on each research site (Section 4.1). The data collected on both the Control and the ‘vegetated’ units were then processed in Excel for direct comparison via a series of calculations (Section B.2.2) to create temperature profiles that could be analysed further. The findings from the temperature profile analysis (Section B.3) can thus be used to quantify and examine the statistical significance of the effects of plant density, population size and species mixture on shrub thermal performance in rooftop environment.

B.2.1.1 Experimental design (Year 1): Effects of plant density on shrub thermal performance

The first year of the study (January 2016 to December 2016) was dedicated to the comparison of temperature profiles of shrubs placed in low-density populations with those of shrubs placed in high-density populations, with the objective of evaluating the effects of plant density on the shrubs' ability to cool rooftop temperatures in the summer and maintain warmer temperatures in the winter. These populations were composed of individuals belonging to *only one species* ('monospecific populations'), with each species placed in two different types of populations:

1) **Low-density populations**: the 9 units were evenly spread out in '*sparse*' groupings, and
2) **High-density populations**: the 9 units were placed in close proximity to one another in '*dense*' groupings.

For example, nine units of *V. tinus* were placed in a low-density population and the other nine were placed in a high-density population. The same was done for the other five species, for a total of six populations per experimental site (Section 4.1). This allowed for the quantification of the impact of both **plant density** and **species choice** on the ability of shrubs to to 'buffer' or abate extreme rooftop temperatures. (N.B. The deciduous species, *Elaeagnus* and *Cotinus*, and *Buddleja* were omitted from the analysis of temperature profiles in the winter months, as their canopies were either completely lacking or had very little foliage.)

B.2.1.2 Experimental design (Year 2): Effects of population size on shrub thermal performance

The second year of the study (January 2017 to December 2017) was dedicated to observing the impact of population size on how plant density affects rooftop temperatures, and therefore compared the temperature profiles of both sparsely- and densely-populated shrubs when placed in either small or relatively larger populations. The objective was to evaluate the effect of population size on the shrubs' ability to cool rooftop temperatures in the summer and maintain warmer temperatures in the winter.

All populations in this experiment were considered ʻpolyspecific' (mixed), or composed of individuals belonging to *three different species*. There were four experimental populations in total, each representing a different combination of plant density and size:

1) **ʻLow-density 3×3' population**: 9 units placed in a *sparsely*-populated *small* group;
2) **ʻLow-density 4×4' population**: 16 units placed in a *sparsely*-populated *large* group;
3) **ʻHigh-density 3×3' population**: 9 units placed in a *densely*-populated *small* group, and
4) **ʻHigh-density 4×4' population**: 16 units placed in a *densely*-populated *large* population.

For example, one small (9-unit) and one large (16-unit) population composed of a mix of *V. tinus*, *C.* × *hybridus* and *E. angustifolia* were sparsely populated, whereas the other small and large population composed of the same three species were densely populated (Section 4.1). This allowed for the quantification of the impact of both **population size** and **plant density** on the ability of shrubs to ʻbuffer' or abate extreme rooftop temperatures. (N.B. The deciduous species, *Elaeagnus* and *Cotinus*, and *Buddleja* were omitted from the analysis of temperature profiles in the winter months, as their canopies were either completely lacking or had very little foliage.)

B.2.1.3 Experimental design (Year 3): Effects of species mixture on shrub thermal performance

The third and final year of the study (January 2018 to August 2018) was dedicated to the comparison of temperature profiles of shrubs placed in ʻmonospecific populations' (i.e. formed by individuals of *only one species*) against the temperature profiles of those placed in mixed or ʻpolyspecific populations' (i.e. formed by individuals of *three different species*), with the objective of evaluating the effects of *species mixture* on the shrubs' ability to cool rooftop temperatures in the summer and maintain warmer temperatures in the winter.

For each research site, the shrubs were placed in six high-density populations, three of which were dedicated to the ʻmonospecific' category (i.e. consisting of *only one species*) while the other three were dedicated to the ʻpolyspecific' category (i.e. consisting of *3 different species*), as described in a previous chapter (Section 4.1) and in more detail below:

On the Lower Hicks roof:

1) A **monospecific population of only *V. tinus*** (9 units);
2) A **polyspecific population** consisting of *V. tinus* (3 units), *C.* × *hybridus* (3 units) and *E. angustifolia* (3 units), **with *V. tinus* at the centre**;
3) A **monospecific population of only *C.* × *hybridus*** (9 units);

4) A **polyspecific population** consisting of *V. tinus* (3 units), *C.* × *hybridus* (3 units) and *E. angustifolia* (3 units), **with *C.* × *hybridus* at the centre**;
5) A **monospecific population of only *E. angustifolia*** (9 units), and
6) A polyspecific population consisting of *V. tinus* (3 units), *C.* × *hybridus* (3 units) and *E. angustifolia* (3 units), **with *E. angustifolia* at the centre**.

On the Hadfield roof garden:

1) A **monospecific population of only *C. thyrsiflorus*** (9 units);
2) A **polyspecific population** consisting of *C. thyrsiflorus* (3 units), *B. davidii* (3 units) and *C. coggygria* (3 units), **with *C. thyrsiflorus* at the centre**;
3) A **monospecific population of only *B. davidii*** (9 units);
4) A **polyspecific population** consisting of *C. thyrsiflorus* (3 units), *B. davidii* (3 units) and *C. coggygria* (3 units), **with *B. davidii* at the centre**;
5) A **monospecific population of only *C. coggygria*** (9 units), and
6) A **polyspecific population** consisting of *C. thyrsiflorus* (3 units), *B. davidii* (3 units) and *C. coggygria* (3 units), **with *C. coggygria* at the centre**.

This allowed for the quantification of the impact of both **species mixture** and **species choice** on the ability of shrubs to ‘buffer’ or abate extreme rooftop temperatures. Findings from these experiments could also give an indication of how particular types of mixtures (e.g. all evergreen species, mix of evergreen and deciduous, all tall shrubs, mix of tall and short shrubs) could impact rooftop temperatures and therefore provide useful information to better tailor plant selection for a green roof vegetation that enhances thermal performance. (N.B. The deciduous species, *Elaeagnus* and *Cotinus*, were omitted from the analysis of temperature profiles in the winter months, as their canopies were devoid of foliage.)

B.2.2 Calculating Δ*T* to compare temperature profiles and quantify shrub thermal performance

The temperature profiles of the different shrub species were created based on the temperature data collected during the monitoring of plant canopy microclimate and were analysed in relation to the temperature profiles of bare substrate (Control). The temperature sensors recorded data at a rate of one record of temperature per minute over the course of three years, a sufficiently high resolution that allowed for very detailed analysis of the temperature profiles. The following subsections describe the calculation of Δ*T*, used to quanify:

- The effects of species and plant density on shrub thermal performance – Year 1 (Sections 2.2.1 and 2.2.2);
- The effect of population size on shrub thermal performance – Year 2 (Sections 2.2.3 and 2.2.4), and
- The effect of species mixture on shrub thermal performance – Year 3 (Sections 2.2.5 and 2.2.6).

In all three years of the study, shrub performance was calculated in terms of both insulating (in winter) and cooling (in summer) of the rooftop environment.

B.2.2.1 Calculating ΔT in winter and the effects of species and plant density on shrub insulating performance (Year 1)

Temperature profiles were used to quantify the effects of species and plant density on shrub insulating performance. These profiles were created based on calculations that used temperature data recorded during 58 winter days in Year 1 of the study. Specifically, these calculations were used to compare the total mean temperature difference (ΔT) between Control (bare substrate) and the shrub populations by category (i.e. by species and by plant density) during the coldest hours of the day (00:00–04:00). (Only three species were observed in the winter months in Year 1, as the other three lacked foliage during this period and therefore would not have been able to offer a distinct microclimate underneath their plant canopies.)

The assumption was that in the winter mean temperature on Control would likely be *lower* than mean temperature under a plant canopy, due to the foliage creating a barrier that would protect it from external conditions (i.e. plant canopy microclimate). Therefore, the calculation of ΔT refers to the mean temperature difference in degrees Celsius between the mean temperature reached below the plant canopy (T_B) and that reached on bare substrate (T_C) at any given minute between the hours of 00:00 and 04:00, as below:

$$\Delta T = ([T_B] - [T_C]).$$

As the temperature sensors logged one record per minute, the calculation of mean temperature for T_B will have consisted in the average of 240 recordings of temperature during the coldest hours of the day (i.e. 60 minutes × 4 hours) per winter day (240 minutes × 58 days) per species (13,920 minutes × 3 species) per the two plant density categories (41,760 minutes × 2), for a total of 83,520 minutes or 1,392 hours worth of temperature data. The calculation of T_C was based on 240 recordings per winter day (240 minutes × 58 days) per species (13,920 minutes × 3 species), for a total of only 41,760 minutes or 696 hours worth of temperature data, as Control units were limited to only one per species. A total of 9 temperature sensors were used during this period.

B.2.2.2 Calculating Δ*T* in summer and the effects of species and plant density on shrub cooling performance (Year 1)

Temperature profiles were used to quantify the effects of species and plant density on shrub cooling performance. These profiles were created based on calculations that used temperature data recorded during 71 summer days in Year 1 of the study. Specifically, these calculations were used to compare the total mean temperature difference (ΔT) between Control (bare substrate) and the shrub populations by category (i.e. by species and by plant density) during the warmest hours of the day (12:00–16:00). (Six species of shrubs were observed during this period, as all had sufficient foliage to provide a distinct microclimate underneath their plant canopies.)

The assumption was that in the summer mean temperature on Control would likely be *higher* than mean temperature under a plant canopy, due to the shading foliage shading it from external conditions (i.e. plant canopy microclimate). Therefore, the calculation of ΔT refers to the mean temperature difference in degrees Celsius between the mean temperature reached on bare substrate (T_C) and that reached below the plant canopy (T_B) at any given minute between the hours of 12:00 and 16:00, as below:

$$\Delta T = ([T_C] - [T_B]).$$

As the temperature sensors logged one record per minute, the calculation of mean temperature for T_B will have consisted in the average of 240 recordings of temperature during the coldest hours of the day (i.e. 60 minutes × 4 hours) per summer day (240 minutes × 71 days) per species (17,040 minutes × 6 species) per the two plant density categories (102,240 minutes × 2), for a total of 204,480 minutes or 3,408 hours worth of temperature data. The calculation of T_C was based on 240 recordings per summer day (240 minutes × 71 days) per species (17,040 minutes × 6 species), for a total of only 102,240 minutes or 1,704 hours worth of temperature data, as Control units were limited to only one per species. A total of 18 temperature sensors were used during this period.

B.2.2.3 Calculating Δ*T* in winter and the effect of population size on shrub insulating performance (Year 2)

Temperature profiles were used to quantify the effects of population size on shrub insulating performance. These profiles were created based on calculations that used temperature data recorded during 83 winter days in Year 2 of the study. Specifically, these calculations were used to compare the total mean temperature difference (ΔT) between Control (bare substrate) and the shrub populations by category (i.e. by population size and by plant density) during the coldest hours of the day (00:00–04:00). (N.B. This data takes into consideration the effects of population size on the combined thermal performance of all species, as all shrubs in Year 2 were arranged in 'polyspecific' populations, or populations in which species that had foliage during winter were mixed in with those that did not. However, temperature sensors were placed only under three of the species – *Viburnum, Cistus* and *Ceanothus* – as the other three lacked foliage during this period and therefore would not have been able to offer a distinct microclimate underneath their plant canopies.)

Like the previous year, the assumption was that in the winter mean temperature on Control would likely be *lower* than mean temperature under a plant canopy, due to the foliage creating a barrier that would protect it from external conditions (i.e. plant canopy microclimate). Therefore, the calculation of ΔT refers to the mean temperature difference in degrees Celsius between the mean temperature reached below the plant canopy (T_B) and that reached on bare substrate (T_C) at any given minute between the hours of 00:00 and 04:00, as below:

$$\Delta T = ([T_B] - [T_C]).$$

As the temperature sensors logged one record per minute, the calculation of mean temperature for T_B will have consisted in the average of 240 recordings of temperature during the coldest hours of the day (i.e. 60 minutes × 4 hours) per winter day (240 minutes × 83 days) per population size category (19,920 minutes × 2) per plant density category (39,840 minutes × 2) per research site (79,680 × 2), for a total of 159,360 minutes or 2,656 hours worth of temperature data. Control units were limited to only two per research site and therefore the mean value of T_C was calculated based on 240 recordings per winter day (240 minutes × 83 days) per population size category (19,920 minutes × 2) per research site (39,840 × 2), for a total of 79,680 minutes or 1,328 hours worth of temperature data. A total of 16 temperature sensors were used.

B.2.2.4 Calculating ΔT in summer and the effect of population size on shrub cooling performance (Year 2)

Temperature profiles were used to quantify the effects of species and plant density on shrub cooling performance. These profiles were created based on calculations that used temperature data recorded during 67 summer days in Year 2 of the study. Specifically, these calculations were used to compare the total mean temperature difference (ΔT) between Control (bare substrate) and the shrub populations by category (i.e. by species and by plant density) during the warmest hours of the day (12:00–16:00). (Six species of shrubs were observed during this period, as all had sufficient foliage to provide a distinct microclimate underneath their plant canopies.)

Like the previous year, the assumption was that in the summer mean temperature on Control would likely be *higher* than mean temperature under a plant canopy, due to the foliage shading it from external conditions (i.e. plant canopy microclimate). Therefore, the calculation of ΔT refers to the mean temperature difference in degrees Celsius between the mean temperature reached on bare substrate (T_C) and that reached below the plant canopy (T_B) at any given minute between the hours of 12:00 and 16:00, as below:

$$\Delta T = ([T_C] - [T_B]).$$

As the temperature sensors logged one record per minute, the calculation of mean temperature for T_B will have consisted in the average of 240 recordings of temperature during the warmest hours of the day (i.e. 60 minutes × 4 hours) per summer day (240 minutes × 67 days) per species (16,080 minutes × 6 species) per population size category (96,480 minutes × 2), per plant density category (192,960 × 2), for a total of 385,920 minutes or 6,432 hours worth of temperature data. Control units were limited to only two per research site and therefore the calculation of the mean value of T_C was based on 240 recordings per summer day (240 minutes × 67 days) per population size category (16,080 × 2) per research site (32,160 minutes × 2), for a total of only 64,320 minutes or 1,072 hours worth of temperature data. A total of 16 temperature sensors were used.

B.2.2.5 Calculating ΔT in winter and the effect of species mixture on shrub insulating performance (Year 3)

Temperature profiles were used to quantify the effect of species mixture on shrub insulating performance. These profiles were created based on calculations that used temperature data recorded during 58 winter days in Year 3 of the study. Specifically, these calculations were used to compare the total mean temperature difference (ΔT) between Control (bare substrate) and the shrub populations by category (i.e. by species and by species mixture) during the coldest hours of the day (00:00–04:00). (Only four species were observed in the winter months in Year 1, as the other two lacked foliage during this period and therefore would not have been able to offer a distinct microclimate underneath their plant canopies.)

(N.B. Further to the last note above: With regards to the ‘polyspecific’ populations, the data takes into consideration the effects of species mixture on the combined thermal performance of all species, as all shrubs that were arranged in populations in which species that had foliage in the winter were mixed in with those without. However, temperature sensors were placed only under four of the species – *Viburnum*, *Cistus*, *Ceanothus* and *Buddleja* – as the other two lacked foliage during this period. With regards to the ‘monospecific’ populations, the same applies: as *Viburnum*, *Cistus*, *Ceanothus* and *Buddleja* were the only species with foliage in the winter, the ‘monospecific’ populations of the deciduous shrubs *Elaeagnus* and *Cotinus* were excluded from the analysis.)

As in previous years, the assumption was that in the winter mean temperature on Control would likely be *lower* than mean temperature both *above* and *below* a plant canopy, due to the foliage creating a barrier that could reduce wind speed (i.e. *above*-plant microclimate) and provide shelter from the elements (i.e. *below*-plant canopy microclimate). Therefore, the calculation of ΔT refers to the mean temperature difference in degrees Celsius (°C):

1) between the mean temperature reached above (T_A) and that reached on bare substrate (T_C):

$$\Delta T = ([T_A] - [T_C])$$

2) and between the mean temperature reached below the plant canopy (T_B) and that reached on bare substrate (T_C):

$$\Delta T = ([T_B] - [T_C])$$

at any given minute between the hours of 00:00 and 04:00.

As the temperature sensors logged one record per minute, the calculation of mean temperature for T_A and T_B will each have consisted in the average of 240 recordings of temperature during the coldest hours of the day (i.e. 60 minutes × 4 hours) per winter day (240 minutes × 58 days) per species (13,920 minutes × 4 species) per the two species mixture categories (55,680 minutes × 2), for a total of 111,360 minutes or 1,856 hours worth of temperature data. Control units were limited to only two per research site and therefore the calculation of the mean value of T_C will have consisted in the average of 240 recordings of temperature during the coldest hours of the day (i.e. 60 minutes × 4 hours) per winter day (240 minutes × 58 days) per the two species mixture categories (13,920 minutes × 2) per the two research sites (27,840 × 2), for a total of 55,680 minutes or 928 hours worth of temperature data. A total of 20 temperature sensors were used.

B.2.2.6 Calculating Δ*T* in summer and the effect of species mixture on shrub cooling performance (Year 3)

Temperature profiles were used to quantify the effect of species mixture on shrub cooling performance. These profiles were created based on calculations that used temperature data recorded during 61 summer days in Year 3 of the study. Specifically, these calculations were used to compare the total mean temperature difference (ΔT) between Control (bare substrate) and the shrub populations by category (i.e. by species and by species mixture) during the warmest hours of the day (12:00–16:00). (N.B. Six species of shrubs were observed during this period, as all had sufficient foliage to provide a distinct microclimate underneath their plant canopies.)

As in previous years, the assumption was that in the summer mean temperature on Control would likely be *higher* than mean temperature both *above* and *below* a plant canopy, due to the higher albedo and shading provided by foliage (i.e. plant canopy microclimate). Therefore, the calculation of ΔT refers to the mean temperature difference in degrees Celsius (°C):

1) between the mean temperature reached on bare substrate (T_C) and that reached above the plant canopy (T_A):

$$\Delta T = ([T_C] - [T_A])$$

2) and between the mean temperature reached on bare substrate (T_C) and that reached below the plant canopy (T_B):

$$\Delta T = ([T_C] - [T_B])$$

at any given minute between the hours of 12:00 and 16:00.

As the temperature sensors logged one record per minute, the calculation of mean temperature for T_A and T_B will each have consisted in the average of 240 recordings of temperature during the warmest hours of the day (i.e. 60 minutes × 4 hours) per summer day (240 minutes × 61 days) per species (14,640 minutes × 6 species) per the two species mixture categories (87,840 minutes × 2), for a total of 175,680 minutes or 2,928 hours worth of temperature data. Control units were limited to only two per research site and therefore the calculation of the mean value of T_C will have consisted in the average of 240 recordings of temperature during the warmest hours of the day (i.e. 60 minutes × 4 hours) per summer day (240 minutes × 61 days) per the two species mixture categories (14,640 minutes × 2) per the two research sites (29,280 × 2), for a total of 58,560 minutes or 976 hours worth of temperature data. A total of 26 temperature sensors were used.

B.3 Results of the temperature profile analysis

This section of Study ‘B’ presents the main findings from the temperature profile analysis, which was based on temperature data recorded during the winter and summer months of Year 1 (Section B.3.1), Year 2 (Section B.3.2) and Year 3 (Section B.3.3) of the study. The purpose of this analysis was to compare the temperature profiles of the different shrub species and to evaluate the effects of plant density, population size and species mixture on the ability of woody shrubs to increase temperature (i.e. insulate the rooftop) in the winter and reduce temperature (i.e. cool the rooftop) in the summer. The findings from this study may provide a better understanding of how species-specific characteristics and different spatial arrangements can influence shrub thermal performance.

B.3.1 The effects of species and plant density on shrub thermal performance (Year 1)

This subsection presents the results of temperature profile analysis for temperature data recorded during the winter and summer months of Year 1. Specifically, it analysed temperature recorded during 58 winter days and 71 summer days and compared the total mean temperature differences (ΔT) between Control (bare substrate) and the shrub populations by category (i.e. by species and by plant density) during the coldest hours of the day in winter (00:00–04:00) and the warmest hours of the day in summer (12:00–16:00). The ability to insulate in the winter (Section B.3.1.1) and to cool in the summer (Section B.3.1.2) by the different shrub species was evaluated in relation to how the shrubs were arranged on the rooftop – either in low-density (‘sparse’) or in high-density (‘dense’) shrub populations (Section B.2.1.1) – in order to compare the effect of plant density on the species’ temperature profiles.

B.3.1.1 The effects of species and plant density on shrub insulating performance (Winter)

The assumption was that in the winter mean temperature on Control (T_C) would likely be *lower* than mean temperature under a plant canopy (T_B), due to the protective barrier created by the plant canopy. Therefore, the calculations for the mean value of ΔT – or the temperature difference between plant canopy and bare substrate (i.e. T_B–T_C) at any given mintue – were in relation to the belief that the Control units would present more extreme conditions compared to the plant units (Section B.2.2.1). For the vast majority of the time this assumption was true and that was how ΔT was calculated to compare the species’ temperature profiles and evaluate the the effects of plant density on the insulating capacity of the three woody shrubs.

During the winter of Year 1, it was found that, on average, shrub populations on the rooftop increased substrate temperature compared to Control (Δ*T*) by only 0.73±0.04 °C. The lowest mean temperature reduction (Δ*T*) by the average shrub during this period was a negative value, of –0.11±0.04 °C, while the highest mean temperature reduction (Δ*T*) was of 1.62±0.05 °C. The maximum Δ*T* reached by a shrub population during this period was of 3.04 °C, in the high-density shrub populations of *Cistus*. In other words, an evergreen shrub during the coldest hours of winter maintained a microclimate underneath the plant canopy that was on average less than 1 °C warmer than bare substrate, with some days unable to increase temperatures above those of bare substrate (i.e. negative values of Δ*T*) but the majority of the time capable of doing so with by more than 1 °C, up to a maximum of 3 °C.

The mean Δ*T* reached by shrubs in low-density populations during winter was lower (0.69±0.05 °C) than that reached by shrubs in high-density populations (0.77±0.06 °C). However, this difference was not significant (*P*=0.327) (Fig. 17). Therefore, plant density did not affect overall shrub thermal performance in the winter.

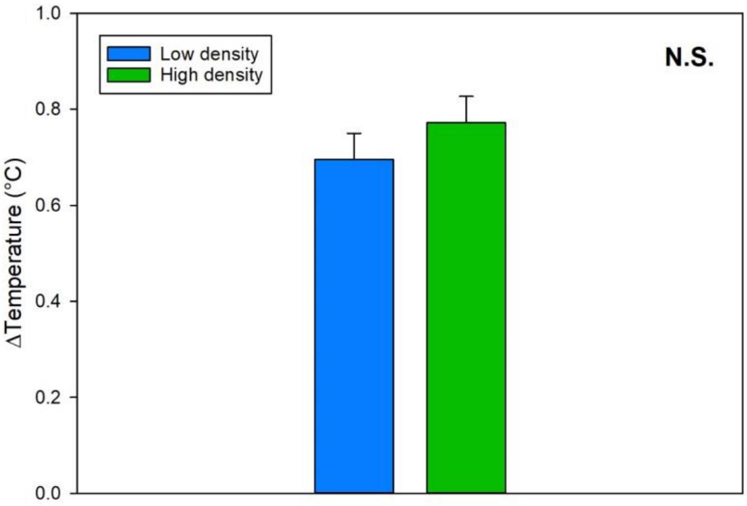


Figure 17. Comparison of low-density and high-density shrub populations. Vertical bar graphs with error bars comparing the mean temperature difference (Δ*T*, °C) reached in low-density populations with those reached in high-density populations, in relation to Control. The two shrub populatons were not significantly different.

Plant density did not have a significant effect on shrub thermal performance at species-level either (Table 42). However, *Cistus* maintained noticeably higher mean Δ*T* on high-density (0.80±0.07 °C) compared to low-density populations (0.68±0.06 °C). *Ceanothus* also maintained slightly warmer temperatures when placed in a 'dense' shrub population, but this difference was negligible. Despite providing the best insulation, *Viburnum* was unequivocally not affected by plant density (*P*=0.938).

Table 42. Mean temperature increase (Δ*T*) in relation to Control, for each species and for each category of plant density: low-density ('Sparse') and high-density ('Dense'). The *p*-values are the results of the analysis testing the differences between the mean values of 'Sparse' for the shrubs growing in the sparse population and the mean values of 'Dense' for those growing in the dense population, within each species.

	Δ*T* (°C)			
Species	**Total**	**Sparse**	**Dense**	***P*-value**
Viburnum tinus	**0.783**±0.039	**0.786**±0.064	**0.780**±0.051	0.938
Cistus × hybridus	**0.740**±0.046	**0.676**±0.062	**0.803**±0.069	0.172
Ceanothus thyrsiflorus	**0.441**±0.032	**0.428**±0.050	**0.454**±0.051	0.720

More interesting were the contrasting temperature profiles of the three shrubs. The total mean temperature increase (Δ*T*) for the winter was significantly less in *Ceanothus* (0.44±0.03 °C) compared to that of the other two species (Table 42 and Fig. 18).

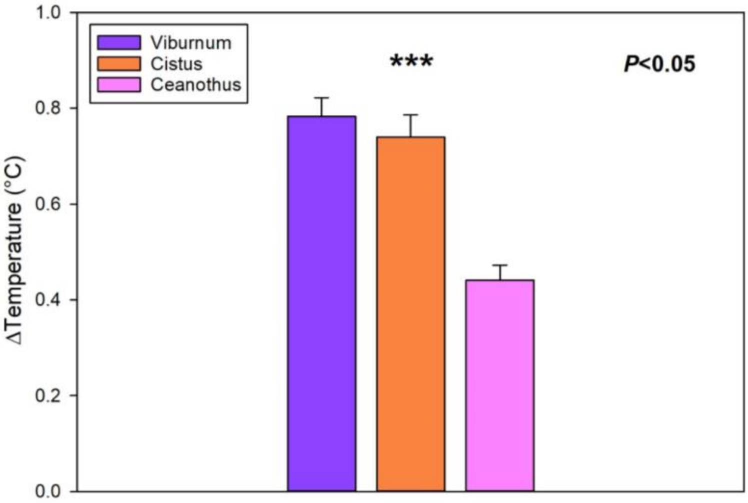


Figure 18. Total mean temperature increase (Δ*T*) by the shrubs during winter. Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by the three species, in relation to Control. *Ceanothus* insulated significantly less compared to the other two species.

In fact, *Viburnum* and *Cistus* maintained significantly higher temperatures compared to *Ceanothus* throughout the entire period, whether they were placed in low-density (Fig. 19a and Fig. 19b) or in high-density shrub populations (Fig. 20a and Fig. 20b). Moreover, there were days during this period in which mean temperature under the *Ceanothus* plant canopy was lower than Control (i.e. Δ*T* was negative), effectively indicating that this species sporadically performed worse than bare substrate. Therefore, *Viburnum* and *Cistus* were significantly better at providing insulatation during the coldest hours of the day in winter than was *Ceanothus*, regardless of plant density.

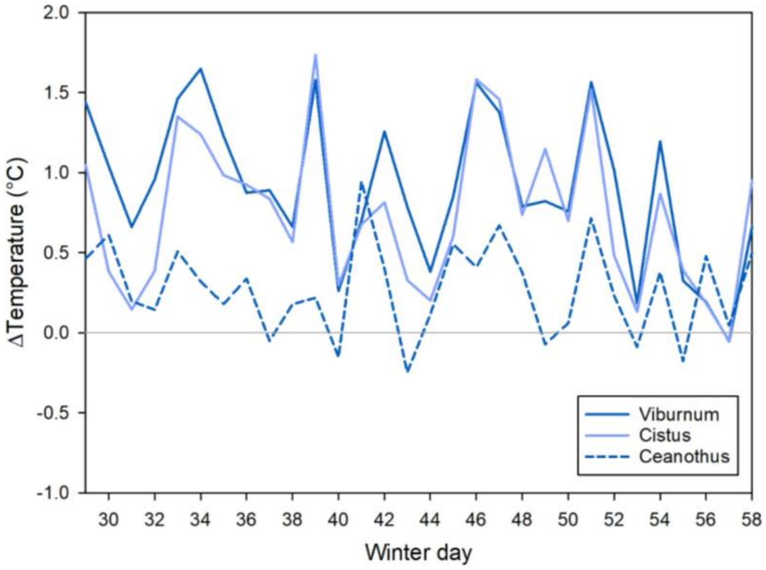


Figure 19a. Temperature profiles of sparsely-populated shrubs.
Time series with line graphs comparing the mean temperature difference (Δ*T*, °C) of the three species placed in low-density populations, in relation to Control.

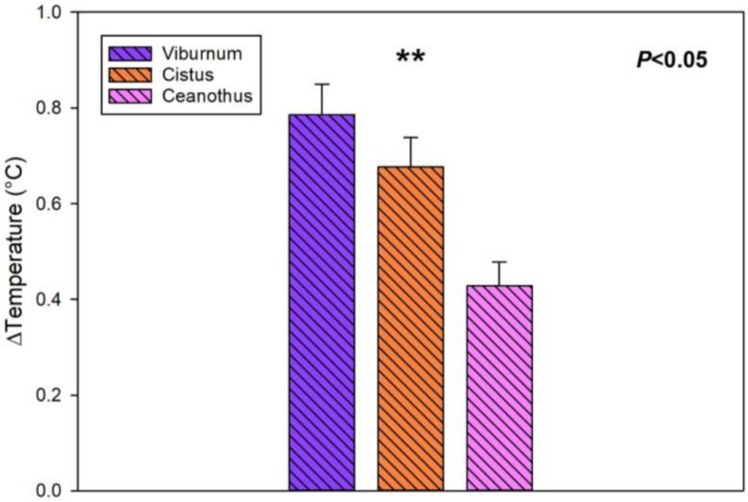


Figure 19b. Mean temperature increase (Δ*T*) by sparsely-populated shrubs.
Vertical bar graphs with error bars comparing the mean temperature difference (Δ*T*, °C) reached by the three species placed in low-density populations, in relation to Control. The insulating capacity among the species was significantly different.

Figure 20a. Temperature profiles of densely-populated shrubs.
Time series with line graphs comparing the mean temperature difference (Δ*T*, °C) of the three species placed in high-density populations, in relation to Control.

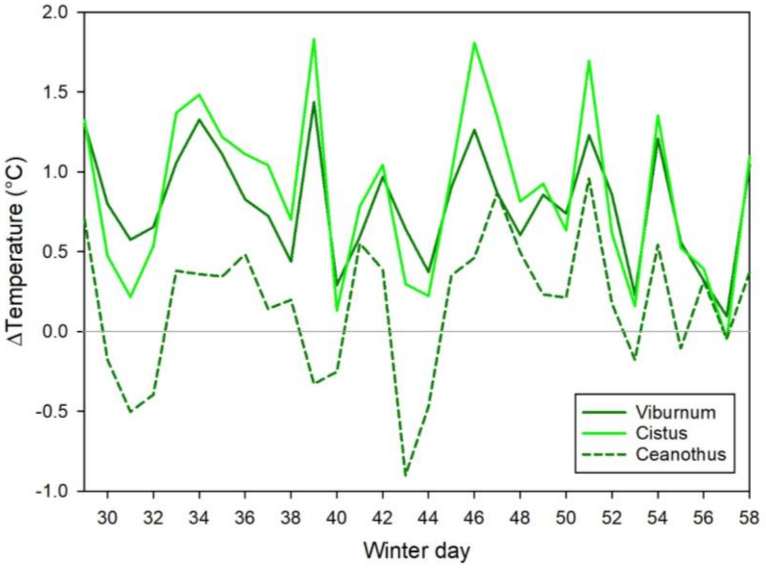
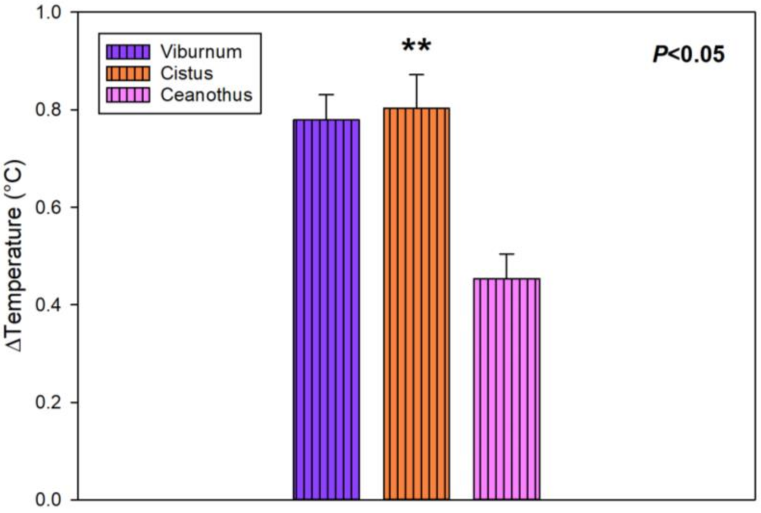


Figure 20b. Mean temperature increase (Δ*T*) by densely-populated shrubs.
Vertical bar graphs with error bars comparing the mean temperature difference (Δ*T*, °C) reached by the three species placed in high-density populations, in relation to Control. The insulating capacity of *Ceanothus* was significantly lower compared to the other species.



Plant density affected the three species in significantly different ways and this disparity was most intense when the conditions on the rooftop were extreme, as in particularly cold and windy days. The species' temperature profiles on such days enabled the closer observation of the trend noted previously, that in which plant density seemed to affect the shrubs in the following order: *Cistus* > *Ceanothus* > *Viburnum*, with *Cistus* noticeably affected, *Viburnum* not affected and *Ceanothus* somewhere in the middle. The analysis of temperature profiles on one markedly cold winter morning (00:00–4:00 on 02/03/2016), for example, clearly showed how both *Viburnum* (Fig. 21a) and *Cistus* (Fig. 22a) nearly always maintained temperatures above those of *Control* throughout those hours, but while plant density did not have any effect on *Viburnum* (Fig. 21b), in *Cistus* plant density had a significant effect and led this species to perform better when placed in high-density populations (Fig.

22b). Despite performing worse compared to the other species, *Ceanothus* was significantly affected by plant density in a similar way to *Cistus* (Fig. 23a and 23b); however, the way plant density affected *Ceanothus* could be classed as 'intermediate' between the other two species. Therefore, in the winter plant density influenced plant canopy microclimate differently depending on the *species*, a phenomena that foreshadowed what would later be observed in the summer months of the same year as a much more intense and complex phenomena.

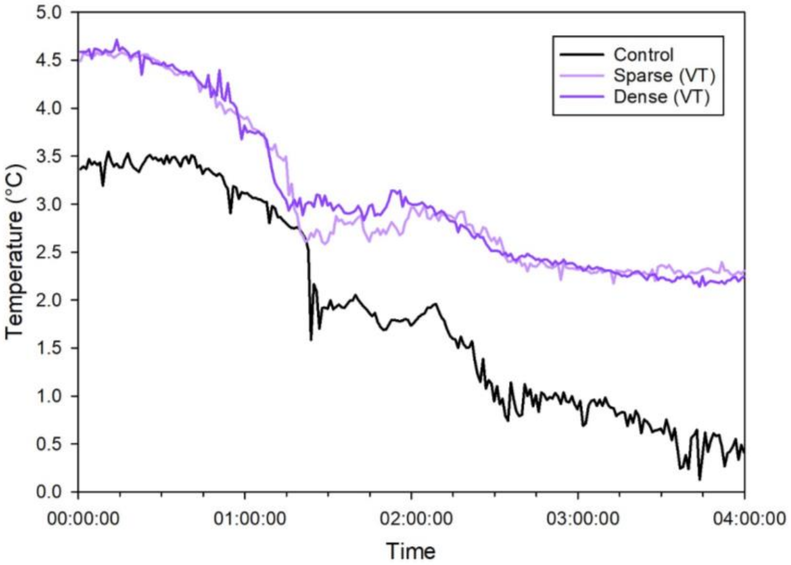
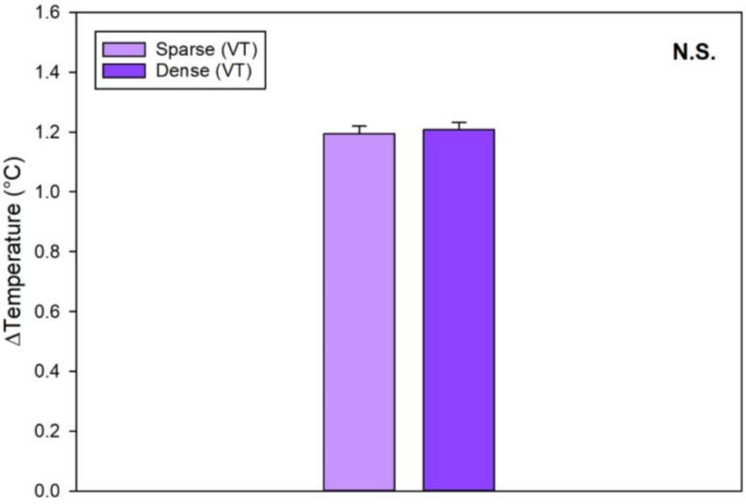


Figure 21a. Temperatures recorded on Control and on low- and high-density shrub populations of *Viburnum* on 02/03/2016. Time series with line graphs comparing the temperature (*T*, °C) recorded on Control and on *Viburnum* (VT) – in low-density ('Sparse') and on high-density ('Dense') populations – during one particularly cold morning.

Figure 21b. Mean temperature increase (Δ*T*) by sparsely vs densely-populated *Viburnum* shrubs on 02/03/2016. Vertical bar graphs with error bars comparing the mean temperature difference (Δ*T*, °C) reached by *Viburnum* (VT) in low- ('Sparse') and high-density ('Dense') populations, in relation to Control. The two categories were not significantly different.



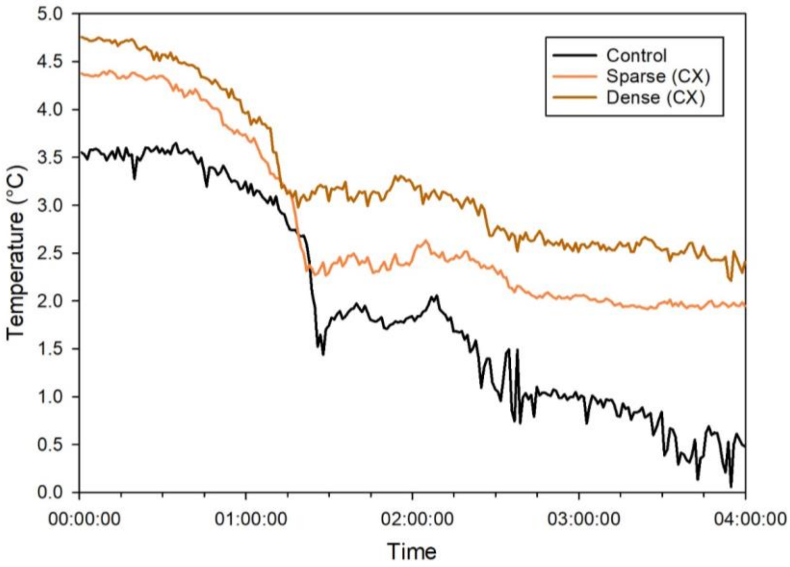
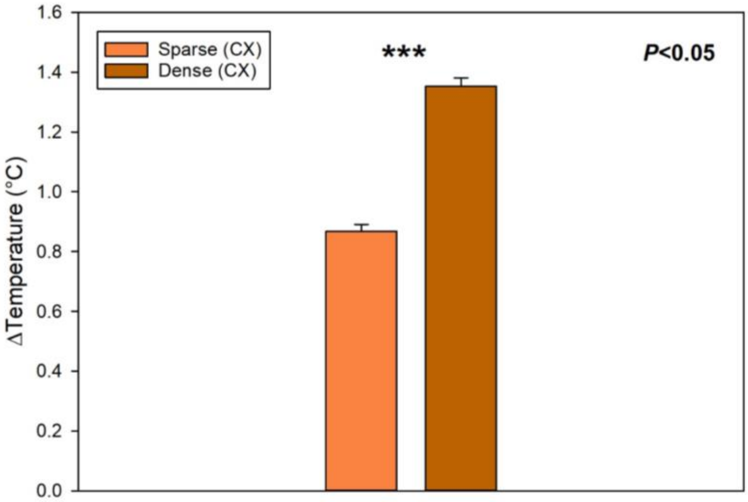


Figure 22a. Temperatures recorded on Control and on low- and high-density shrub populations of *Cistus* on 02/03/2016. Time series with line graphs comparing the temperature (*T*, °C) recorded on Control and on *Cistus* (CX) – in low-density ('Sparse') and on high-density ('Dense') populations – during one particularly cold morning.

Figure 22b. Mean temperature increase (Δ*T*) by sparsely vs densely-populated *Cistus* shrubs on 02/03/2016. Vertical bar graphs with error bars comparing the mean temperature difference (Δ*T*, °C) reached by *Cistus* (CX) in low- ('Sparse') and high-density ('Dense') populations, in relation to Control. The two categories were significantly different.



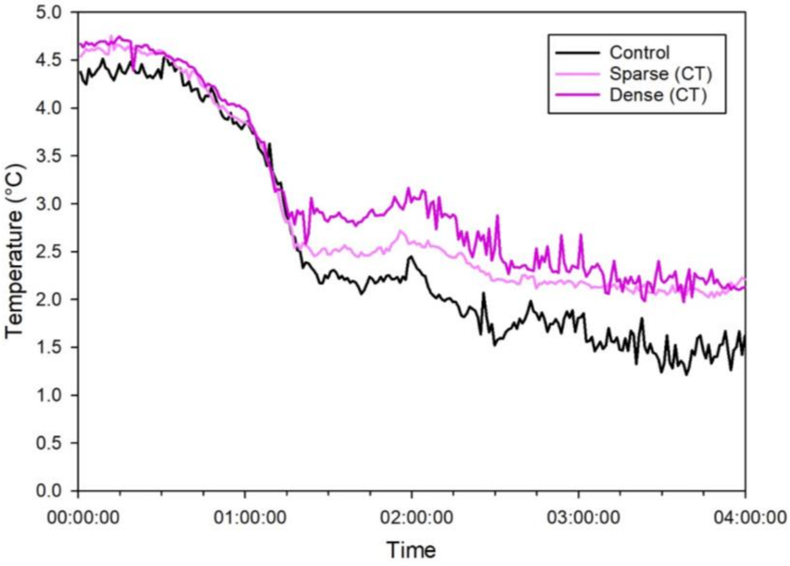
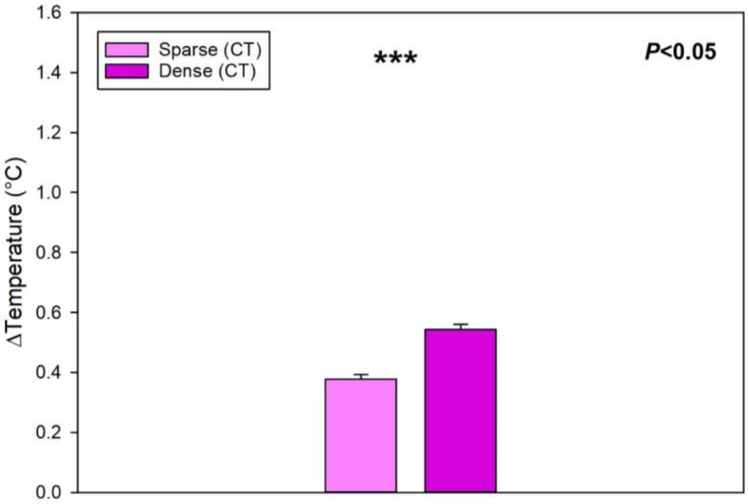


Figure 23a. Temperatures recorded on Control and on low- and high-density shrub populations of *Ceanothus* on 02/03/2016. Time series with line graphs comparing the temperature (*T*, °C) recorded on Control and on *Ceanothus* (CT) – in low-density ('Sparse') and on high-density ('Dense') populations – during one particularly cold morning.

Figure 23b. Mean temperature increase (Δ*T*) by sparsely vs densely-populated *Ceanothus* shrubs on 02/03/2016. Vertical bar graphs with error bars comparing the mean temperature difference (Δ*T*, °C) reached by *Ceanothus* (CT) in low- ('Sparse') and high-density ('Dense') populations, in relation to Control. The two categories were significantly different.



B.3.1.2 The effects of species and plant density on shrub cooling performance (Summer)

The assumption was that in the summer mean temperature on Control would likely be *higher* than mean temperature under a plant canopy, due to the shade created by the plant canopy. Therefore, the calculations for the mean value of Δ*T* – or the temperature difference between bare substrate and plant canopy (i.e. $T_C – T_B$) at any given mintue – were in relation to the belief that the Control units would present more extreme conditions compared to the plant units (Section B.2.2.2). For the vast majority of the time this assumption was true and that was how Δ*T* was calculated to compare the species' temperature profiles and evaluate the the effects of plant density on the cooling capacity of the six woody shrubs.

During the summer of Year 1, it was found that, on average, shrub populations on the rooftop decreased substrate temperature compared to Control (Δ*T*) by 4.44±0.28 °C. The lowest mean temperature reduction (Δ*T*) by the average shrub during this period was of 0.52±0.04 °C and the highest mean Δ*T* was of 10.46±0.71 °C. The highest *maximum* Δ*T* were reached in the high-density populations of *Cistus* (18.89 °C) and of *Viburnum* (18.82 °C). In other words, a woody shrub during the warmest hours of summer maintained a microclimate underneath the plant canopy that was always at least 4 °C (but normally could be over 10 °C) cooler than bare substrate, with the potential at any given time to be nearly 19 °C cooler.

The mean Δ*T* reached by shrubs in low-density populations during summer (3.85±0.25 °C) was significantly lower (P=0.003) than that reached by shrubs in high-density populations (5.03±0.31 °C) (Fig. 24). Therefore, plant density significantly affected the overall shrub thermal performance in the summer, with shrubs in high-density populations cooling by over 1 °C more than those in low-density populations.

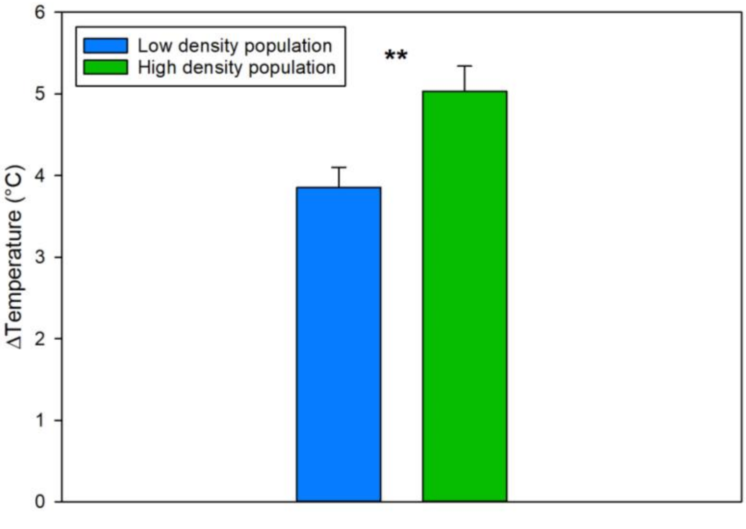


Figure 24. Comparison of low-density and high-density shrub populations. Vertical bar graphs with error bars comparing the mean temperature difference (Δ*T*, °C) reached in low-density populations with those reached in high-density populations, in relation to Control. The two shrub populatons were significantly different.

At species level, plant density also had a significant effect on the temperature profiles of the different shrubs. Half of the species were significantly affected by plant density: the deciduous shrubs (*Elaeagnus* and *Cotinus*) and the semi-deciduous *Cistus* (Table 43). These three species maintained significantly higher mean Δ*T* – and therefore had greater cooling capacity – when placed in high-density ('dense') populations than when in low-density ('sparse') ones. The evergreen shrubs (*Viburnum* and *Ceanothus*) and the semi-deciduous *Buddleja* also maintained slightly cooler temperatures when in dense shrub populations, but when compared to their respective sparse populations the difference was not significant. Despite providing the best cooling, *Viburnum* was unequivocally not affected by plant density.

Table 43. Mean temperature reduction (Δ*T*) in relation to Control, for each species and for each category of plant density: low-density ('Sparse') and high-density ('Dense'). The *p*-values are the results of the analysis testing the differences between the mean values of 'Sparse' for the shrubs growing in the sparse population and the mean values of 'Dense' for those growing in the dense population, within each species.

	Δ*T* (°C)			
Species	**Total**	**Sparse**	**Dense**	***P*-value**
Viburnum tinus	**5.874**±0.509	**5.719**±0.510	**6.028**±0.511	0.671
Ceanothus thyrsiflorus	**4.833**±0.723	**4.650**±0.681	**5.253**±0.759	0.559
Elaeagnus angustifolia	**4.822**±0.355	**3.866**±0.310	**5.779**±0.409	**<0.001**
Cistus × hybridus	**4.655**±0.355	**4.021**±0.319	**5.289**±0.411	**0.017**
Cotinus coggygria	**4.376**±0.287	**3.73**±0.252	**5.246**±0.324	**<0.001**
Buddleja davidii	**3.043**±0.250	**2.882**±0.248	**3.205**±0.264	0.376

A valuable feature of temperature profile analysis was the opportunity to observe the 'cooling' range of the six shrub species (Fig. 25). The cooling capacity was significantly different amongst the species (P<0.001). The total mean temperature reduction (Δ*T*) in the summer was significantly less by *Buddleja* (3.04±0.25 °C) compared to the other species, especially compared to *Viburnum* (5.87±0.51 °C). Thereby, the cooling capacity of the shrubs can be ranked in the following order: *Viburnum* > *Ceanothus* > *Elaeagnus* > *Cistus* > *Cotinus* > *Buddleja*. Therefore, *Viburnum* (the best performing shrub) cooled by nearly 3 °C more than *Buddleja* (the worst performing shrub).

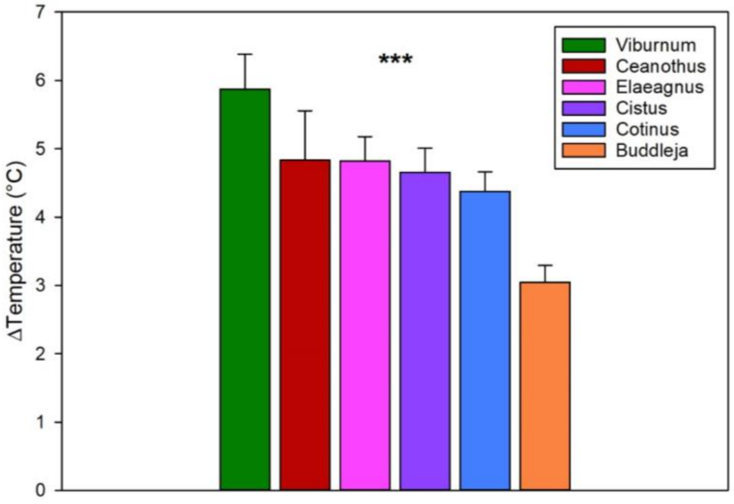


Figure 25. The shrubs' cooling capacity in summertime.
Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by the six species, in relation to Control. *Buddleja* cooled significantly less compared to the other species.

Another noteworthy trend observed in the summer was the fact that the shrub vegetation, especially 'dense' or high-density shrub vegetation, had a tendency to *delay* the reaching of peak midday temperatures compared to Control. This trend was observed by comparing the time in which air or ambient temperature (i.e. as logged by the weather station on each research site) reached the highest ('peak') temperature between 12:00 and 16:00 of each summer day to the time in which Control, low-density ('sparse') shrub populations and high-density shrub populations reached peak temperatures during the same time interval. Findings showed that, for the majority of the time, all three categories reached peak temperatures *before* air temperature did (i.e. *anticipated*), which is not a positive finding if the purpose of woody shrub vegetation is to delay maximum temperature on a rooftop. However, the times when the three categories delayed rather than anticipated the reaching of peak temperature compared to air temperature *increased* going from Control (i.e. no vegetation) to low-density shrub populations (i.e. little or sparse vegetation) to high-density shrub populations (i.e. dense vegetation) – from only 2.4% of the time on Control (Fig. 26a), to 11.0% on low-density vegetation (Fig. 26b) to 32.2% on high-density vegetation (Fig. 26c). Therefore, high-density woody vegetation has the ability to delay the reaching of peak high temperatures on a rooftop by nearly a third of the time.

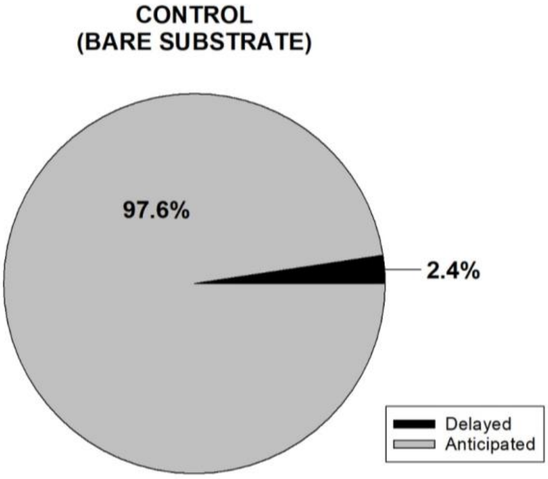


Figure 26a. The effect of bare substrate on the reaching of peak midday temperatures.
Pie graph comparing the percentage of time in which bare substrate, or Control, either delayed (black) or anticipated (grey) the reaching of peak temperatures on the rooftop in relation to air temperature.

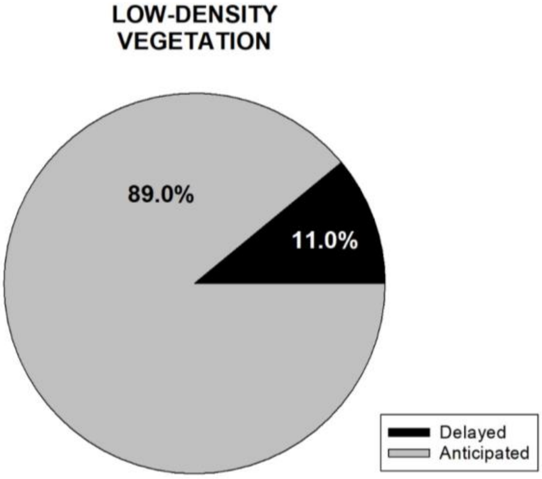


Figure 26b. The effect of low-density vegetation on the reaching of peak midday temperatures.
Pie graph comparing the percentage of time in which low-density shrub vegetation, or 'sparse' populations, either delayed (black) or anticipated (grey) the reaching of peak temperatures on the rooftop in relation to air temperature.

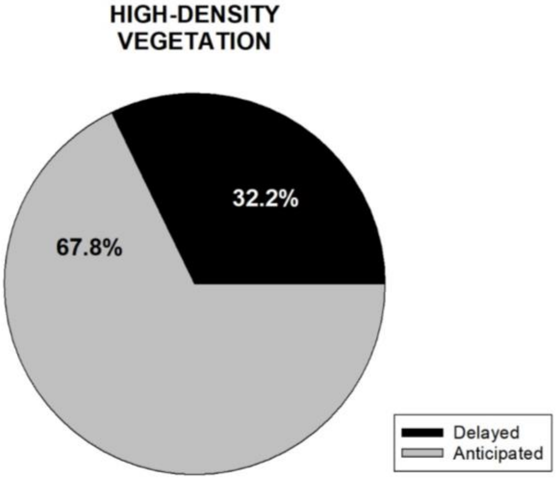


Figure 26c. The effect of high-density vegetation on the reaching of peak midday temperatures.
Pie graph comparing the percentage of time in which high-density shrub vegetation, or 'dense' populations, either delayed (black) or anticipated (grey) the reaching of peak temperatures on the rooftop in relation to air temperature.

B.3.2 The effect of population size on shrub thermal performance (Year 2)

This subsection presents the results of temperature profile analysis for temperature data recorded during the winter and summer months of Year 2. Specifically, it analysed temperature recorded during 83 winter days and 67 summer days and compared the total mean temperature differences (ΔT) between Control (bare substrate) and the shrub populations by category (i.e. by species, by population size and by plant density) during the coldest hours of the day in winter (00:00–04:00) and the warmest hours of the day in summer (12:00–16:00). The ability to insulate in the winter (Section B.3.2.1) and to cool in the summer (Section B.3.2.2) by the different shrub species was evaluated in relation to how they were arranged on the rooftop: either in low-density small populations (‘sparse’ & ‘3×3’), low-density large populations (‘sparse’ & ‘4×4’), high-density small populations (‘dense’ & ‘3×3’) or high-density large populations (‘dense’ & ‘4×4’) of shrubs (Section B.2.1.2).

B.3.2.1 The effect of population size on shrub insulating performance (Winter)

The assumption was that in the winter mean temperature on Control would likely be *lower* than mean temperature under a plant canopy, due to the protective barrier created by the plant canopy. Therefore, the calculations for the mean value of ΔT – or the temperature difference between plant canopy and bare substrate (i.e. T_B–T_C) at any given mintue – were in relation to the belief that the Control units would present more extreme conditions compared to the plant units (Section B.2.2.3). For the vast majority of the time, this assumption was true and that was how ΔT was calculated to compare the species’ temperature profiles and evaluate the the effects of both population size and plant density on the insulating capacity of the three woody shrubs.

During the winter of Year 2, the four categories of woody shrub populations – ‘low-density small populations’, ‘low-density large populations’, ‘high-density small populations’ and ‘high-density large populations’ – were found to be significantly different (P=0.010) and that shrub performance in terms of insulation seemingly increased with both population size and plant density (Fig. 27).

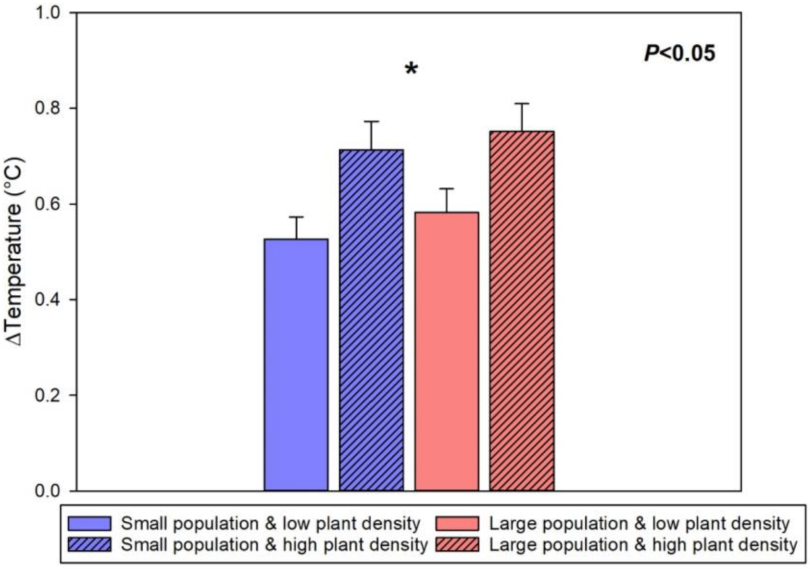


Figure 27. Shrub performance increased with population size and plant density. Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by woody shrubs, in relation to Control. The four categories of shrub populations (small & low density; small & high density; large & low density; large & high density) were significantly different.

However, when the temperature data was combined and analysed to compare only the two population categories (i.e. small and large shrub populations) to determine whether population size had a significant effect on the shrubs' insulating performance, it emerged that population size was not an influencing factor (Fig. 28). The thermal performance of the average shrub was therefore not affected by how big the shrub population was (i.e. by the number of individual plants), but rather by how dense it was (i.e. how close the individual plants were to one another) (Fig. 29). In fact, the average shrub placed in high-density populations (0.73±0.06 °C) performed significantly better (*P*=0.023) compared to a shrub placed in low-density populations (0.56±0.05 °C). This difference between the two plant density categories can be observed throughout the winter, with shrubs in high-density populations nearly always performing better than those in low-density populations (Fig. 30).

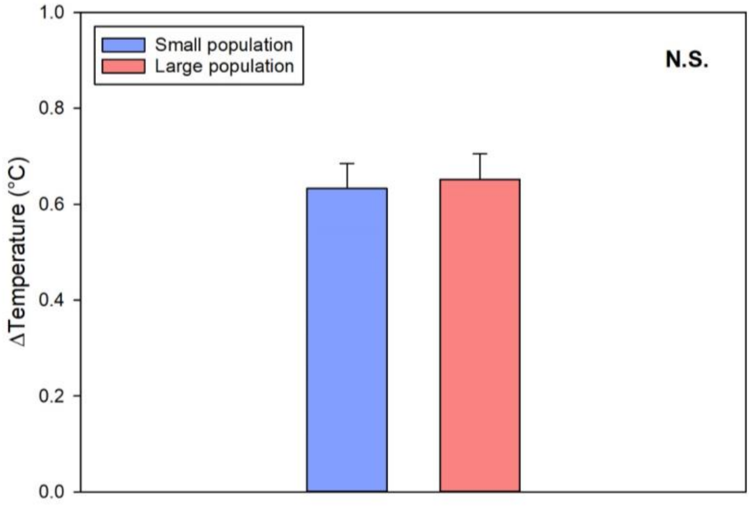


Figure 28. Shrub performance was not influenced by population size. Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by small and large populations of woody shrubs, in relation to Control. Population size was not a factor that determined how well a shrub provided insulation.

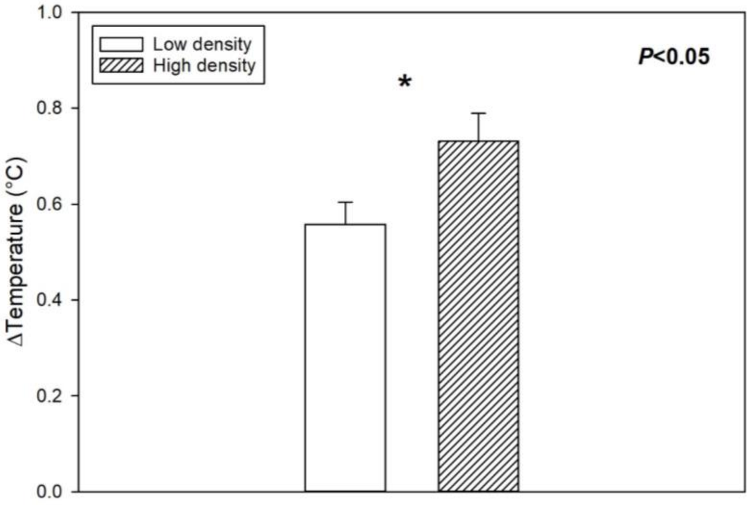


Figure 29. Shrub performance was primarily affected by plant density. Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by low-density and high-density populations of woody shrubs, in relation to Control. Plant density was a significant factor in determining how well a shrub provided insulation and higher plant density meant better-performing shrubs.

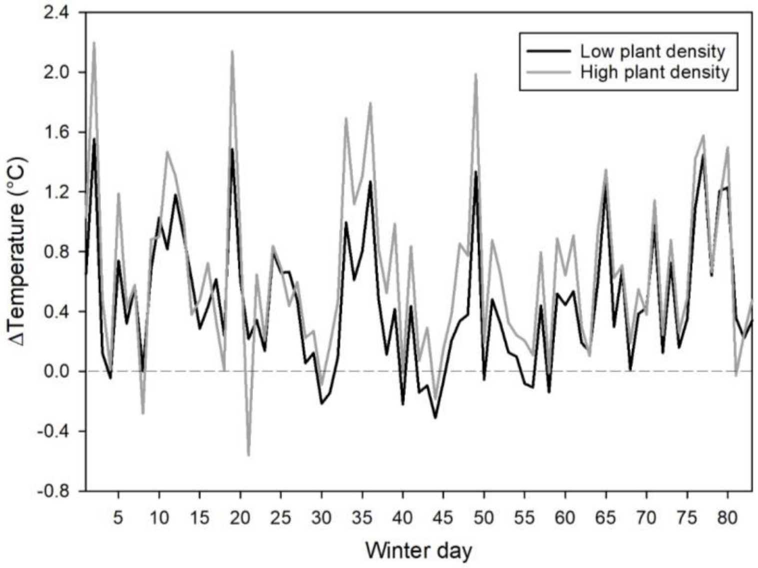


Figure 30. Temperature profiles of low-density and high-density shrub populations in wintertime. Time series with line graphs comparing the mean temperature increase (Δ*T*, °C) by the average shrub when placed in low-density (black) and high-density (grey) populations during winter, in relation to Control. High plant density guaranteed better shrub performance throughout.

Moreover, the 'insulating' capacities of the three shrub species were clearly distinct (Fig. 31). The total mean temperature increase (Δ*T*) in the winter was significantly lower ($P<0.001$) by *Ceanothus* (0.46±0.05 °C) compared to *Cistus* (0.72±0.09 °C) and especially to *Viburnum* (1.18±0.12 °C). Thereby, the insulating capacity of the shrubs can be ranked in the following order: *Viburnum* > *Cistus* > *Ceanothus*, with *Viburnum* performing the best and insulating nearly double the amount as *Ceanothus*, regardless of the category of shrub population (i.e. the four combinations of population size and plant density) they were placed in (Fig. 32).

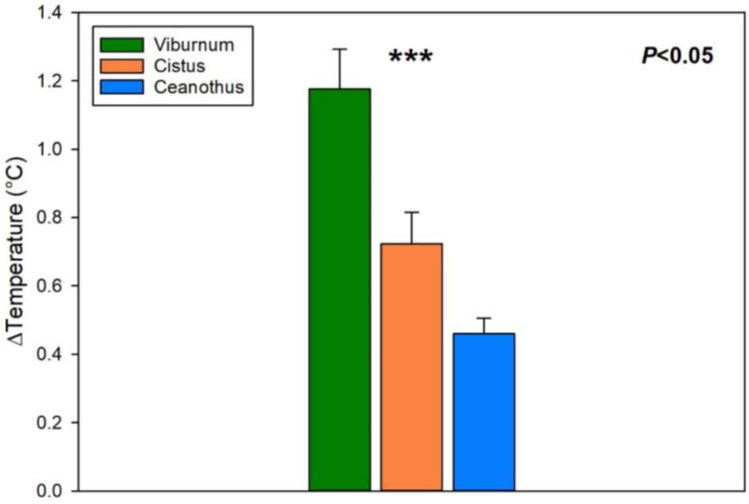


Figure 31. The shrubs' insulating capacity in wintertime.
Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by the three species, in relation to Control. *Ceanothus* insulated significantly less compared to the other species.

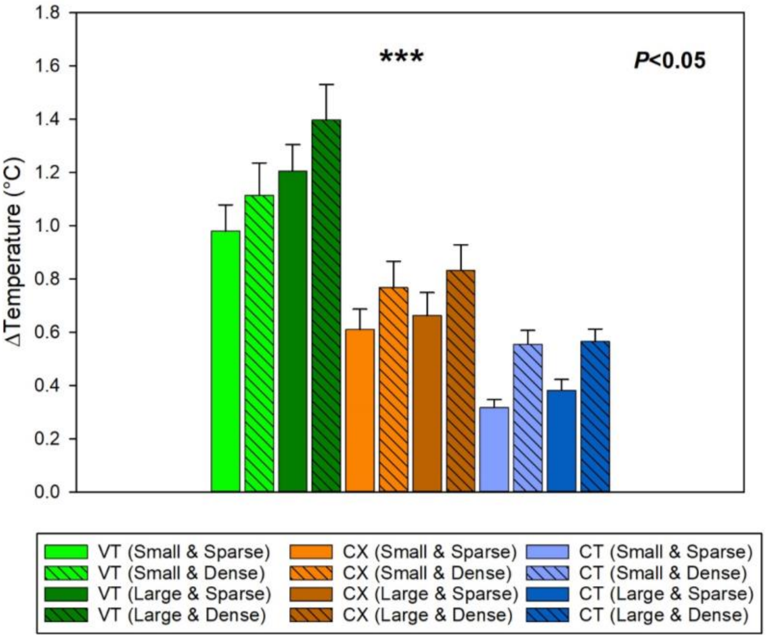


Figure 32. The effect of population size and plant density on the shrubs' insulating capacity in wintertime.
Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by *Viburnum* (VT), *Cistus* (CX) and *Ceanothus* (CT), in relation to Control and as affected by the four experimental categories: small population & low density; small population & high density; large population & low density and large population and high density.

B.3.2.2 The effect of population size on shrub cooling performance (Summer)

The assumption was that in the summer mean temperature on Control would likely be *higher* than mean temperature under a plant canopy, due to the shade created by the plant canopy. Therefore, the calculations for the mean value of ΔT – or the temperature difference between bare substrate and plant canopy (i.e. $T_C – T_B$) at any given mintue – were in relation to the belief that the Control units would present more extreme conditions compared to the plant units (Section B.2.2.4). For the vast majority of the time, this assumption was true and that was how ΔT was calculated to compare the species' temperature profiles and evaluate the the effects of both population size and plant density on the cooling capacity of the six woody shrubs.

During the summer of Year 2, it was found that the four categories of woody shrub populations – 'low-density small population', 'low-density large population', 'high-density small population' and 'high-density large population' – were found to be significantly different ($P<0.001$) and that shrub performance in terms of cooling seemingly increased with plant density but not with population size (Fig. 33). In fact, it would seem that the worst combination in terms of shrub cooling performance was that of 'low-density' and 'large population' (Fig. 34).

When the temperature data was combined and analysed to compare only the two population categories (i.e. small and large shrub populations) to determine whether population size had a significant effect on the shrubs' insulating performance, it emerged that population size was not an influencing factor (Fig. 35). The thermal performance of the average shrub was therefore not affected by how big the shrub population was (i.e. by the number of individual plants), but rather by how dense it was (i.e. how close the individual plants were to one another) (Fig. 36). In fact, the average shrub placed in high-density populations (3.73±0.29 °C) performed significantly better ($P<0.001$) compared to a shrub placed in low-density populations (2.21±0.22 °C). This difference between the two plant density categories can be observed throughout the summer, with shrubs in high-density populations almost always performing better than those in low-density populations (Fig. 37).

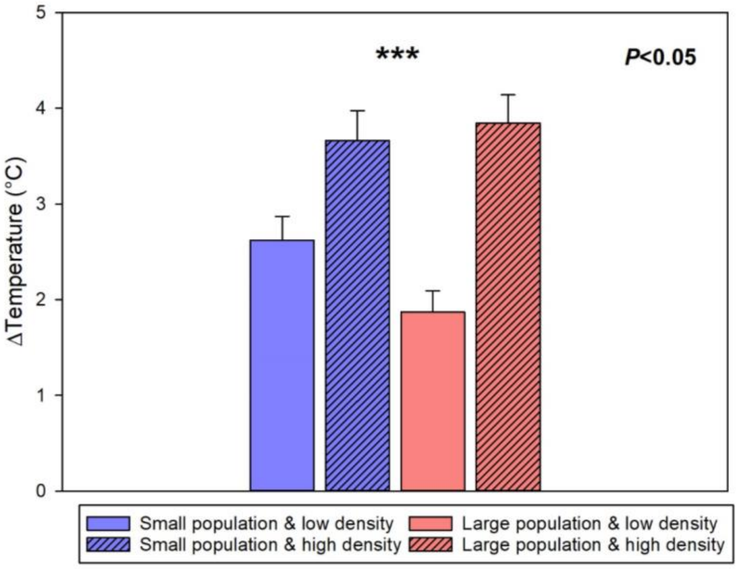


Figure 33. Shrub performance increased with plant density but not with population size.
Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by woody shrubs, in relation to Control. The four categories of shrub populations (small & low density; small & high density; large & low density; large & high density) were significantly different. Shrub cooling performance increased with plant density but not with population size.

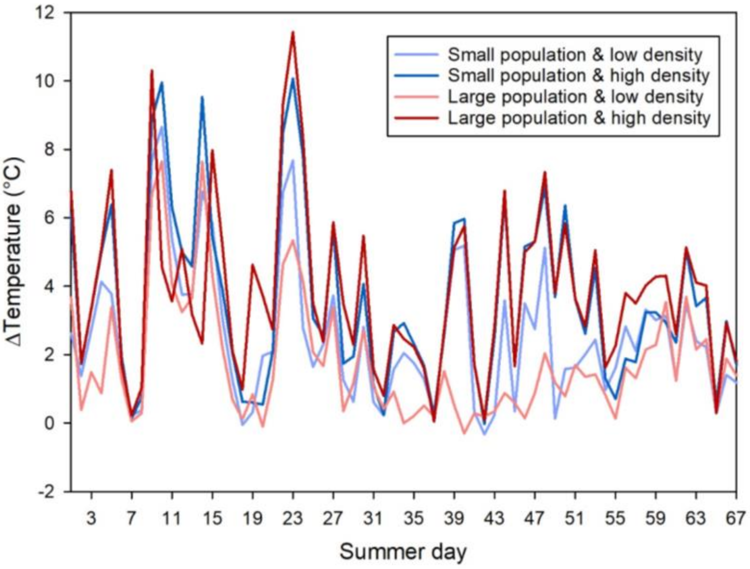


Figure 34. Temperature profiles of the four categories of shrub populations in summertime.
Time series with line graphs comparing the mean temperature reduction (Δ*T*, °C) by the average shrub when placed in each of the four categories of shrub population. The combination of large shrub population with low plant density resulted in the worst cooling performance by the shrubs throughout the summer.

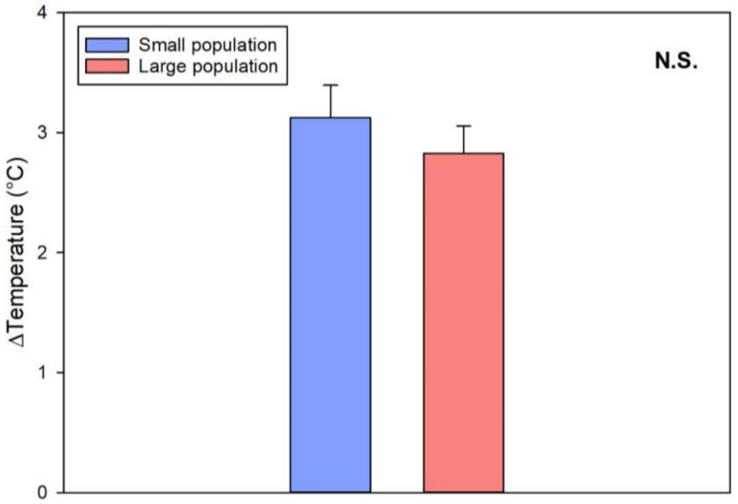


Figure 35. Shrub performance was not influenced by population size.
Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by small and large populations of woody shrubs, in relation to Control. Population size was not a factor that determined how well a shrub cooled.

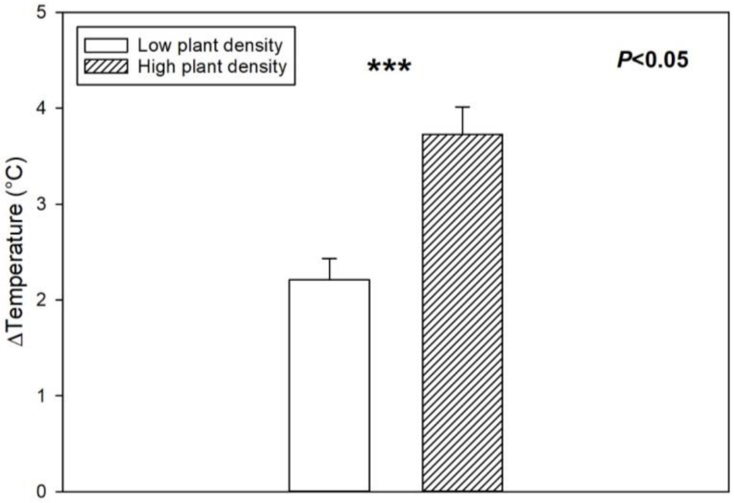


Figure 36. Shrub performance was primarily affected by plant density. Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by low-density and high-density populations of woody shrubs, in relation to Control. Plant density was a significant factor in determining how well a shrub cooled and higher plant density meant better-performing shrubs.

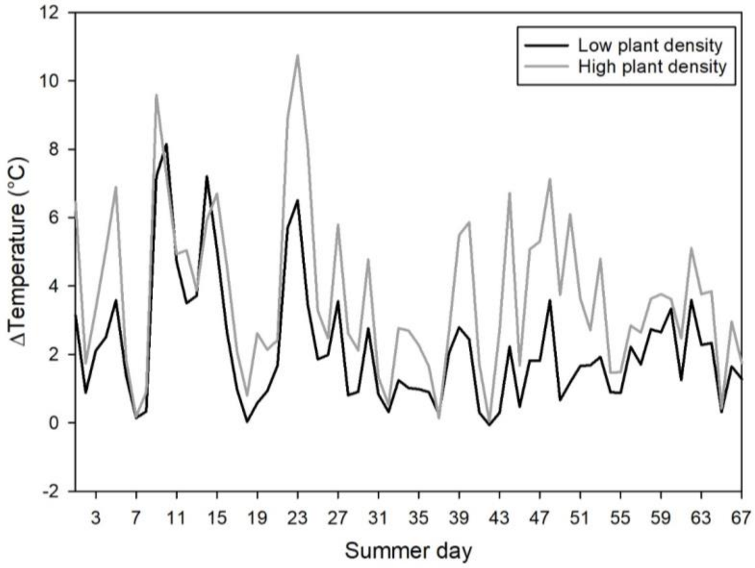


Figure 37. Temperature profiles of low-density and high-density shrub populations in the summer. Time series with line graphs comparing the mean temperature reduction (Δ*T*, °C) by the average shrub when placed in low-density (black) and high-density (grey) populations during summer, in relation to Control. High plant density guaranteed better shrub performance throughout.

On average, the ‘cooling’ range of the six shrub species was between approximately 2.5 °C and 7.0 °C, with *Buddleja* performing the worst and *Viburnum* exhibiting a clearly superior cooling capacity (Table 44). In fact, *Viburnum* was able to reduce temperatures compared to Control (Δ*T*) by between 4.0 °C and 4.5 °C more than all other shrubs. Despite the disparity in cooling performance amongst the species, the majority of them were significantly affected by the different experimental categories and displayed common theme with regards to the combination of large population and low plant density, in which all species performed worst (Fig. 38a–38f). Despite not significantly affecting shrubs in general (Fig. 35), population size did have an effect at species level, with some (e.g. *Ceanothus* and *Cotinus*) clearly showing greater cooling capacity with an increase in both plant density *and* population size (Fig. 38d and Fig. 38e, respectively).

Table 44. The cooling performances of each species and for each experimental category. Mean temperature reduction (Δ*T*) in relation to Control, for each species and for each combination of population size and plant density. The species are listed as VT (*Viburnum*); CX (*Cistus*); CC (*Cotinus*); CT (*Ceanothus*); EA (*Elaeagnus*) and BD (*Buddleja*). The four categories are small low-density population ('Small & Sparse'); small high-density population ('Small & Dense'), large low-density population ('Large & Sparse') and large high-density population ('Large & Dense'). *P*-values are the result of testing the differences between mean values per experimental category, within each species.

	Δ*T* (°C)					
Species	**Total**	**Small & Sparse**	**Small & Dense**	**Large & Sparse**	**Large & Dense**	***P*-value**
VT	**7.092**±0.751	**7.334**±0.720	**8.003**±0.784	**5.478**±0.621	**7.552**±0.786	0.084
CX	**3.060**±0.382	**2.587**±0.279	**3.758**±0.420	**2.093**±0.260	**3.832**±0.450	**0.001**
CC	**2.941**±0.448	**2.543**±0.349	**2.925**±0.473	**2.302**±0.375	**3.936**±0.531	**0.044**
CT	**2.846**±0.453	**1.980**±0.272	**3.291**±0.443	**1.766**±0.264	**4.006**±0.541	**<0.001**
EA	**2.748**±0.442	**3.73**±0.252	**5.246**±0.324	**6.028**±0.511	**6.028**±0.511	**0.003**
BD	**2.524**±0.516	**2.256**±0.336	**3.571**±0.471	**1.422**±0.340	**3.191**±0.406	0.066

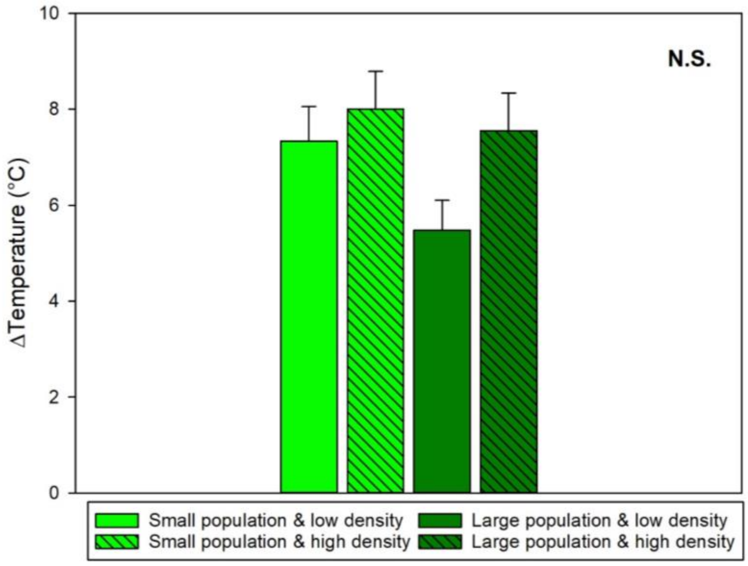


Figure 38a. *Viburnum*'s cooling capacity was not affected by plant density or population size. Vertical bar graphs with error bars comparing the total mean temperature reduction (Δ*T*, °C) by *Viburnum*, in relation to Control and to the four experimental categories: small low-density population; small high-density population; large low-density population and large high-density. None of the combinations had a significant effect on the cooling capacity of *Viburnum*.

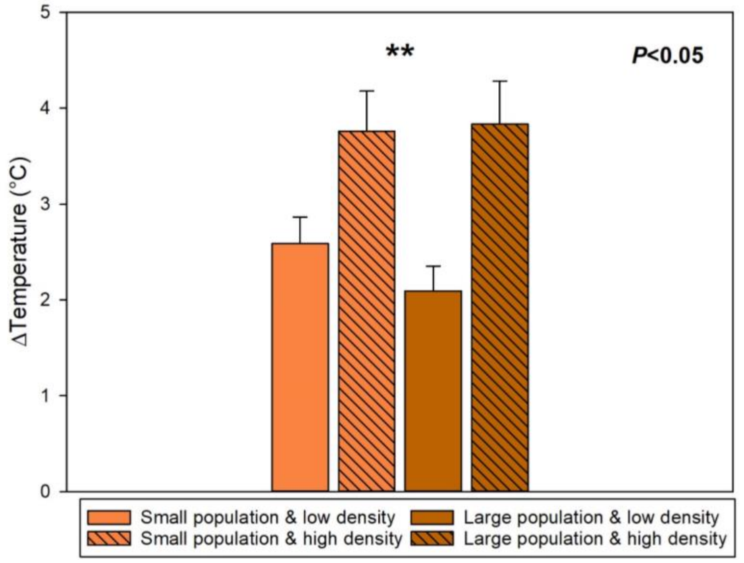


Figure 38b. ***Cistus'* cooling capacity was primarily affected by plant density.** Vertical bar graphs with error bars comparing the total mean temperature reduction (Δ*T*, °C) by *Cistus*, in relation to Control and to the four experimental categories: small low-density population; small high-density population; large low-density population and large high-density. The combinations did have a significant effect on the cooling capacity of *Cistus*, but primarily in terms of plant density.

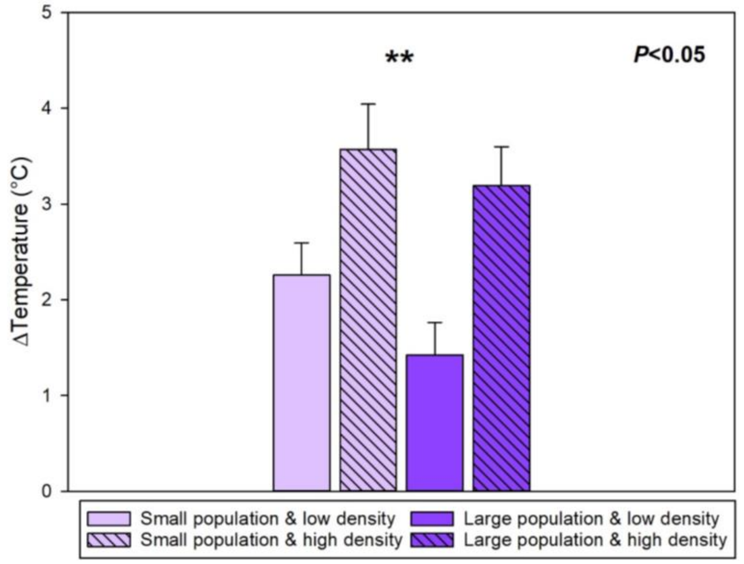


Figure 38c. ***Elaeagnus'* cooling capacity was affected by both plant density and population size.** Vertical bar graphs with error bars comparing the total mean temperature reduction (Δ*T*, °C) by *Elaeagnus*, in relation to Control and to the four experimental categories: small low-density population; small high-density population; large low-density population and large high-density. The combinations had an overall significant effect on the cooling capacity of *Elaeagnus*.

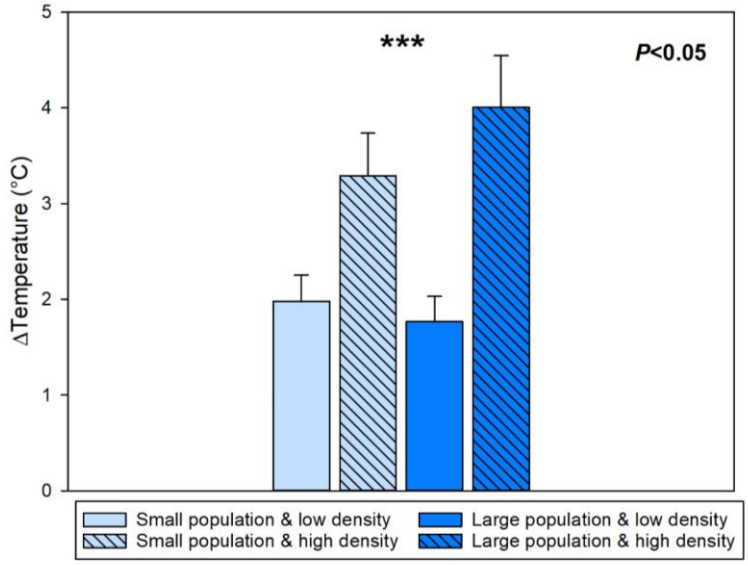


Figure 38d. ***Ceanothus'* cooling capacity was affected by both plant density and population size.** Vertical bar graphs with error bars comparing the total mean temperature reduction (Δ*T*, °C) by *Ceanothus*, in relation to Control and to the four experimental categories: small low-density population; small high-density population; large low-density population and large high-density. The combinations had an overall significant effect on the cooling capacity of *Ceanothus*.

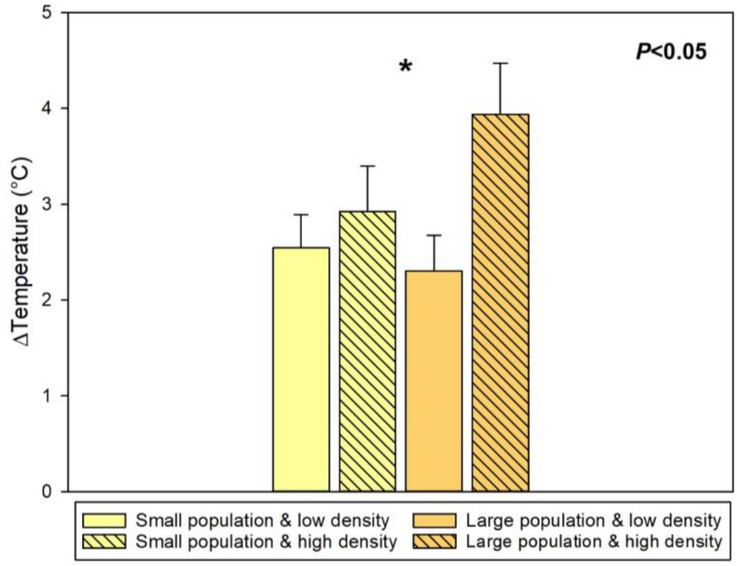


Figure 38e. ***Cotinus'*** **cooling capacity was affected by both plant density and population size.**
Vertical bar graphs with error bars comparing the total mean temperature reduction (Δ*T*, °C) by *Cotinus*, in relation to Control and to the four experimental categories: small low-density population; small high-density population; large low-density population and large high-density. The combinations had an overall significant effect on the cooling capacity of *Cotinus*.

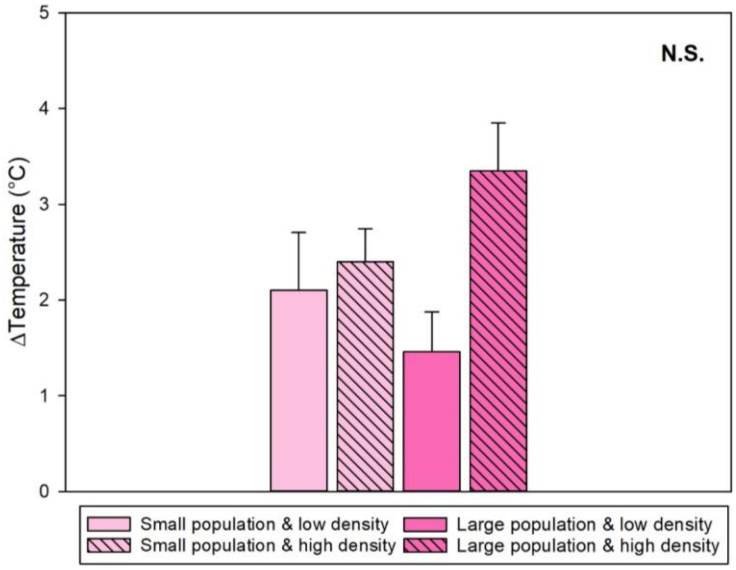


Figure 38f. ***Buddleja*'s cooling capacity was not affected by plant density or population size.**
Vertical bar graphs with error bars comparing the total mean temperature reduction (Δ*T*, °C) by *Buddleja*, in relation to Control and to the four experimental categories: small low-density population; small high-density population; large low-density population and large high-density. The combinations did not have a significant effect on the cooling capacity of *Buddleja*.

B.3.3 The effect of species mixture on shrub thermal performance (Year 3)

This subsection presents the results of temperature profile analysis for temperature data recorded during the winter and summer months of Year 3. Specifically, it analysed temperature recorded during 58 winter days and 61 summer days and compared the total mean temperature differences (ΔT) between Control (bare substrate) and the shrub populations by category (i.e. by species and by species mixture) during the coldest hours of the day in winter (00:00–04:00) and the warmest hours of the day in the summer (12:00–16:00). The ability to insulate in the winter (Section B.3.3.1) and to cool in the summer (Section B.3.3.2) by the different shrub species was evaluated in relation to how the shrubs were arranged on the rooftop – either in monospecific (single-species) or in polyspecific ('mixed') shrub populations (Section B.2.1.3) – in order to compare the effect of species mixture on the species' temperature profiles.

B.3.3.1 The effect of species mixture on shrub insulating performance (Winter)

The assumption was that in the winter mean temperature on Control would likely be *lower* than mean temperature under a plant canopy, due to the protective barrier created by the plant canopy. Therefore, the calculations for the mean value of ΔT – or the temperature difference between above- or below-plant canopy and bare substrate (i.e. T_A–T_C or T_B–T_C, respectively) at any given mintue – were in relation to the belief that the Control units would present more extreme conditions compared to the plant units (Section B.2.2.5). For the vast majority of the time, this assumption was true and that was how ΔT was calculated to compare the species' temperature profiles and evaluate the the effects of species mixture on the insulating capacity of the four woody shrubs.

During the winter of Year 3, it was found that all the study species, in both monospecific and polyspecific populations, increased temperatures compared to Control in the winter, buffering extreme low temperatures at the coldest times of the day and therefore insulating the substrate when placed on rooftops (Fig. 39). The mean buffering capacity by the shrub canopies (ΔT_B) in winter ranged from 1.30±0.12 °C in *Viburnum* to 0.59±0.05 °C in *Buddleja* in the monospecific populations and from 1.15±0.13 °C in *Viburnum* to –0.33±0.08 °C in *Buddleja* in the polyspecific or mixed populations. Unsurprisingly, the difference in thermal performance by the four shrubs in winter was significant ($P<0.001$, Fig. 42). In most cases, the monospecific population of shrubs had a greater ability to buffer low temperatures compared to the polyspecific (or mixed) population of shrubs, with *Buddleja* even presenting negative temperature differences between Control and the polyspecific population below the canopy (ΔT_B). However, the difference between the ΔT_B in monospecific and polyspecific populations was only significant in *Buddleja* ($P<0.001$).

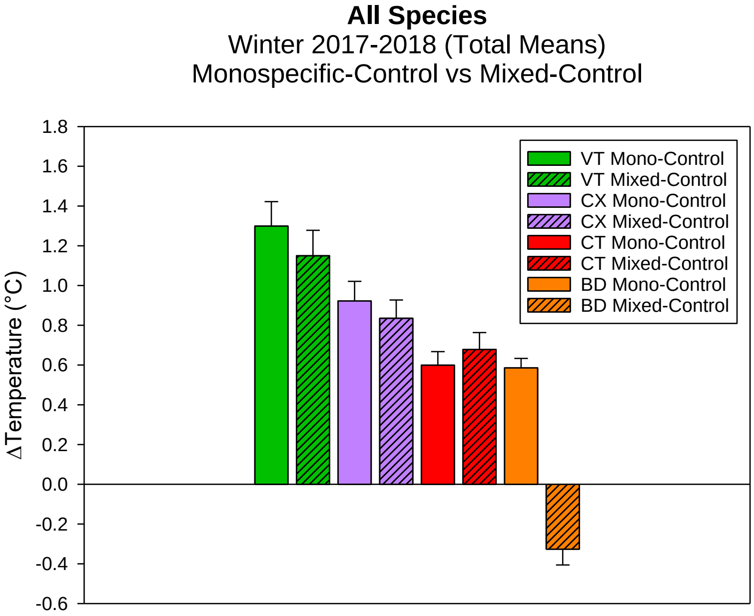


Figure 39. The effect of species mixture on mean ΔT in the winter. Bar graphs comparing the mean differences in temperature (ΔTemperature, °C) between the temperature reached by Control and that reached by the various categories of shrubs in the winter months of 2018: monospecific populations ("Mono–Control") and polyspecific populations ("Mixed–Control"), for all study species. These mean temperature differences relate to winter data at coldest peak of the day (00:00–04:00) for 58 days, as collected in 2018.

The difference between the temperature reached on Control and that reached in all vegetated categories (i.e. below- and above-canopy temperatures in both monospecific and polyspecific populations) was significant in all four species ($P<0.001$), with the exception of *Cistus* in the monospecific population ($P=0.146$) and *Ceanothus* in the monospecific population ($P=0.375$). However, the comparison of the ΔT of the two categories of species mixture in terms of their impact on below- (ΔT_B) and above-canopy (ΔT_A) temperatures (Fig. 40 and 41) highlighted the fact that the mean temperature reached above the canopy was unexpectedly and significantly higher than Control in all species ($P<0.001$), even higher than the mean temperature reached below the canopy of *Buddleja* in both the monospecific (Fig. 40) and the polyspecific population (Fig. 41). Moreover, the difference between the ΔT_A in monospecific populations and the ΔT_A in polyspecific populations was significant in all species ($P<0.001$ in *Cistus*, $P<0.05$ in *Viburnum* and *Buddleja*) except in *Ceanothus* ($P=0.479$). Though still maintaining higher mean temperatures compared to Control, *Ceanothus* in fact showed little difference in how its shrubs performed below- and above the canopy (Fig. 43). What is also counter-intuitive is the fact that, unlike ΔT_A, mean values of ΔT_B were not significantly different between the monospecific and the polyspecific populations of any of the species except for *Buddleja* (P<0.001), since it presented negative mean values of below-canopy temperatures compared to Control when placed in the polyspecific population (i.e. below-canopy temperatures were lower than Control). This curiosity can be easily observed when comparing the ΔT_B and ΔT_A of the different species and of the different categories of species mixture (Fig. 44a and 44b).

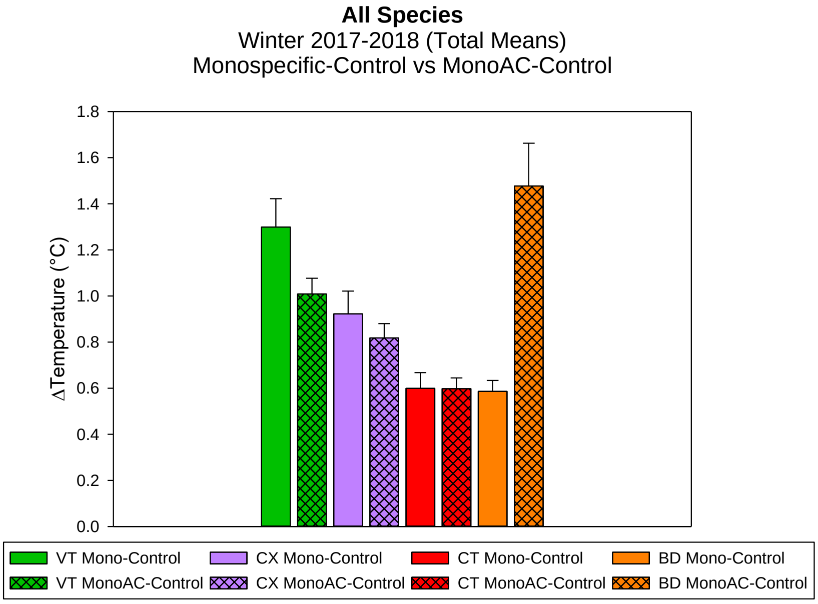


Figure 40. The effect of monospecific populations on below- and above-canopy ΔT. Bar graphs comparing the mean differences in temperature (ΔTemperature, °C) between the temperature reached by Control and that reached below and above the canopy of shrubs in the monospecific populations in the winter months of 2018, for all study species. These mean temperature differences relate to winter data at coldest peak of the day (00:00–04:00) for 58 days, as collected in 2018.

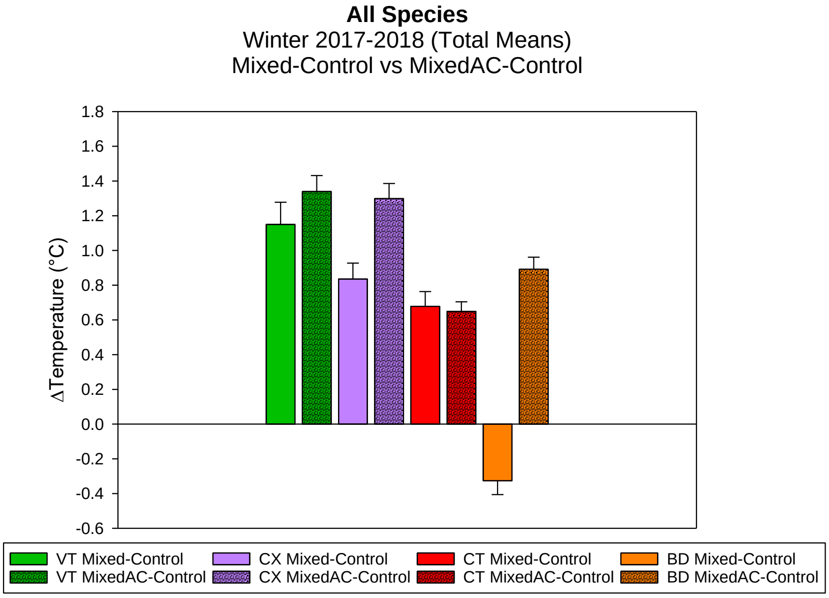
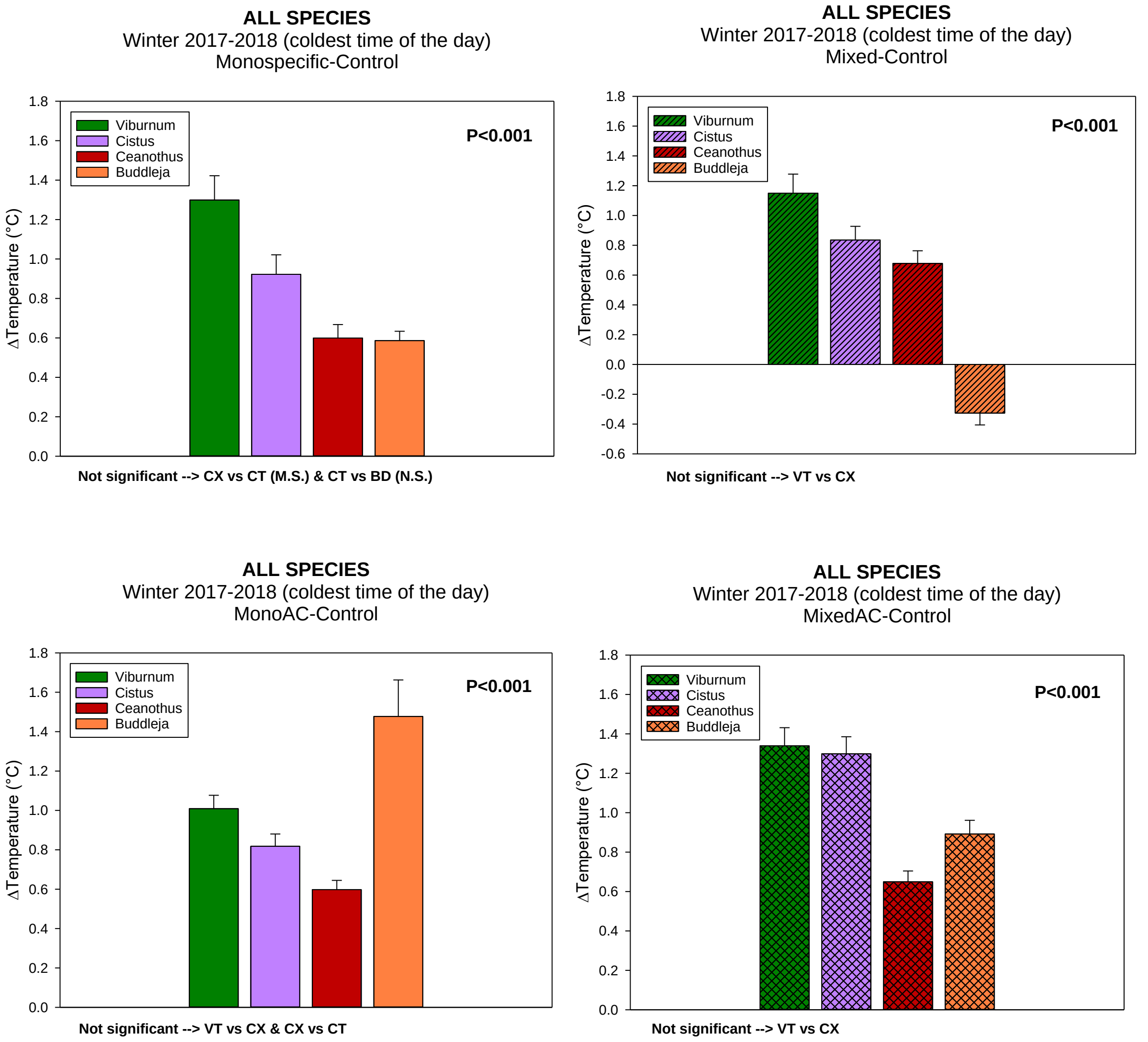


Figure 41. The effect of polyspecific populations on below and above-canopy ΔT. Bar graphs comparing the mean differences in temperature (ΔTemperature, °C) between the temperature reached by Control and that reached below and above the canopy of shrubs in the polyspecific populations in the winter months of 2018, for all study species. These mean temperature differences relate to winter data at coldest peak of the day (00:00–04:00) for 58 days, as collected in 2018.



ALL SPECIES
Winter 2017-2018 (coldest time of the day)
Monospecific-Control

Not significant --> CX vs CT (M.S.) & CT vs BD (N.S.)

ALL SPECIES
Winter 2017-2018 (coldest time of the day)
Mixed-Control

Not significant --> VT vs CX

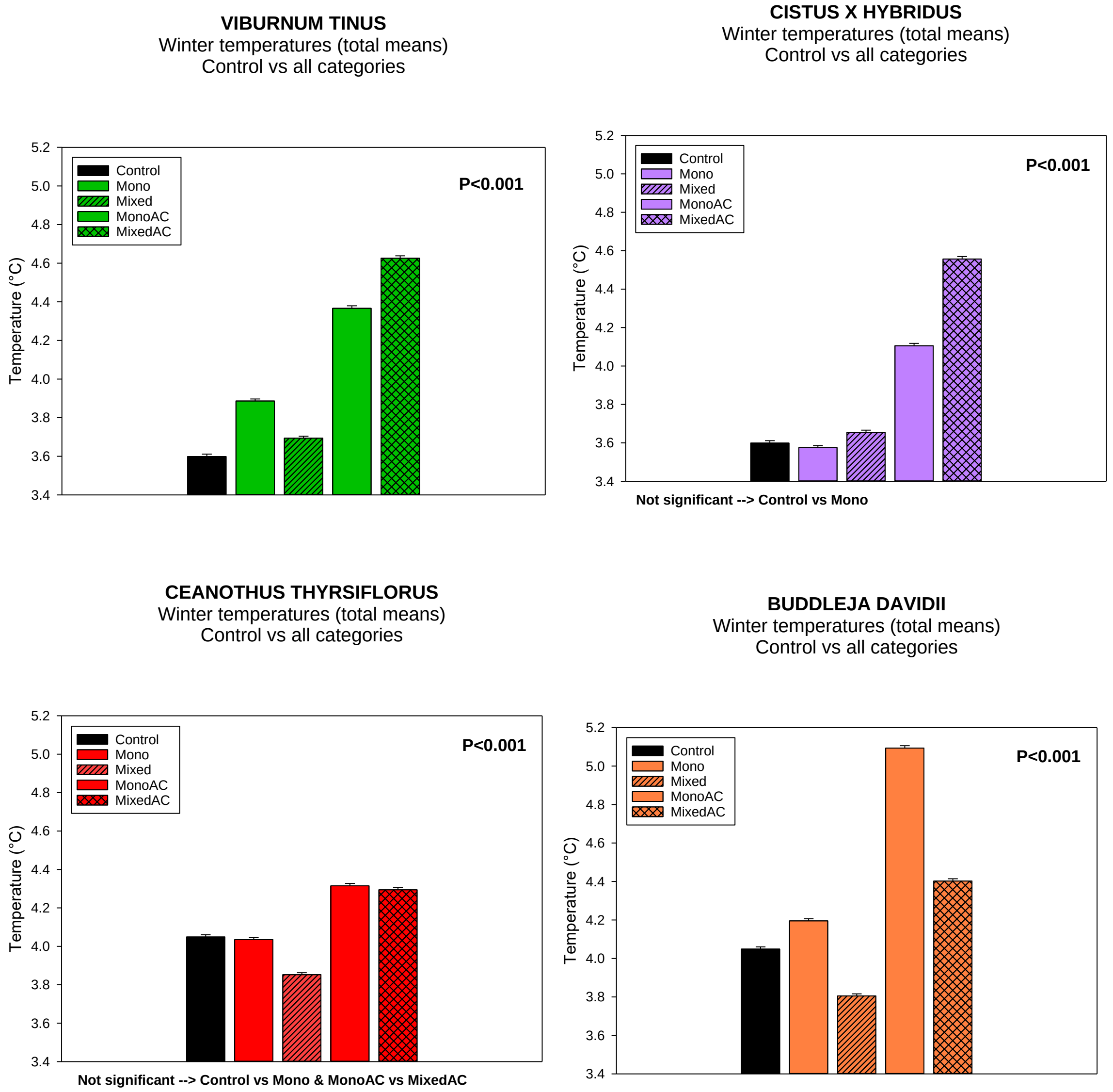
ALL SPECIES
Winter 2017-2018 (coldest time of the day)
MonoAC-Control

Not significant --> VT vs CX & CX vs CT

ALL SPECIES
Winter 2017-2018 (coldest time of the day)
MixedAC-Control

Not significant --> VT vs CX

Figure 42. Comparison of the effects of species mixture on ΔT in the different shrub species in the winter. Bar graphs comparing the mean differences in temperature (ΔTemperature, °C) between the temperature reached by Control and that reached by the various categories of shrubs in the winter months of 2018: below-canopy in monospecific populations (top left); below-canopy in polyspecific or mixed populations (top right); above-canopy in monospecific populations (bottom left), and above-canopy in polyspecific or mixed populations (bottom right). These mean temperature differences relate to winter data at coldest peak of the day (00:00–04:00) for 58 days, as collected in 2018.



VIBURNUM TINUS
Winter temperatures (total means)
Control vs all categories

CISTUS X HYBRIDUS
Winter temperatures (total means)
Control vs all categories

Not significant --> Control vs Mono

CEANOTHUS THYRSIFLORUS
Winter temperatures (total means)
Control vs all categories

Not significant --> Control vs Mono & MonoAC vs MixedAC

BUDDLEJA DAVIDII
Winter temperatures (total means)
Control vs all categories

Figure 43. Mean temperatures reached by Control vs vegetated categories in winter. Bar graphs comparing the mean temperatures (°C) reached Control and the various categories of shrubs in the winter months of 2018: below-canopy in monospecific populations; below-canopy in polyspecific or mixed populations; above-canopy in monospecific populations and above-canopy in polyspecific or mixed populations, for *Viburnum* (top left), *Cistus* (top right), *Ceanothus* (bottom left) and *Buddleja* (bottom right). These mean temperatures relate to winter data at coldest peak of the day (00:00–04:00) for 58 days, as collected in 2018.

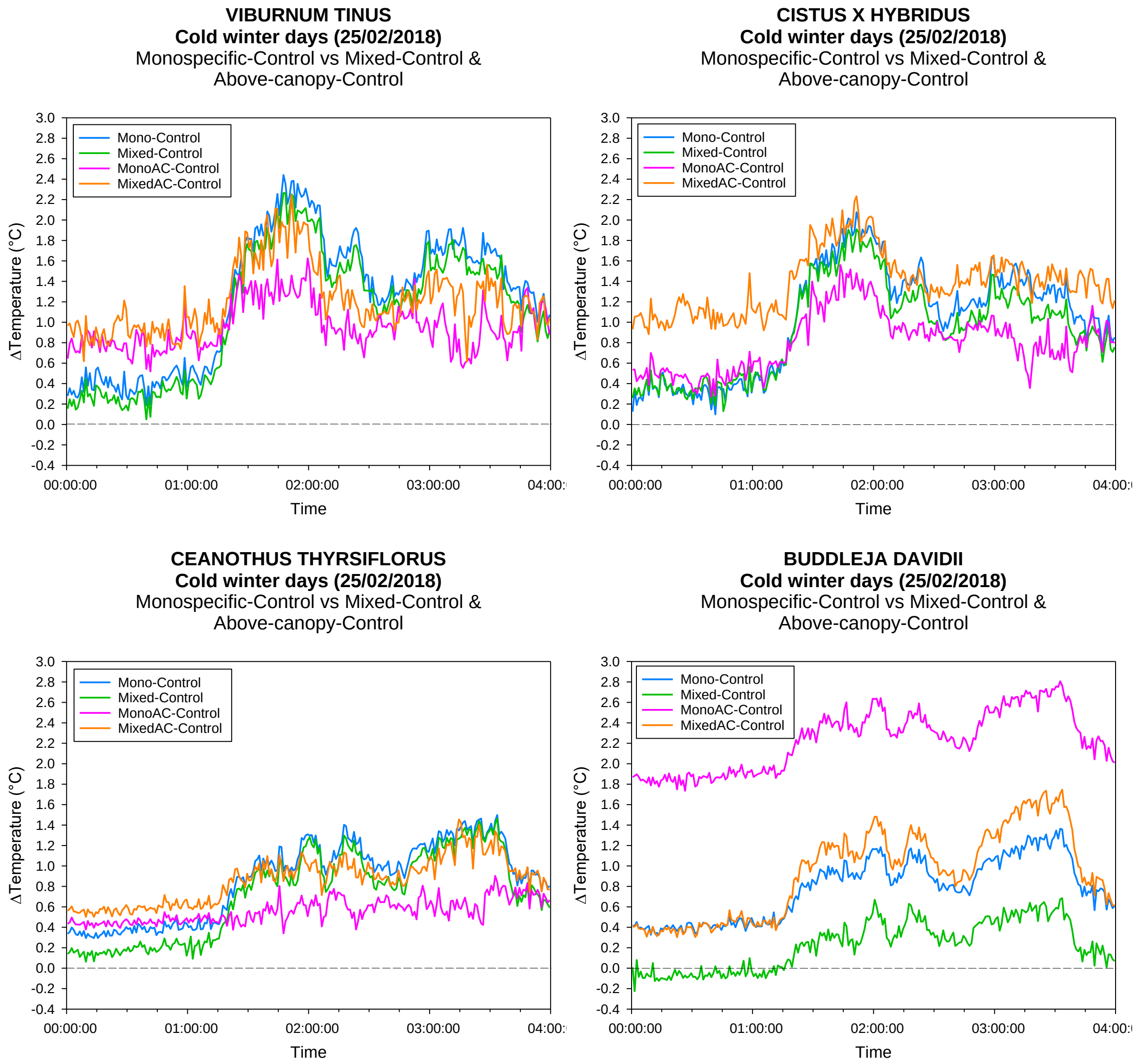


Figure 44a. Time series comparing the effects of species mixture on mean winter ΔT in four shrubs on a specific winter day. Time series graphs comparing the mean differences in temperature (ΔTemperature, °C) between the temperature reached by Control and that reached by the various categories of shrubs on a specific winter day in 2018 (below-canopy in monospecific populations, below-canopy in polyspecific or mixed populations, above-canopy in monospecific populations and above-canopy in polyspecific or mixed populations) in *Viburnum* (top left), *Cistus* (top right), *Ceanothus* (bottom left) and *Buddleja* (bottom right). These mean temperature differences relate to winter data at coldest peak of the day (00:00–04:00) on 25 February 2018.

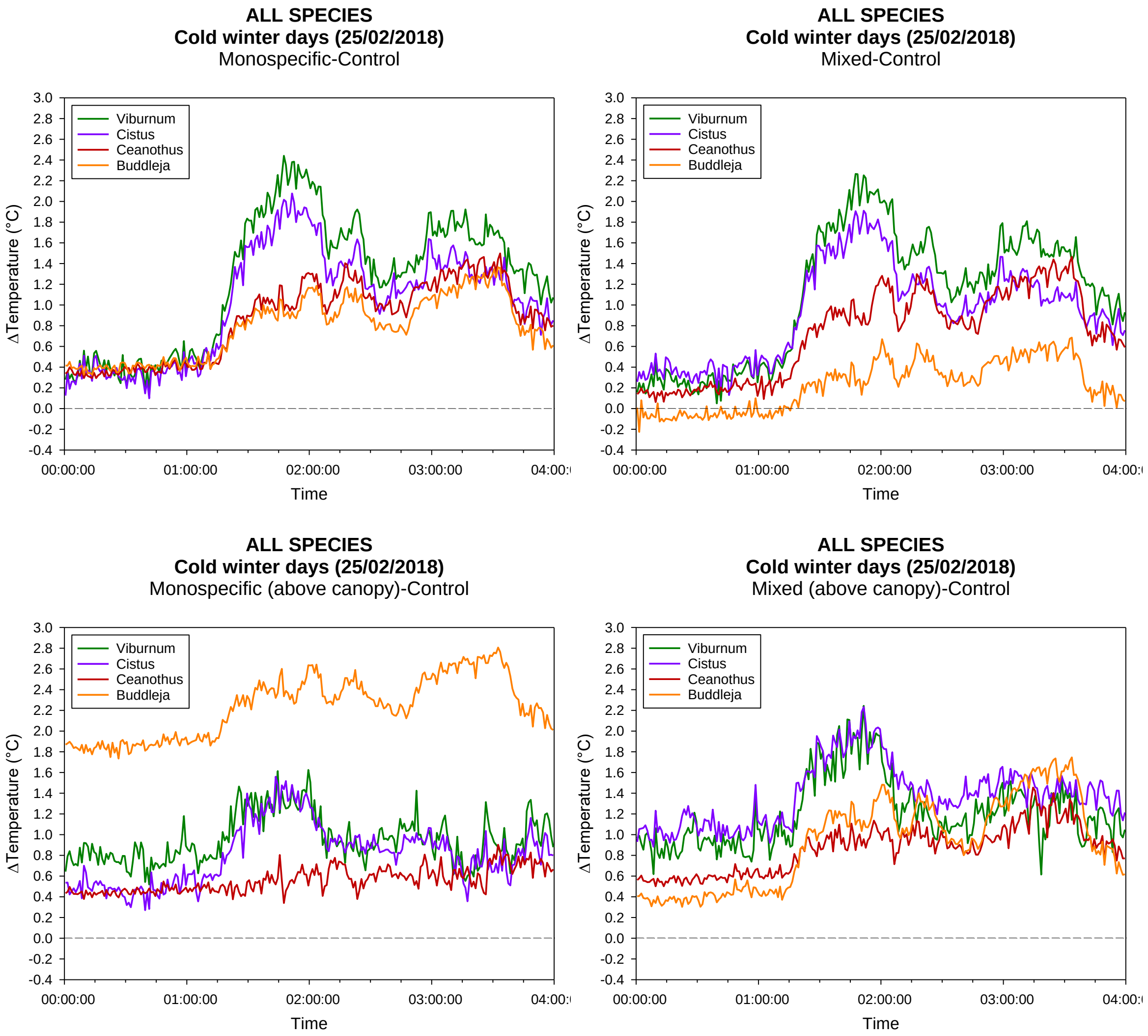


Figure 44b. Time series comparing the effects of species mixture on below- and above-canopy mean ΔT of four shrubs on a specific winter day. Time series graphs comparing the mean differences in temperature (ΔTemperature, °C) between the temperature reached by Control and that reached by the various categories of shrubs on a specific winter day in 2018 (per species): below-canopy in monospecific populations (top left), below-canopy in polyspecific or mixed populations (top right), above-canopy in monospecific populations (bottom left), and above-canopy in polyspecific or mixed populations (bottom right). These mean temperature differences relate to winter data at coldest peak of the day (00:00–04:00) on 25 February 2018.

B.3.3.2 The effect of species mixture on shrub cooling performance (Summer)

The assumption was that in the summer mean temperature on Control would likely be *higher* than mean temperature under a plant canopy, due to the shade created by the plant canopy. Therefore, the calculations for the mean value of ΔT – or the temperature difference between bare substrate and above- or below-plant canopy (i.e. T_C–T_A or T_C–T_B, respectively) at any given minute – were in relation to the belief that the Control units would present more extreme conditions compared to the plant units (Section B.2.2.6). For the vast majority of the time this assumption was true and that was how ΔT was calculated to compare the species' temperature profiles and evaluate the the effects of species mixture on the cooling capacity of the six woody shrubs.

During the summer of Year 3, it was found that all the study species significantly reduced temperatures compared to Control in the summer when placed in both a monospecific and a polyspecific population (P<0.001), thereby buffering extreme high temperatures at peak midday hours of the day and cooling the substrate on a rooftop (Fig. 45). The mean buffering capacity by the shrub canopies (ΔT_B) in summer ranged from 7.14±0.49 °C in *Viburnum* to 5.31±0.34 °C in *Elaeagnus* in the polyspecific populations and from 6.41±0.46 °C in *Viburnum* to 3.31±0.23 °C in *Ceanothus* in the monospecific populations. The polyspecific populations on average tended to have a greater buffering capacity of peak midday temperatures compared to the monospecific populations, however only *Ceanothus* showed a significant difference (P<0.001) in thermal performance between the two categories of species mixture. *Cotinus* (P=0.117) tended to have greater cooling capacity in the monospecific population, *Cistus* (P=0.159) tended to have greater cooling capacity in the polyspecific population and *Buddleja* showed the least difference in cooling capacity between the two categories of species mixture (P=0.904). It comes as no surprise then that the thermal performances by the six shrubs in the summer were significantly different, with species differences in thermal performance more significant in the monospecific populations (P<0.001) compared to those in the polyspecific populations (P=0.010). This finding not only strengthens all other findings that point to species-specific factors influencing the ability of shrubs to cool/insulate a rooftop, but it also points at the existence of a general 'flattening' effect by the polyspecific populations on individual species-specific cooling/insulating properties (Fig. 46).

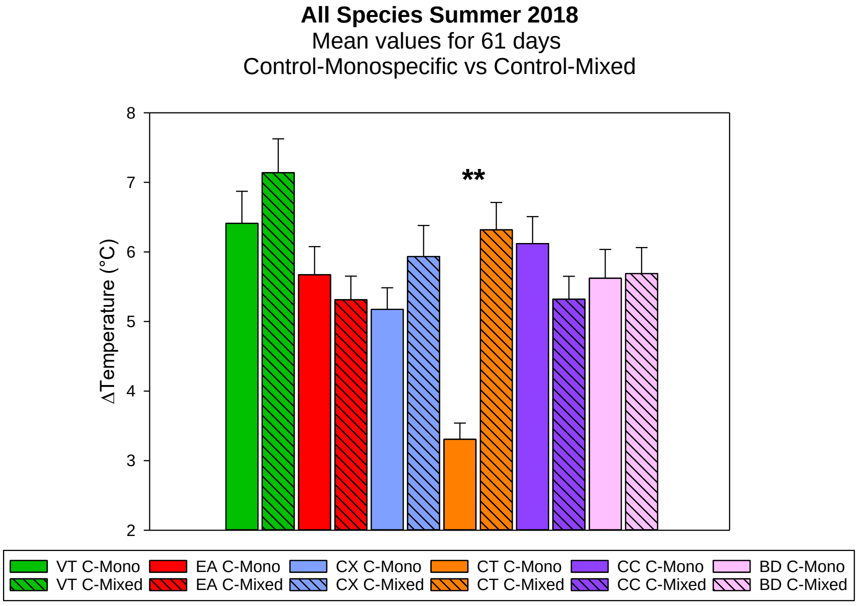


Figure 45. The effect of species mixture on mean ΔT in the summer. Bar graphs comparing mean differences in temperature (ΔT, °C) between Control and monospecific (“Mono–Control”) and polyspecific (“Mixed–Control”) populations of all study species. Mean temperature differences relate to summer data at warmest peak of the day (12:00–16:00) for 61 days in 2018.

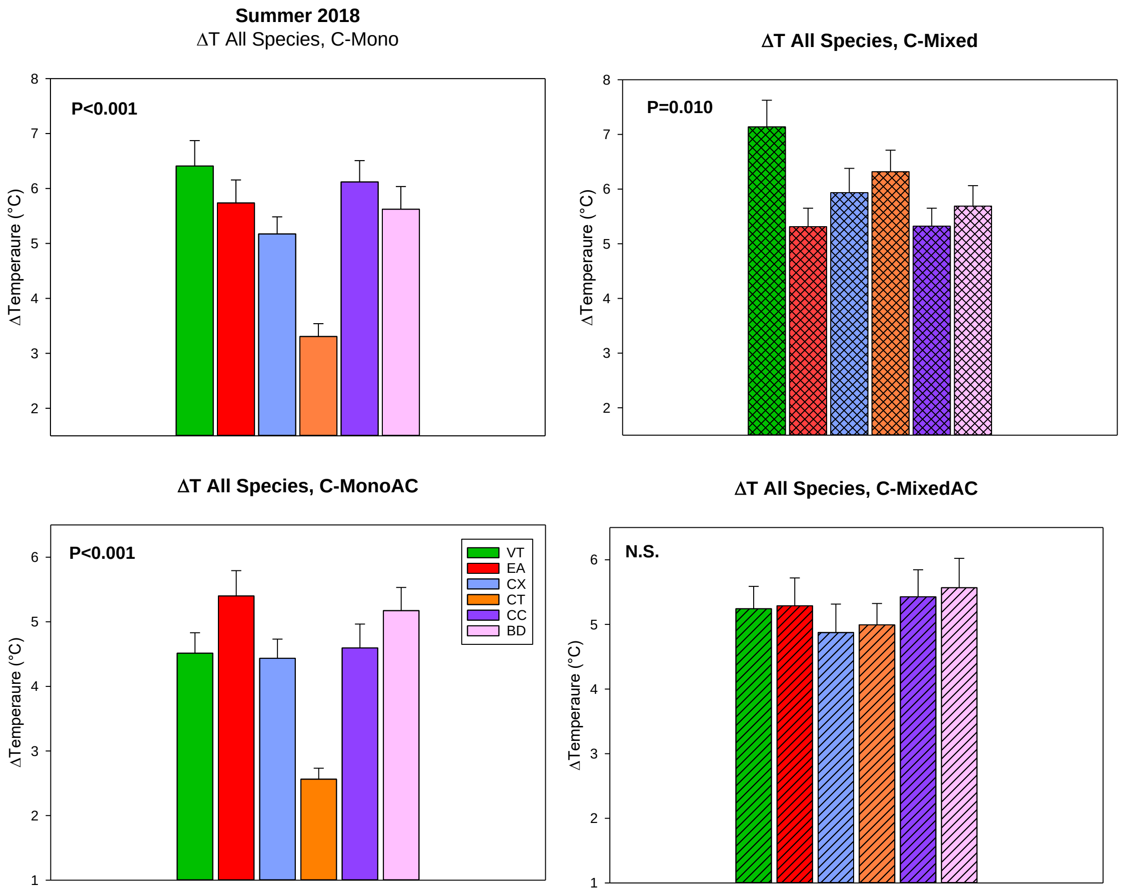


Figure 46. Comparison of the effects of species mixture on ΔT in the different shrub species in the summer. Bar graphs comparing the mean differences in temperature (ΔTemperature, °C) between the temperature reached by Control and that reached by the various categories of shrubs in the summer months of 2018: below-canopy in monospecific populations (top left); below-canopy in polyspecific populations (top right); above-canopy in monospecific populations (bottom left), and above-canopy in polyspecific populations (bottom right). These mean temperature differences relate to summer data at midday peak (12:00–16:00) for 61 days, as collected in 2018.

As was the case in the winter, the mean differences between Control and above-canopy temperatures (ΔT_A) in the summer were surprisingly positive and reached values that were similar to those recorded below the canopy (ΔT_B), though still comparatively less (Fig. 47). Again, *Ceanothus* was the only species to show significantly higher mean ΔT_A ($P<0.001$) in the polyspecific population (4.99±0.33 °C) compared to that in the monospecific population (2.56±0.17 °C), undoubtedly due to the greater shading created by taller shrubs surrounding *Ceanothus* in the mixed-species scenario, so much so that the mean temperatures reached below (T_B) and above (T_A) the canopy were not significant in *Ceanothus* (Fig. 48). On the contrary, the difference between mean T_A and mean T_B in the deciduous species *Elaeagnus* and *Cotinus* were indeed significant ($P<0.001$). This contrast between the two groups of shrubs – a lack of microclimatic difference in above- and below-canopy environment in *Ceanothus* (a short shrub) versus a significant microclimatic difference in above- and below-canopy environment in *Elaeagnus* and *Cotinus* (tall shrubs) may in part be due to plant height but also to particular canopy characteristics.

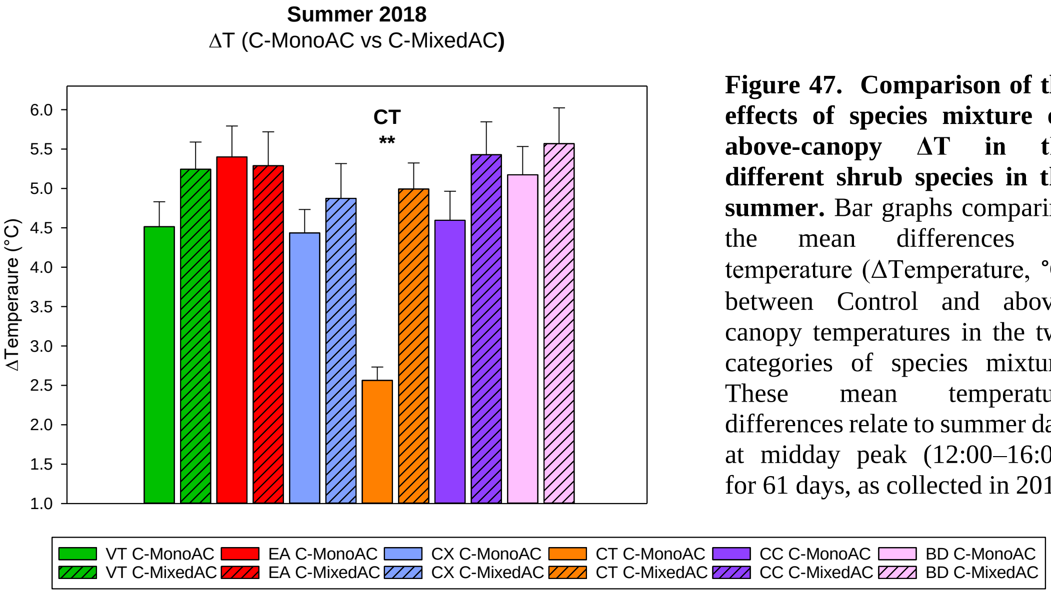


Figure 47. Comparison of the effects of species mixture on above-canopy ΔT in the different shrub species in the summer. Bar graphs comparing the mean differences in temperature (ΔTemperature, °C) between Control and above-canopy temperatures in the two categories of species mixture. These mean temperature differences relate to summer data at midday peak (12:00–16:00) for 61 days, as collected in 2018.

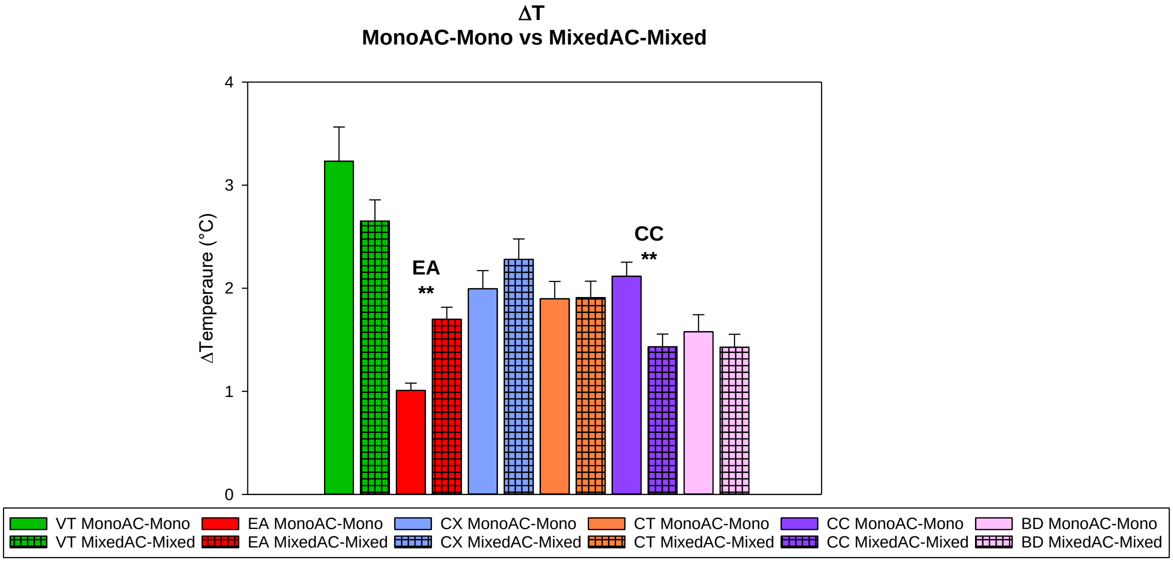


Figure 48. Comparison of the difference between above- and below-canopy ΔT in the different shrub species in the summer. Bar graphs comparing the mean temperatures reached above the canopy to those recorded below-canopy (ΔTemperature, °C). These mean temperature differences relate to summer data at midday peak (12:00–16:00) for 61 days, as collected in 2018.

Finally, the maximum difference in temperature between Control and below-canopy temperatures of a vegetated category (ΔT_B) in summer 2018 was found to be above 25 °C, meaning that at most and on specific moments in the summer the shrubs were able to reduce temperatures by more than 25 °C compared to bare substrate. The highest maximum differences found were:

- 25.69 °C on 11/07/2018 at 13:52;
- 25.66 °C on 06/07/2018 at 13:40;
- 25.63 °C on 24/06/2018 at 13:02, and
- 25.27 °C on 25/06/2018 at 12:59.

All of these temperature differences (ΔT_B) were achieved by *Viburnum* shrubs placed in the polyspecific or mixed populations. For example, it was clear that on 24/06/2018 (Fig. 49a–c**)** *Viburnum*, especially when placed in a mixed-species scenario, was the species with the highest thermal cooling potential. It was also obvious that the trend of ΔT_B for that day followed the course or trend of temperatures on Control on the two rooftops, only at a much reduced degree. Therefore, the ΔT_B trend of the species placed on the Hicks roof had quite a different trend to that of the species on the Hadfield roof, but in both cases all species drastically decreased temperatures compared to Control (e.g. from up to approximately 48 °C on Control down to as low as nearly 26 °C in *Viburnum* on the Hicks roof).

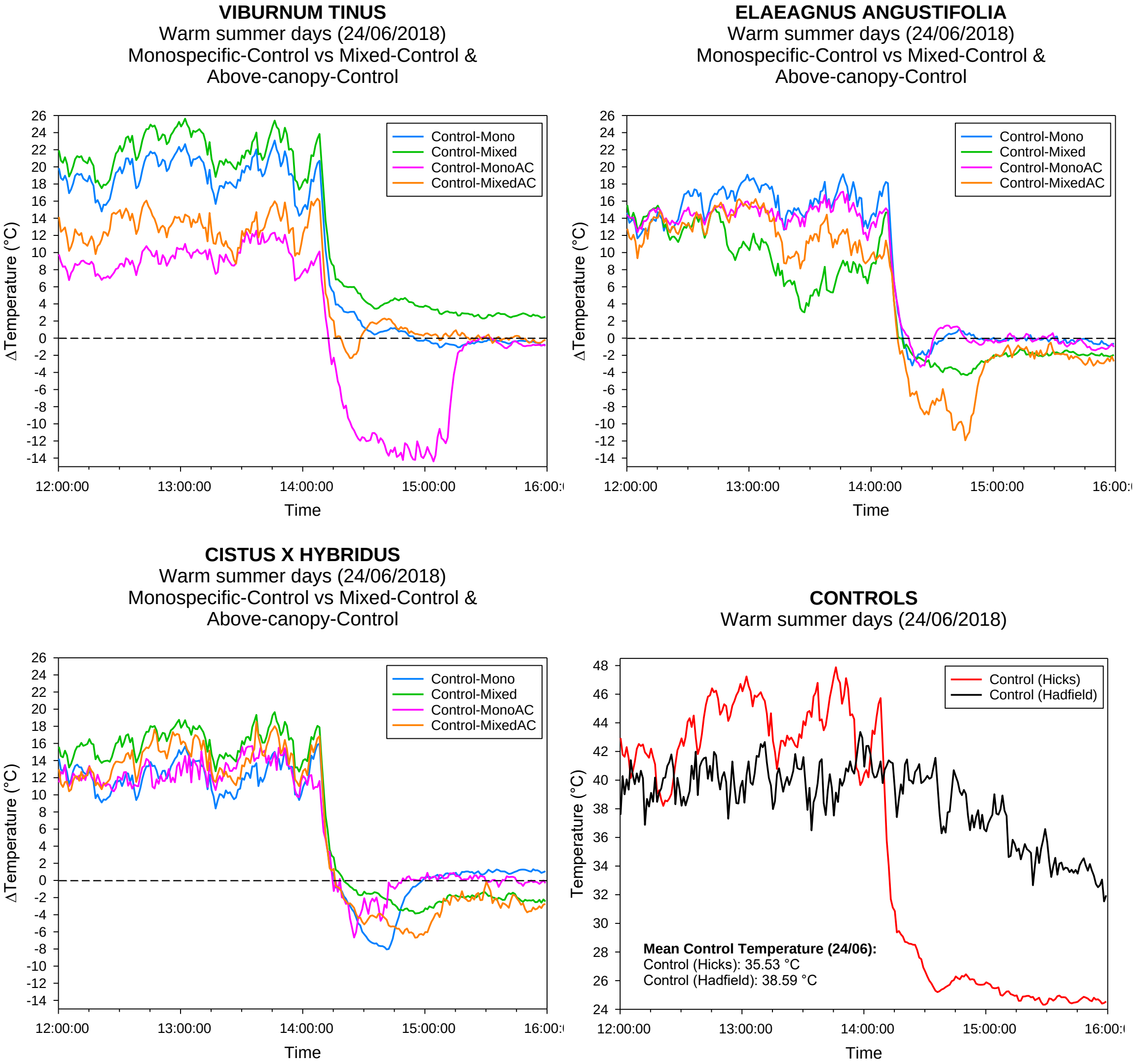


Figure 49a. Time series comparing the effects of species mixture on mean ΔT in the three shrubs on the Hicks roof on a specific summer day. Time series graphs comparing the mean differences in temperature (ΔTemperature, °C) between the temperature reached by Control and that reached by the various categories of shrubs on a specific summer day in 2018 (below-canopy in monospecific populations, below-canopy in polyspecific or mixed populations, above-canopy in monospecific populations and above-canopy in polyspecific or mixed populations) in the shrubs on the Hicks roof: *Viburnum* (top left), *Elaeagnus* (top right), and *Cistus* (bottom left). It is clear that ΔTemperature in all categories and species followed the trend of temperatures on Control throughout the day (bottom right, in red), just at a much lower temperature. These mean temperature differences relate to summer data at midday peak (12:00–16:00) on 24 June 2018.

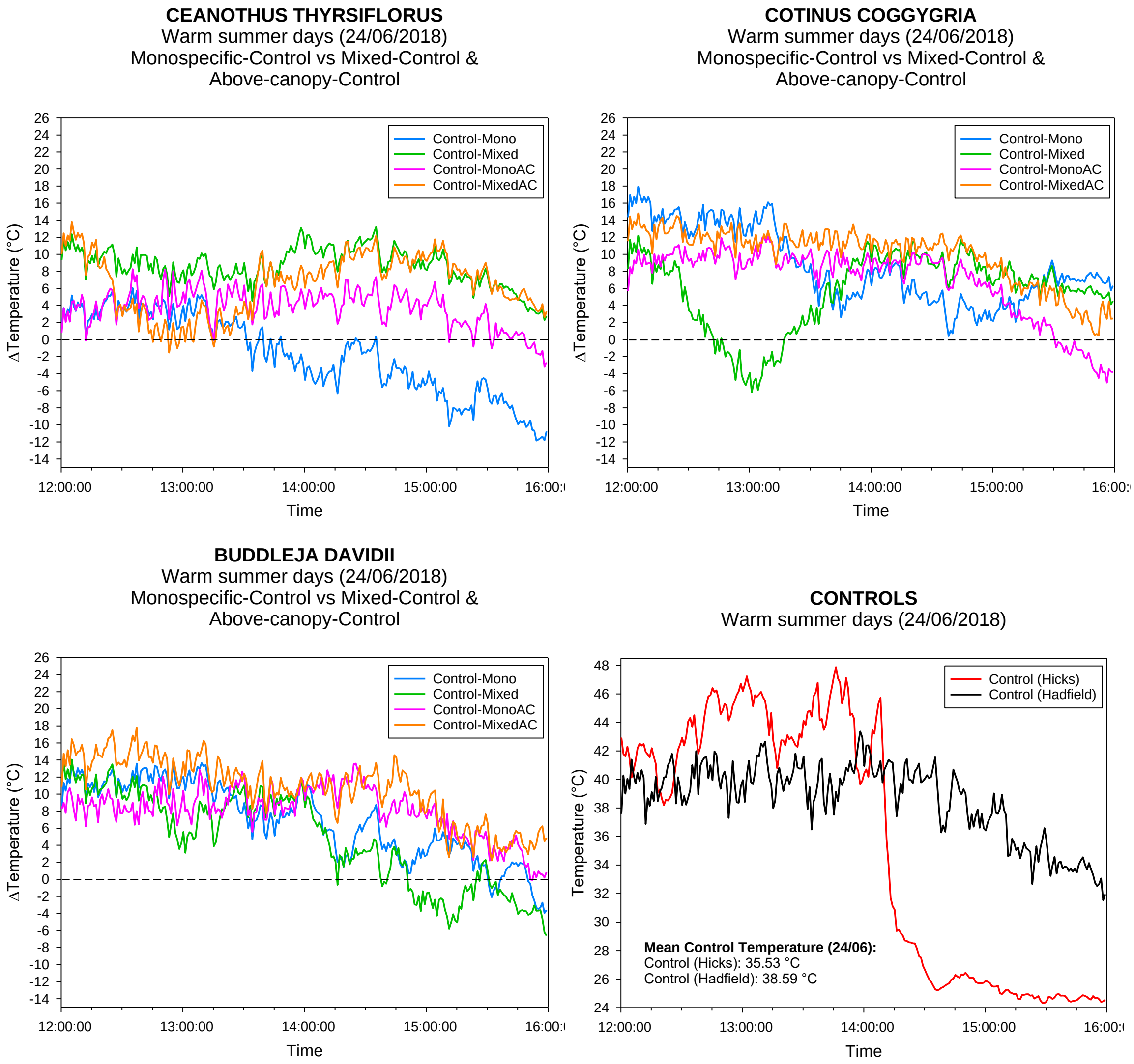


Figure 49b. Time series comparing the effects of species mixture on mean ΔT in the three shrubs on the Hadfield roof on a specific summer day. Time series graphs comparing the mean differences in temperature (ΔTemperature, °C) between the temperature reached by Control and that reached by the various categories of shrubs on a specific summer day in 2018 (below-canopy in monospecific populations, below-canopy in polyspecific or mixed populations, above-canopy in monospecific populations and above-canopy in polyspecific or mixed populations) in the shrubs on the Hadfield roof: *Ceanothus* (top left), *Cotinus* (top right), and *Buddleja* (bottom left). It is clear that ΔTemperature in all categories and species followed the trend of temperatures on Control throughout the day (bottom right, in black), just at a much lower temperature. These mean temperature differences relate to summer data at midday peak (12:00–16:00) on 24 June 2018.

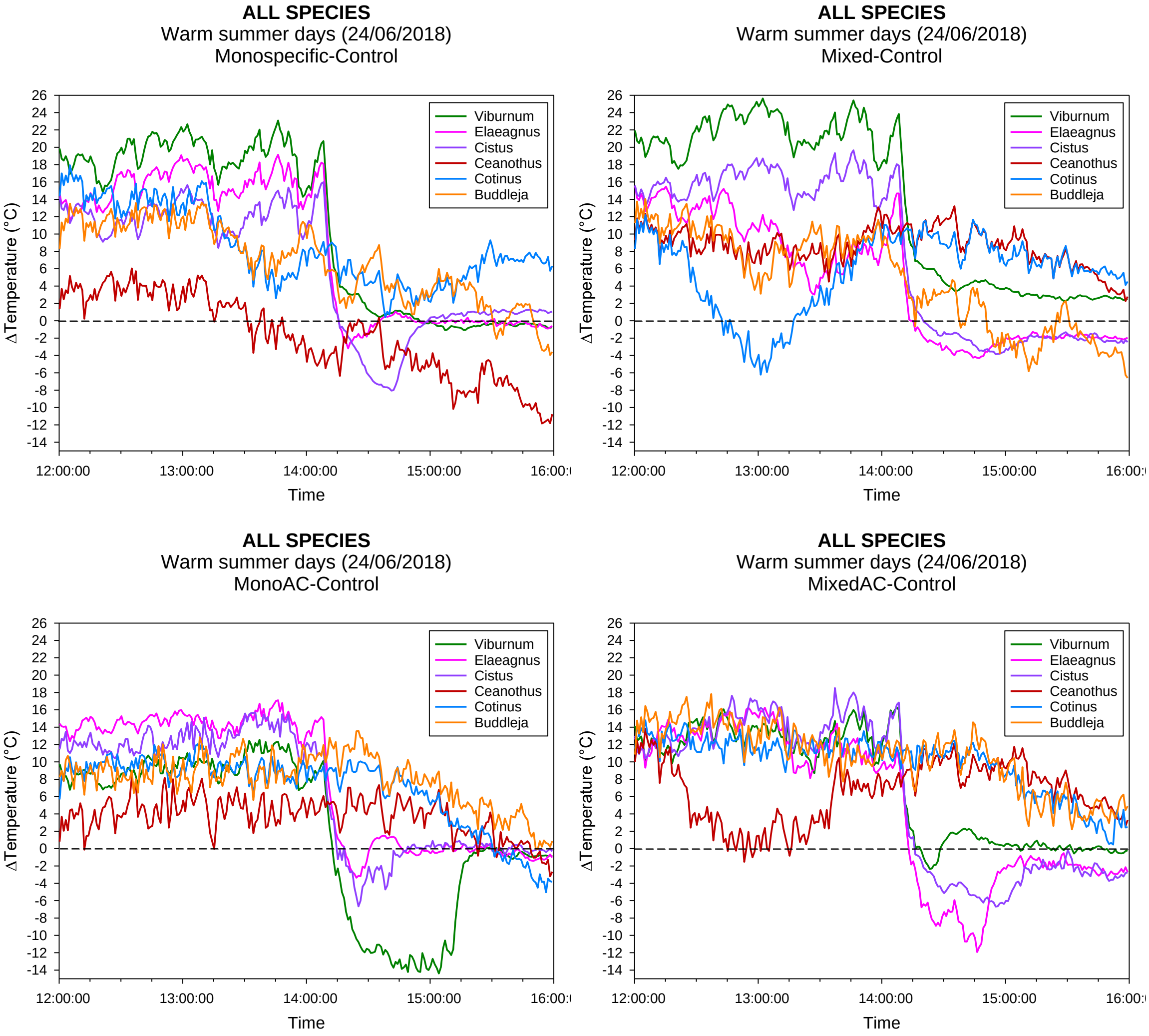


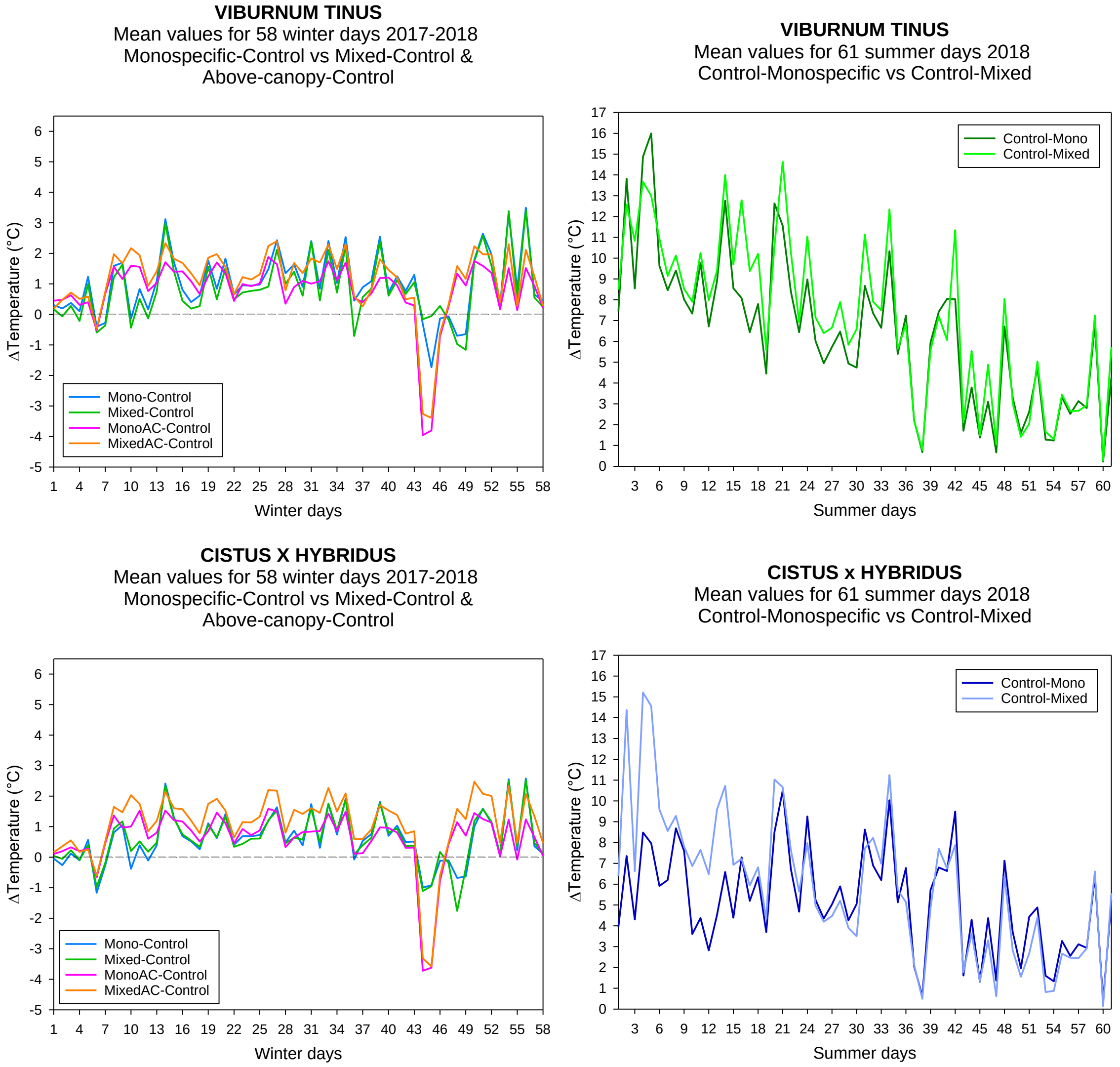
Figure 49c. Time series comparing the effects of species mixture on below- and above-canopy mean ΔT of four shrubs on a specific summer day. Time series graphs comparing the mean differences in temperature (ΔTemperature, °C) between the temperature reached by Control and that reached by the various categories of shrubs on a specific summer day in 2018 (per species): below-canopy in monospecific populations (top left); below-canopy in polyspecific populations (top right); above-canopy in monospecific populations (bottom left), and above-canopy in polyspecific populations (bottom right). These mean temperature differences relate to summer data at midday peak (00:00–04:00) on 24 June 2018.

B.3.3.3 Shrub performance: the winter vs summer contrast and the decline over time

One of the most notable findings from the final year of the study was observing the stark difference in the shrubs' ability to buffer extreme temperatures between summer and winter. In fact, the various shrubs were able to reduce extreme temperatures (in relation to Control, ΔT) by a much larger degree in the summer months compared to the winter months (Fig. 50a–50c). The mean differences between temperature on Control and that below the canopy of the study species (ΔT_B) in the summer were as high as 15.99±0.46 °C in *Viburnum* (an average reached on 25/06/2018 within the monospecific population), meaning that *Viburnum* on one particular summer day was able reduce peak midday temperatures *on average* by nearly 16 °C compared to bare substrate. By contrast, the mean ΔT_B in the winter only reached 3.12±0.03 °C, on 26/01/2018 again in *Viburnum* within the monospecific population (N.B.: It further reached 3.50±0.04 °C on 14/03/2018, when weather was milder after the "Beast from the East" in early March). This means that *Viburnum* on one particular winter day at most was able to increase extreme low temperatures on average by just over 3°C compared to bare substrate.

It is evident from that a short period of unusually intense cold wind and snow (i.e. Storm Hartmut in late February to early March 2018, then nicknamed the "Beast from the East") between winter days 40 and 49 temporarily suppressed the ability of all shrubs to buffer cold temperatures on the rooftop (Fig. 50a–50c), although the negative effect of the storm on the temperature profiles was much less severe in the below-canopy temperature differences (ΔT_B) compared to the above-canopy ones (ΔT_A). In fact, temperatures were maintained between approximately 0 and –2 °C below the canopies while above the canopies temperatures reached nearly –5 °C. The shrub canopies were therefore able to buffer temperature extremes despite the harsh weather conditions and create their own milder microclimate below the canopies.

It is also clear that shrub thermal performance decreased dramatically from the beginning to the end of summer in all species (Fig. 50a–50c), with a mean ΔT_B of nearly 16 °C at the beginning in some cases to nearly 0 °C at the end of summer. Interestingly, monospecific populations of *Ceanothus* saw about a third of summer days (all at the beginning of summer) with negative mean values of ΔT_B (i.e. negative performance), the only group (and species) to present this behaviour. Compared to their thermal performance in the summer, the thermal performance of all shrubs in the winter (albeit at a much lower degree of performance) was at least consistent and fluctuations in both ΔT_B and ΔT_A were less severe throughout the season.

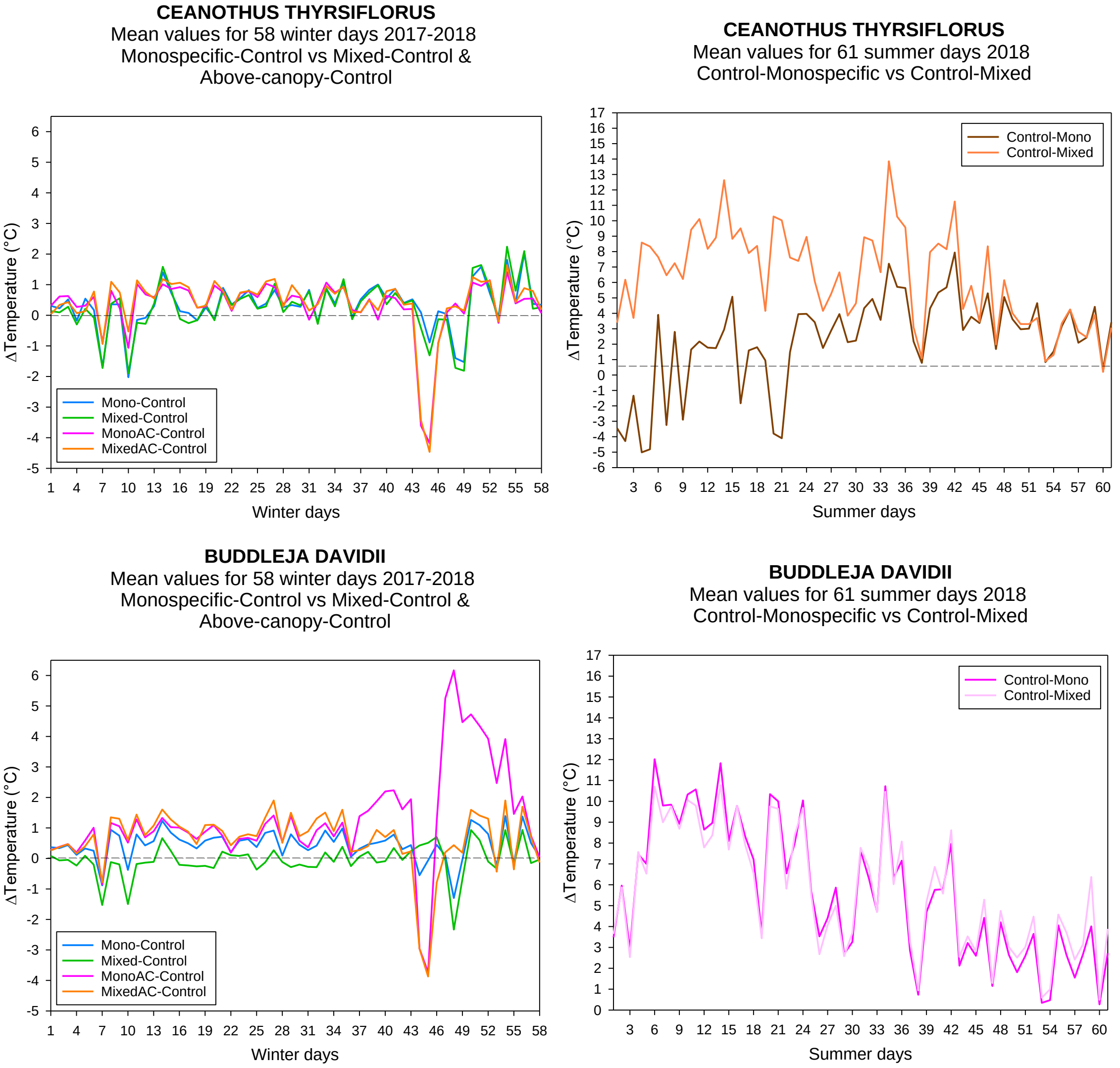

VIBURNUM TINUS
Mean values for 58 winter days 2017-2018
Monospecific-Control vs Mixed-Control &
Above-canopy-Control

VIBURNUM TINUS
Mean values for 61 summer days 2018
Control-Monospecific vs Control-Mixed

CISTUS X HYBRIDUS
Mean values for 58 winter days 2017-2018
Monospecific-Control vs Mixed-Control &
Above-canopy-Control

CISTUS x HYBRIDUS
Mean values for 61 summer days 2018
Control-Monospecific vs Control-Mixed

Figure 50a. Time series comparing the effects of species mixture on mean summer and winter ΔT in *Viburnum* and *Cistus*. Time series graphs of the differences in temperature (ΔTemperature, °C) between the mean temperature reached by Control and that reached by the various categories of shrubs: monospecific populations ("Mono–Control" in winter; "Control–Mono" in summer) and polyspecific populations ("Mixed–Control" in winter; "Control–Mixed" in summer), as well as above-canopy differences in temperature (e.g. "MixedAC–Control") for each study species on the Hicks roof – *Viburnum* above, *Cistus* below. For each species, the time series graphs on the left relate to winter data at coldest hours of the day (00:00–04:00) for 58 days, while the graphs on the right relate to summer data at warmest peak of the day (12:00–16:00) for 61 days, as collected in 2018.



CEANOTHUS THYRSIFLORUS
Mean values for 58 winter days 2017-2018
Monospecific-Control vs Mixed-Control &
Above-canopy-Control

CEANOTHUS THYRSIFLORUS
Mean values for 61 summer days 2018
Control-Monospecific vs Control-Mixed

BUDDLEJA DAVIDII
Mean values for 58 winter days 2017-2018
Monospecific-Control vs Mixed-Control &
Above-canopy-Control

BUDDLEJA DAVIDII
Mean values for 61 summer days 2018
Control-Monospecific vs Control-Mixed

Figure 50b. Time series comparing the effects of species mixture on mean summer and winter ΔT in *Ceanothus* and *Buddleja*. Time series graphs of the differences in temperature (ΔTemperature, °C) between the mean temperature reached by Control and that reached by the various categories of shrubs: monospecific populations ("Mono–Control" in winter; "Control–Mono" in summer) and polyspecific populations ("Mixed–Control" in winter; "Control–Mixed" in summer), as well as above-canopy differences in temperature (e.g. "MixedAC–Control") for each study species on the Hadfield roof – *Ceanothus* above and *Buddleja* below. For each species, the time series graphs on the left relate to winter data at coldest hours of the day (00:00–04:00) for 58 days, while the graphs on the right relate to summer data at warmest peak of the day (12:00–16:00) for 61 days, as collected in 2018.

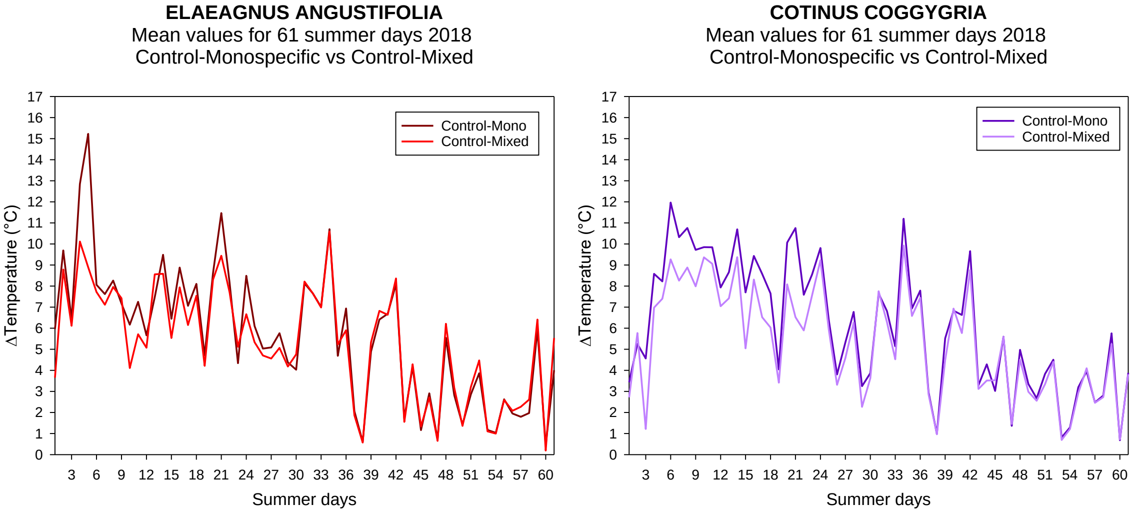


Figure 50c. Time series comparing the effects of species mixture on mean summer ΔT in *Elaeagnus* and *Cotinus*. Time series graphs of the differences in temperature (ΔTemperature, °C) between the temperature reached by Control and that reached by the various categories of shrubs in the summer months of 2018: monospecific populations ("Control–Mono") and polyspecific populations ("Control–Mixed") for the deciduous species (*Elaeagnus* on the left, *Cotinus* on the right). For each species, the time series graphs relate to summer data at warmest peak of the day (12:00–16:00) for 61 days, as collected in 2018.

B.3.4 The effects of species, plant density, population size and species mixture on overall shrub thermal performance in winter and summer

This section is dedicated to the analysis of the combined temperature data through the three years of the study, with the purpose of confirming the trends observed previously during the year-on-year analysis. Specifically, this section wants to determine the overarching effects of plant density, species mixture, species-specific characteristics and time on the thermal performance of an average woody shrub.

What is probably evident by now is that there is an obvious contrast distinction in the way the woody shrubs performed depending on the season of the year – shrubs were significantly more “active”, better performing and overall providing more of a “service” in the summer rather than in the winter (Fig. 51). The ability of shrubs to buffer extreme temperatures (i.e. ΔT, to increase them during the hours in which temperature is lowest in the winter and lower them during the hours in which temperature is highest in the summer, compared to Control) was highly and significantly different ($P<0.001$) between winter (0.69±0.04 °C) and summer (4.31±0.18 °C). Therefore, the season in which shrubs were observed definitely determined the *levels* of provision by shrubs in terms of abating temperature extremes and summer represented the season in which shrubs provided the greatest level of thermal provision. In fact, shrubs provided six times more “cooling service” in the summer than they provided “insulating” service in the winter.

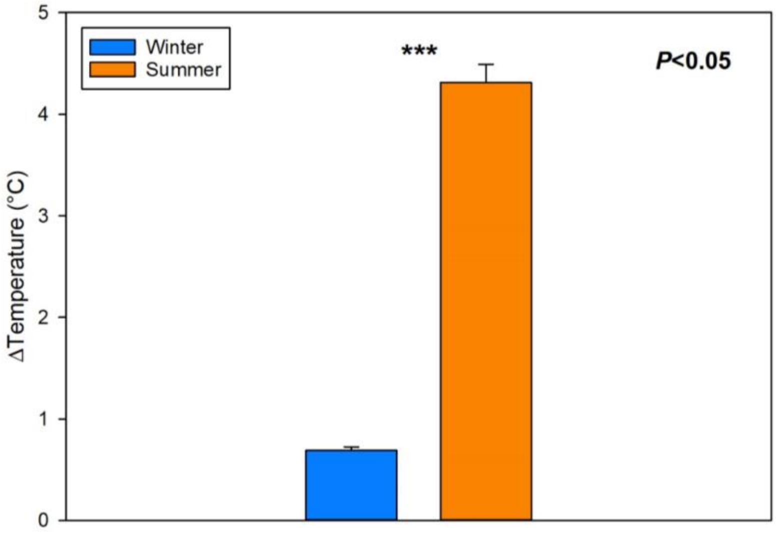


Figure 51. Shrub thermal performance was significantly higher in the summer than in the winter.
Vertical bar graphs with error bars comparing the total mean temperature difference (ΔT, °C) reached by shrubs in the winter and in the summer, in relation to Control. Season was a significant factor in determining the *levels* of thermal performance.

Plant density was a significant factor in influencing shrub thermal performance in both the winter (P=0.004, Fig. 52) and the summer months ($P<0.001$, Fig. 53) and in both cases *high* plant density (mean Δ*T* of 0.74±0.04 °C in the winter and mean Δ*T* of 4.76±0.19 °C in the summer) provided shrubs with superior conditions for extreme temperature abatement compared to low plant density (mean Δ*T* of 0.58±0.03 °C in the winter and mean Δ*T* of 3.07±0.18 °C in the summer). However, the effect of plant density was again more pronounced in the summer than in the winter, with high-density shrub populations cooling on average nearly 1.7 °C more than the low-density ones during peak midday temperatures in the summer, compared to just approximately 0.15 °C in the winter.

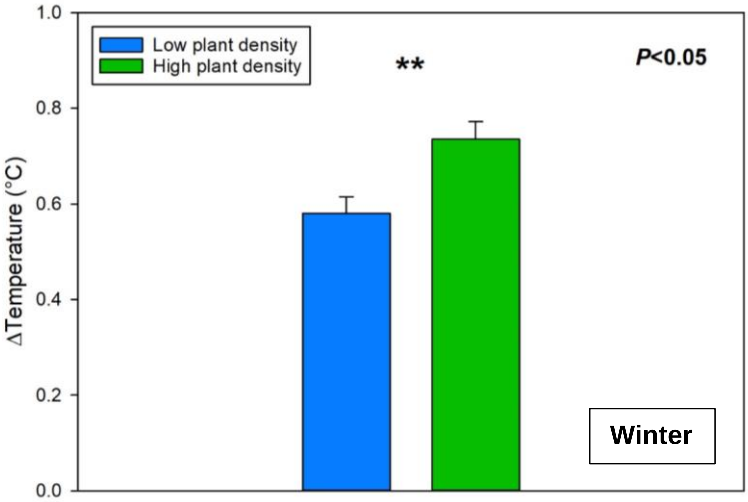


Figure 52. Insulation was significantly greater in high-density shrub populations. Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by shrubs in low-density and high-density populations, in relation to Control. Plant density was significant in affecting shrub insulating performance in the winter.

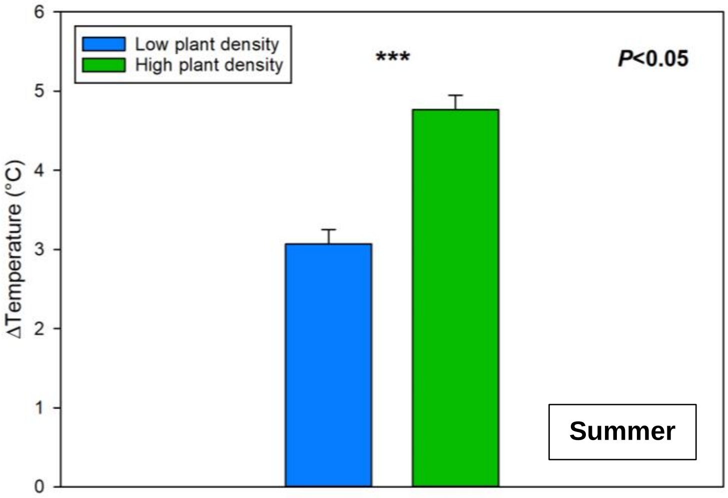


Figure 53. Cooling was significantly greater in high-density shrub populations. Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by shrubs in low-density and high-density populations, in relation to Control. Plant density was significant in affecting shrub cooling performance in the summer.

Species mixture – or the variety of species used in a shrub population – was not found to have affected shrub thermal performance significantly, either in the winter (*P*=0.595, Fig. 54) or in the summer (*P*=0.247, Fig. 55), despite observing slightly better performances in monospecific or single-species populations (mean Δ*T* of 0.75±0.05 °C in winter and mean Δ*T* of 4.79±0.21 °C in summer) compared to polyspecific or ‘mixed’ populations (mean Δ*T* of 0.71±0.05 °C in winter and mean Δ*T* of 4.41±0.25 °C summer).

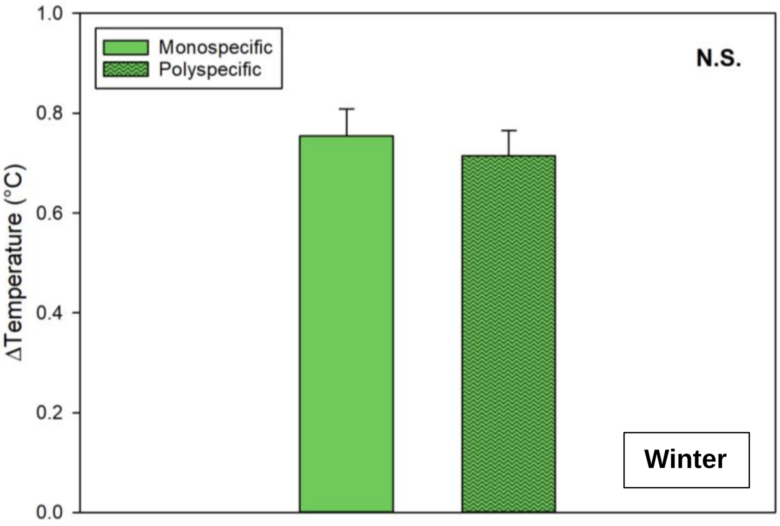


Figure 54. Insulation was not affected by species mixture.
Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by shrubs in monospecific and polyspecific populations, in relation to Control. Species mixture was not a factor affecting shrub insulating performance in the winter.

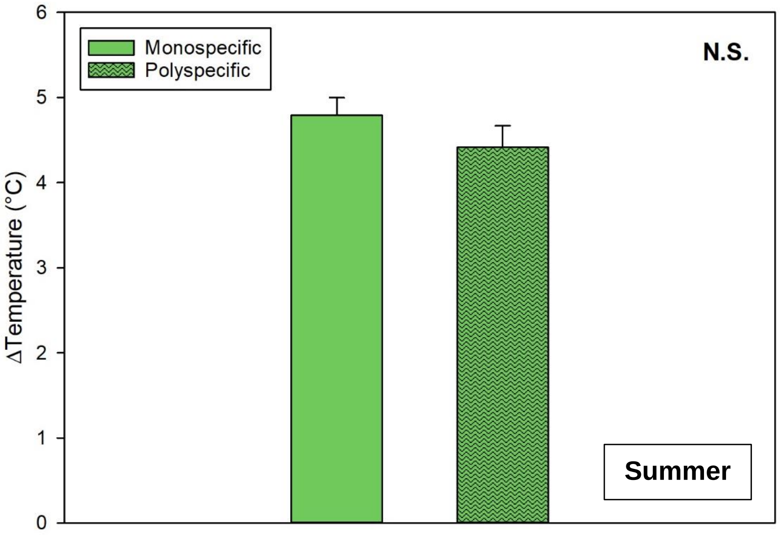


Figure 55. Cooling was not affected by species mixture.
Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by shrubs in monospecific and polyspecific populations, in relation to Control. Species mixture was not a factor affecting shrub cooling performance in the summer.

In terms of how species-specific characteristics affected the thermal performance of the different shrub species, it was clear that certain species had a significantly greater ability to cool (P<0.001, Fig. 56) and to insulate (P<0.001, Fig. 57) than others. *Viburnum* was the species with the greatest overall insulating (mean Δ*T* of 0.97±0.05 °C) and cooling (mean Δ*T* of 6.57±0.32 °C) capacity for all winter and summer months, respectively, and in every year of the study. At the other end of the spectrum was *Ceanothus*, the other evergreen species, which had the overall worst insulating (mean Δ*T* of 0.46±0.03 °C) and cooling (mean Δ*T* of 3.97±0.24 °C) capacity out of all the species in the study. Therefore, the average best-performing shrub in the winter maintained twice the the amount of warmth as the average worst-performing shrub, and the best-performing shrub in the summer maintained temperatures under the canopy that were more than 2.5 °C cooler compared to the average worst-performing shrub.

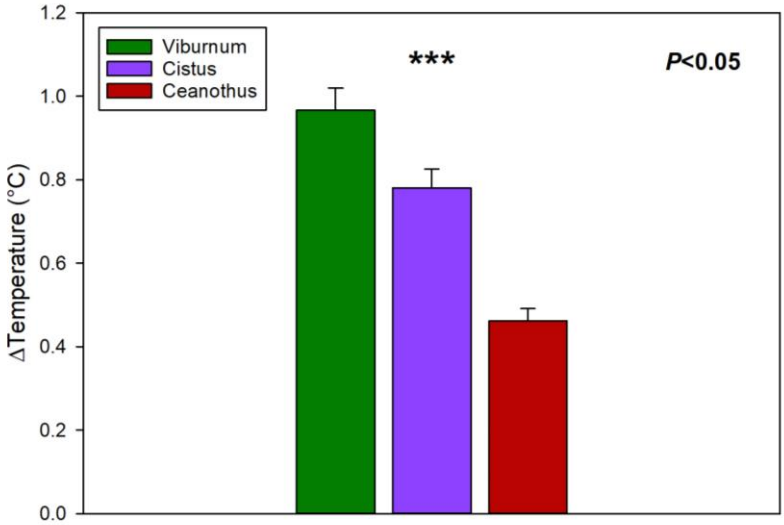


Figure 56. Insulation was significantly affected by species-specific characteristics. Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by the three shrubs in winter, in relation to Control. The choice of shrub species was significant in determining how a shrub population insulated the rooftop.

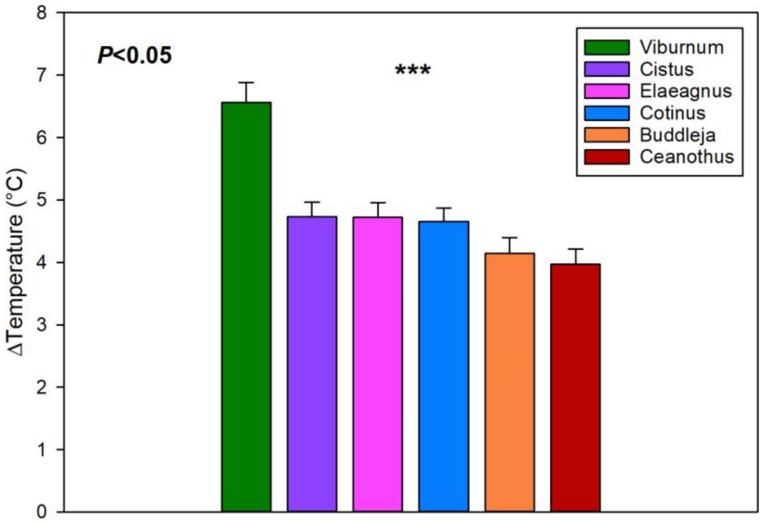


Figure 57. Cooling was significantly affected by species-specific characteristics. Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by six shrubs in the summer, in relation to Control. The choice of shrub species was significant in determining how a shrub population cooled the rooftop.

The final part of this section is dedicated to assessing the impact of time on mean shrub thermal performance. “Time” is an all-encompassing term used here to represent all the factors (positive and negative) that may have influenced shrub thermal performance through the three years of the study, for example the growth and aging of the shrubs and the constant exposure and adaptation by the shrubs to wind, rain and high levels of heat, irradiance and evapotranspiration common to the rooftop environment. The study found that, overall, shrub thermal performance significantly improved over the years, both in the winter ($P=0.008$, Fig. 58) and in the summer ($P<0.001$, Fig. 59). The improvement over time of the shrubs' insulating capacity in the winter was negligible between the first (mean Δ*T* of 0.61±0.05 °C) and second (mean Δ*T* of 0.63±0.05 °C) year of the study, while the final year saw a substantial increase in shrub performance (mean Δ*T* of 0.86±0.08 °C). On the contrary, the shrubs' cooling capacity in the summer saw a noticeable reduction going from the first (mean Δ*T* of 4.44±0.28 °C) to the second (mean Δ*T* of 2.99±0.24 °C) year of the study, but again shrub performance remarkably recovered during the final year (mean Δ*T* of 5.58±0.33 °C).

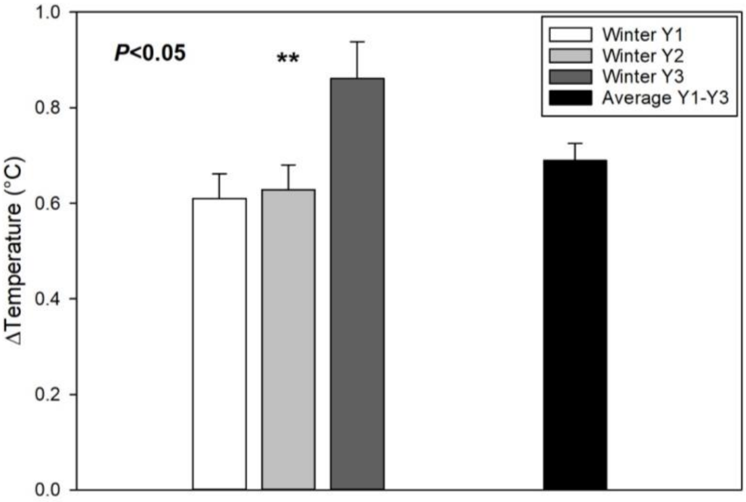


Figure 58. Insulation by woody shrubs increased during the study.
Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by woody shrubs in winter, in relation to Control. Shrub thermal performance in the winter significantly improved with time, especially in the last year of the study.

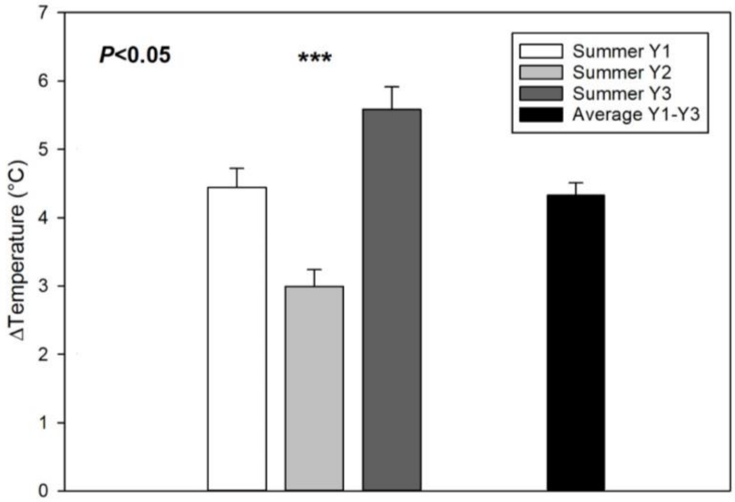


Figure 59. Cooling by woody shrubs increased during the study.
Vertical bar graphs with error bars comparing the total mean temperature difference (Δ*T*, °C) reached by woody shrubs in winter, in relation to Control. Overall, shrub thermal performance in the summer significantly improved with time, despite a dip in the second year of the study.

B.4 Discussion

Study 'B' of the research project was a 3-year study that had the aim of evaluating shrub thermal performance, or the ability of six woody shrubs to: 1) insulate rooftops from low temperatures during the coldest hours of the day in the winter and 2) to cool rooftops during the warmest hours of the day in the summer. The same experimental shrubs and research sites were used as in Study 'A': a total of 324 individual shrubs, belonging to six different species, two of which were evergreen (*Viburnum tinus* and *Ceanothus thyrsiflorus*), two were semi-deciduous (*Cistus* × *hybridus* and *Buddleja davidii*) and two were deciduous (*Elaeagnus angustifolia* and *Cotinus coggygria*). An evergreen, a semi-deciduous and a deciduous species were placed on each of the two research sites, two nearby but separate building rooftops each provided with a weather station for the monitoring of rooftop conditions. The spatial arrangement of these shrub populations changed each year to assess the effects of species-specific characteristics, plant density, population size and species mixture on plant canopy microclimate. Shrub thermal performance was quantified through the monitoring of plant canopy microclimate, which was carried out through the collection of temperature data via sensors placed on bare substrate (Control) and on experimental shrub populations. Temperature profiles were thus created based on this temperature data to capture the direct temperature increases or decreases by the shrubs with respect to Control and to translate these as their insulating or cooling performances, respectively. The analysis of the temperature profiles of the different species of shrubs and of the different experimental categories tested the differences in temperature amongst the different species, between high and low plant density, between small and large shrub population size and between single-species and mixed-species shrub populations, to evince their influence on plant canopy microclimate. The analysis also included a reflection on the "delaying effect" of shrub vegetation on peak summer temperatures and the potential repercussions of time and season on long-term shrub thermal performance.

Fundamental to both the first and second years of 'Study B' was observing the effects of **plant density** on shrub thermal performance. Apart from the first winter, plant density played an overall significant role in influencing plant canopy microclimate throughout the entire study irrespective of season, with shrubs in high-density populations (i.e. individuals spaced closer together) representing the best condition for increasing the insulating and cooling services they provide. This was also true regardless of the size of the shrub population (i.e. number of individual plants) – plant density still had a significant effect on canopy microclimate whether the shrubs were placed in relatively small or large populations. On the other hand, population size was not found to influence temperatures, despite some species showing slightly poorer performances in the combination "large and sparse" (i.e. higher number of individuals that were spread further apart). **The spatial arrangement of**

woody vegetation, especially in terms of how far apart individual plants are spaced, may therefore represent a crucial planning aspect if the intent of installing a intensive green roof or other green infrastructure is to lower costs associated with energy consumption for the heating and cooling of buildings.

Unlike population size, **season** had a major impact not only on plant density but on shrub performance in general, as unquestionably the greatest influence on plant canopy microclimate. The average shrub increased temperatures in the winter compared to Control in the range of 0.5 – 1.0 °C, whereas the average shrub lowered temperatures in the summer compared to Control in the range of 4.0 and 6.6 °C. Moreover, the effect of plant density on temperature was significantly greater in the summer than it was in the winter, with shrubs in high-density populations cooling on average nearly 1.7 °C more than those in low-density populations, compared to only a 0.2 °C difference between the two categories in the winter. **In this sense, season determined the *levels* of temperature abatement by shrubs and summer was the season in which shrubs provided the greatest level of thermal provision. In fact, shrubs provided overall six times more "cooling service" in the summer than they provided "insulating service" in the winter.** Using woody shrubs as the main type of vegetation on green roofs would consequently provide minimal insulating service in the winter but a six-fold greater cooling service in the summer. The study was carried out in the UK where the climate is temperate and heating is one of the main culprits of excessive energy consumption in this nation, thereby selecting green infrastructure that favours functionality in the colder rather than the warmer months would seem more advantageous for a country like the UK. However, energy consumption for cooling in the warmer months will only become more important in the future with the impact of climate change, so discovering ways to use vegetation on green infrastructure in a way that renders it uniformly functional year-round in terms of thermal performance would be a worthwhile undertaking for further studies.

The seasonal contrast in thermal provision observed in this study could be caused by a number of factors. It could be due to the research sites (building rooftops) potentially being prone to more extreme conditions during the summer than in the winter and therefore to the shrubs responding accordingly. In other words, provision may have increased with an increase in stress and consequently in physiological and morphological responses that allowed shrubs to endure these conditions. Another reason could be linked to dormancy – plants are mostly dormant in the winter and therefore are physiologically and morphologically less active. This fact suggests that perhaps woody shrubs in the winter have only *physical* protection against exposure to harsh weather conditions (depending on the species), mainly on account of their foliage and canopy structure, and that is if the shrubs are evergreen or at least semi-evergreen; otherwise they may be completely exposed and forced into dormancy until late spring. On the contrary, shrubs in the summer have the dual support of both physiological and morphological mechanisms (e.g. cooling mechanisms via stomatal closure, avoidance/tolerance strategies to heat and drought, higher canopy density during periods of fitness or leaf shedding/paused growth to avoid embolisms, leaf/wood growth including plant height, branching and branch length) to combat temperature extremes and other environmental factors that can impede their general fitness, growth and survival. **The strong seasonality in shrub thermal performance is most likely due to a combination of all these hypotheses, but it may not be essential to know why it occurs; it may be more important to find ways of using seasonality to our advantage to enhance plant functionality.**

One of the easiest methods for honing and controlling plant functionality is through the use of specific plants or types of plants that are best suited for certain purposes. What is meant by "easy" is that there is an element of control in choosing a plant by *species*, in that species-specific characteristics represent a species' "ID card" and a way of guaranteeing reliability of sorts when predicting useful plant (or ecosystem) services. In the context of this study, the choice of **species** proved to be crucial in determining the levels of thermal provision by the woody shrubs. **Species had a significant impact on the levels of insulation and cooling provided by the shrubs in the winter and summer, respectively.** In the winter, the average best-performing shrub (*Viburnum*) maintained twice the amount of warmth as the average worst-performing shrub (*Ceanothus*). Likewise in the summer, the average best-performing shrub (*Viburnum*) maintained more than 2.5 °C lower temperatures under the canopy than the average worst-performing shrub (*Ceanothus*). There was also a consistency in the levels of performance by the different species through the years, with *Viburnum* and *Ceanothus* displaying significantly opposing thermal abilities in all scenarios despite both being evergreen and relatively short shrubs. The idiosyncratic characteristics of a species, like average plant height, canopy density, leaf type/thickness, shrub lifeform (e.g. evergreen vs deciduous), habit and branching structure, will *collectively* influence that species' canopy microclimate. For example, species mixture (i.e. species composition of a shrub population) did not have a significant effect on overall shrub thermal performance, meaning that the levels of provision by the shrubs was the same whether they were placed in groups of shrubs composed of only one species ('monospecific') or in groups of three different species ('polyspecific'). However, when comparing the cooling capacity of the different shrubs in the summer, it was found that the differences amongst species were significantly greater in the monospecific populations than in the polyspecific populations. In other words, **the species-specific characteristics of the six woody shrub species were reflected more (i.e. the species differences were more apparent) in the single-species populations than in the mixed-species ones, the latter producing a recognisable 'flattening' or levelling effect on individual species-specific cooling properties.** The question is not which is better – having low or high species diversity – as neither influenced shrub thermal performance in a significant way. The question is instead, **how can we harness the inherently complex concept of 'species' to improve plant functionality?**

Despite not affecting plant microclimate below the canopy, **species mixture** did have a surprising effect on the temperature *above* the canopy of the shrub populations. Depending on the density and characteristics of the foliage, one would expect temperatures below the shrub canopy to be warmer in the winter and cooler in the summer compared to the respective temperatures above the canopy, in that the foliage would protect the understory from atmospheric conditions and create a milder microclimate below the canopy. One would also expect mean temperature just above the shrub canopy to maintain a similar temperature to that of the surrounding ambient or air temperature. Unexpectedly, the mean temperature above the shrub canopy in the winter was significantly higher than that of bare substrate in all species and was even higher than the mean temperature *below* the plant canopy in *Buddleja*. Intriguingly, species mixture in the winter had a significant effect on temperatures above the shrub canopies of all species except *Ceanothus*, which was also the only species without significantly different temperatures above and below the canopy in either the winter or summer. In the summer, the difference between above and below canopy temperatures was significant only for the two deciduous species (*Elaeagnus* and *Cotinus*) and *Ceanothus* was the only species to have temperatures above the canopy significantly affected by species mixture (the opposite to winter). Finally, *Buddleja* was the only species in the winter to insulate significantly more in the monospecific than in the polyspecific populations, whereas *Ceanothus* was the only species in the summer to cool significantly more in the polyspecific than in the monospecific populations. It is difficult to ignore the resemblance of a 'tennis match' between *Ceanothus* and *Buddleja* in this scenario, the two species constantly 'out of sync' which each other. **Plant height** will most likely have been the cause, given that *Buddleja* was the tallest species and *Ceanothus* was the shortest one in the study: *Ceanothus* and *Buddleja* were two of the three species tested on the same research site (Hadfield roof garden) and so when the two were placed in polyspecific (i.e. mixed species) populations alongside *Cotinus*, it is reasonable to think that such a scenario would have been overwhelmingly more advantageous to *Ceanothus* in terms of shade and protection than it was to *Buddleja*, where the latter would have been more exposed surrounded by shorter shrubs. The opposite would also have been true – a monospecific population would have been far more favourable to *Buddleja* (i.e. less exposed due to all shrubs being tall) compared to *Ceanothus* (i.e. more exposed due to all shrubs being short). **By these findings, it is apparent that species was a key factor regulating shrub thermal performance, but that some species-specific characteristics like plant height wielded a greater influence than others.**

Perhaps the simplest indication of species influence on plant canopy microclimate was the observation of the conspicuous differences in **maximum recorded insulation and cooling** by the six woody shrubs during the study. As previously mentioned, the average shrub insulating capacity was relatively minor compared to the average shrub cooling capacity and it reached at most approximately 3.5 °C in *Viburnum* during the last winter of the study. The same species during the summer of same year was able to cool temperatures by more than 25 °C compared to Control! Generally the "best" species in terms of 'maximum cooling' performance was always *Viburnum*, followed at a distance by both *Cistus* and *Elaeagnus*. However, the "worst" performing species was harder to pinpoint, as *Ceanothus*' thermal performance seemed to noticeably decrease over the years while *Buddleja* seemed to remain stabily at the bottom throughout the entire study. This observation thus leads to the broaching of another important aspect of this study – the effect of **time** on shrub thermal performance. For example, the maximum cooling service provided by a shrub in the first year was of approximately 19 °C, but this increased to over 25 °C by the last year of the study, thereby indicating an increase in performance in time.

Overall, shrub thermal performance was indeed found to have significantly improved with time, suggesting that woody shrubs were not only *surviving* in rooftop environment but were largely also *adapting* enough to it to continue growing despite growth-limiting experimental containers. This increase in performance could be due to plant growth (i.e. physical growth in canopy density and structure), however the evident dip in performance in Year 2 could be related to the rearrangement of the shrubs' spatial dispositions to accommodate the different experiments carried out each year (e.g. Year 1 = all monospecific, all dense; Year 2 = all polyspecific, half sparse and half dense, half small and half large; Year 3 = all dense, half monospecific and half polyspecific). It is also true that a deviation from typical seasonal weather (e.g. annual differences in seasonal weather patterns, like a particularly wet summer or mild winter) at any point during the study may also have played a part in the way shrubs performed on the research sites. Constant exposure to the elements and aging will have had a negative impact on the shrubs' physiological and morphological processes, the combination of which may have affected the shrubs' ability to abate temperature extremes. On the other hand, shrub growth and adaptation to rooftop environment will have had a positive impact on fitness and survival, which in turn will have had an overall positive effect on the shrubs' ability to buffer extreme temperatures.

Despite the increase in shrub thermal peformance through the years, performance over the course of a single season was found to decline significantly. In particular, it was observed to decrease significantly in all species from the beginning to the end of summer in the final year of the study. By contrast, the thermal performance of all shrubs in the winter (albeit at a much lower level of performance) was much more consistent and fluctuations in both above- and below-canopy temperatures were less severe throughout the season. Although the phenomenon of declining shrub performance through the summer may undoubtedly be linked to atmospheric conditions that become less extreme as summer progressed, the decreasing performance that can be observed in all species may also be in relation to a gradual reduction in physiological fitness that can occur as drought and heat stress likely took a toll on plant health. **Declining shrub thermal performance throughout the summer was therefore most likely related to the maturing of leaves in the evergreens species or even to the senescence and progressive fall of leaves due to both natural ageing and drought and heat stress.**

The final but not least important aspect of 'Study B' to be discussed is based on the least expected finding of the study – that of the **delaying effect** by shrub vegetation on the reaching of peak maximum temperatures, as observed during the first summer of the study. For the most part, all three categories of that first summer (Control, low-density vegetation and high-density vegetation) *anticipated* rather than delayed the reaching of peak midday temperatures compared to air temperature, meaning that, at any given minute during the warmest four hours of the day, temperature on bare substrate and the vegetated categories most likely reached maximum *before* air temperature did (N.B.: varying by minutes or by hours, depending on the day). However, the number of times when the three categories *delayed* rather than anticipated the reaching of peak maximum temperature compared to air temperature *increased* going from Control (i.e. no vegetation) to low-density shrub populations (i.e. little or sparse vegetation) to high-density shrub populations (i.e. dense vegetation) – from only 2.4% of the time on Control, to 11.0% on low-density vegetation to 32.2% on high-density vegetation. **In other words, high-density woody shrub vegetation had the ability to delay the reaching of peak high temperatures on a rooftop by nearly one out of every three minutes during the warmest four hours of each summer day.** If high-density woody shrub vegetation could be harnessed to delay peak rooftop temperatures and if this effect was directly transferrable to internal building temperature, this finding could have major implications in terms of energy savings. Implementing high-density woody shrub vegetation using high-performing species could consequently also delay the use of energy-consuming ventilation systems for cooling inside building spaces. This finding supports the call for further studies on ways to increase the delaying effect by all vegetation on green roof and other green infrastructure in an effort to reduce the impact of climate change through nature-inspired solutions.

5 Conclusions

The research project was a 3-year study divided into two parts: 1) Study ‘A’, to evaluate shrub morphological and physiological performance, and 2) Study ‘B’, to evaluate shrub thermal performance. The overall aim of the research project was to identify the relationships between the shrub canopy traits observed in Study ‘A’ and the shrub canopy microclimate observed in Study ‘B’, to determine combinations of plant traits and spatial arrangements (or conditions) that can potentially enhance green roof thermal performance when using woody shrubs as green roof vegetation. Study ‘A’ and Study ‘B’ are simply ‘two sides of the same coin’, the ‘coin’ representing the main factors determining the relationship between plant functional traits and plant canopy microclimate. The purpose of this final chapter is therefore to identify these factors by discussing the findings from both studies of the research project as a whole, in the hope of better understanding the cooling/insulating services provided by woody shrubs and how they can be judiciously harnessed to improve green roof thermal performance and bring about energy savings. **The potential benefits of understanding this association – between shrub characteristics and the ability of shrubs to reduce extreme temperatures – include improving the plant selection process for functional green roofs, promoting the use of woody shrubs in green infrastructure and contributing to the knowledge of what makes for high-performing green roof vegetation in terms of thermal insulation, fitness and longevity.**

The effect of species

Species had a significant effect on the levels of insulation and cooling provided by the shrubs in both the winter and summer, respectively. On average, the best-performing shrub (*Viburnum*) insulated twice as much as the worst-performing shrub (*Ceanothus*) in the winter. Similarly, on average the best-performing shrub (*Viburnum*) maintained more than 2.5 °C lower temperatures under the canopy than the worst-performing shrub (*Ceanothus*) in the summer. There was also a consistency in the levels of performance by the different species through the years, with *Viburnum* and *Ceanothus* displaying significantly opposing thermal abilities in all scenarios despite both being evergreen and relatively short shrubs. The average shrub insulating capacity was relatively minor compared to the average shrub cooling capacity and it reached at most approximately 3.5 °C in *Viburnum* during the last winter of the study. The same species during the summer of same year was able to cool temperatures by more than 25 °C compared to Control. In general, the best performing species in terms of maximum cooling was always *Viburnum*, followed at a distance by both *Cistus* and *Elaeagnus*. However, the worst performing species was harder to pinpoint, as *Ceanothus*' thermal performance seemed to noticeably decrease over the years while *Buddleja* seemed to remain stabily at the bottom throughout the entire study.

The evergreen shrubs (*Viburnum* and *Ceanothus*) had the highest canopy or foliage density while the semi-deciduous shrubs (*Buddleja* and *Cistus*) had the lowest. In fact, *Buddleja* had the lowest foliage density with 4 times less leaves than the evergreen shrubs and the lowest values of leaf area index (LAI). Leaf mass per area (or leaf thickness) was also significantly different amongst the species, with highest leaf thickness in the evergreens, intermediate thickness in the semi-deciduous species and lowest thickness in the deciduous shrubs (*Elaeagnus* and *Cotinus*). Consequently, *Buddleja*'s low canopy foliage density, low leaf to branch ratio, intermediate leaf thickness and other leaf and branching characteristics will have contributed to its reduced ability to insulate from wind/frost and to shade from high irradiance, therefore resulting in poor thermal performance.

Species also influenced physiological shrub parameters, usually highlighting a correlation between performane and leaf longevity or certain functional groups (i.e. evergreen habit vs deciduous habit, tall vs short shrubs). There are too many examples to describe, but almost all morphological and physiological parameters were affected more by leaf longevity or functional group than by species. For example, leaf mass per area (or leaf thickness) was highest in the evergreens, intermediate in the semi-deciduous shrubs and lowest in the deciduous shrubs. Similarly, evergreen shrubs were the least affected by water stress and maintained the highest soil water content, whereas the semi-deciduous generally presented the worst water-use efficiency.

Species was therefore key to regulating shrub morphological, physiological and thermal performance, with some species-specific characteristics (i.e. leaf longevity and plant height) displaying a greater influence than others. Additionally, *Viburnum* was the indisputable 'winner' out of the six woody shrub species, presenting the overall best shrub insulating and cooling properties and the highest fitness, adaptability and long-term suitability as a green roof plant. Conversely, *Cistus* was ranked the worst performing species of the study for many reasons outlined in previously chapters, but especially for its incredibly high mortality rate.

The effects of plant density and species mixture

Plant density played an overall significant role in influencing plant canopy microclimate, with shrubs in high-density populations (i.e. individuals spaced closer together) representing the best condition for increasing the insulating and cooling services they provide. Species mixture also played a crucial role in shrub thermal performance, in that it defined the level of 'heterogeneity' vs 'homogeneity', or the 'individuality' vs 'group effort' of insulating and cooling services. In other words, the species differences in thermal performance were more apparent in single-species populations and shrub performance was the result of the individual species effort, whereas species differences were 'flattened' or levelled in mixed-species populations and shrub thermal performance was therefore the result of a 'collective' effort. Additionally, high-density woody shrub vegetation was found to delay the reaching of peak high temperatures by nearly a third of the time during the warmest hours of a summer day.

Plant density also impacted the woody shrubs' morphological and physiological responses in numerous ways, most notably their growth patterns and photosynthetic performance. In fact, growth was significantly lower in high-density shrub populations, potentially due to a greater chance of self-shading by the canopies which may have affected the shrubs' photosynthesis and thereby overall growth. Photosynthesis, as quantified through the measurement of gas exchange parameters, was in fact found to be significantly higher in high-density shrub populations. The way plant density and species mixture affected shrub response could also be very complex. For example, evapotranspiration rate, assimilation and stomatal conductance were not affected by plant height, but plant density had a significantly greater effect on these parameters when the shrubs were in mixed-species populations, thereby suggesting that a more heterogeneous plant height in shrub populations may have significantly affected the way shrubs photosynthesised.

In conclusion, establishing the kind of plant density and type of species mixture both represent key planning areas when installing a intensive green roof or other green infrastructure with the purpose of lower costs associated with energy consumption for the heating and cooling of buildings. Implementing high-density woody shrub vegetation using high-performing species can also potentially delay the use these ventilation systems. Moreover, choosing species that are highly responsive to changes in plant density, for example in terms of increasing leaf thickness in conditions of low-plant density where they would be more exposed to light and other environmental factors, could represent an advantage to woody shrubs growing on green roofs. These findings also highlight the need for further studies on the 'delaying' effect not just by shrubs but by all type of vegetation, in order to study the ways to use and maximise this effect to improve the thermal performance of green roof and other green infrastructure.

The effects of plant height and canopy characteristics

The six woody species presented a wide range of morphological characteristics that affected light interception and therefore plant canopy microclimate, such as differing plant heights and habits, above-ground biomass and area and branching architecture. Both plant height and leaf area index (LAI) influenced the shrub canopy's ability to shade and intercept light and therefore determine canopy microclimate. Plant height also affected physiological shrub response. For example, both leaf area and photosynthetic water-use efficiency (WUE_P) were found to be significantly higher in the 'tall shrubs' (*Buddleja*, *Elaeagnus* and *Cotinus*) than in the 'short shrubs' (*Ceanothus*, *Cistus* and *Viburnum*), suggesting a relationship between taller shrubs, reduced leaf longevity and higher water-use efficiency in photosynthetic processes.

LAI was confirmed as a key parameter for predicting a species' level of light interception and thereby determining shrub thermal performance. Both maximum quantum yield (or photosynthetic performance) and leaf area were found to correlate with LAI – photosynthetic performance of the woody shrubs decreased as LAI increased, and LAI increased with leaf area. Photosynthetic performance and leaf area could therefore be reliable proxies of LAI and are also simpler parameters compared to LAI to measure. LAI was calculated based on canopy (or foliage) density and leaf area and was found to be highest in *Viburnum* and *Cotinus* and lowest in the semi-deciduous shrubs (*Buddleja* and *Cistus*). In particular, the semi-deciduous shrub *Buddleja* (also the tallest shrub) had the lowest canopy density, with 4 times less leaves than the evergreen shrubs. Canopy density was in fact negatively correlated with branch length, meaning that the longer the branches the less dense the foliage. Similarly, leaf area was also significantly affected by plant height – on average, the tallest shrubs had the biggest leaves and the shortest shrubs had smallest leaves. Although neither leaf area nor leaf biomass were correlated with branch length, both branch length and plant height will most likely have affected the species' biomass allocation. Despite having the lowest canopy density and one of the lowest values of LAI, *Buddleja* was still able to intercept about 74% of incident light during an ad hoc experiment, which is a high percentage in spite of having the lowest leaf to branch biomass ratio (i.e. a higher ratio of exposed woody biomass compared to leaf biomass) and therefore a greater predisposition to allow light to pass through the canopy.

The effect of season

Season had the greatest inflence on plant canopy microclimate, impacting not only plant density but also determining the levels of shrub thermal performance in winter and summer. Both insulation and cooling were significantly greater in the summer and therefore shrubs provided the greatest level of thermal provision in the warm season. The average shrub increased temperatures in the winter compared to Control in the range of 0.5 – 1.0 °C, whereas the average shrub lowered temperatures in the summer compared to Control in the range of 4.0 and 6.6 °C. In fact, shrubs provided overall six times more "cooling service" in the summer than they provided "insulating service" in the winter. Using woody shrubs as the main type of vegetation on green roofs would consequently provide minimal insulating service in the winter but a six-fold greater cooling service in the summer. Moreover, the effect of plant density on temperature was significantly greater in the summer than it was in the winter, with shrubs in high-density populations cooling on average nearly 1.7 °C more than those in low-density populations, compared to only a 0.2 °C difference between the two categories in the winter. Therefore, finding ways of using seasonality to our advantage to enhance plant functionality and rendering vegetation on green infrastructure uniformly functional year-round in terms of thermal performance would be a worthwhile undertaking for further studies.

Shrub adaptability to change and their long-term fitness and survival

Shrub thermal performance significantly improved with time, suggesting that woody shrubs were not only *surviving* but were also *adapting* to rooftop environment despite experimental constrictions. For example, the maximum cooling service provided by a shrub in the first year was of approximately 19 °C, but this increased to over 25 °C by the last year of the study. However, performance over the course of a single season was found to decline significantly during the final summer of the study, which was most likely related to the maturing or senescent leaves due to age, drought and heat stress. The shrubs also presented declining levels of soil moisture content in all species, also most likely reflecting the increasing levels of stress experienced over the years. On the contrary, all shrubs increased leaf thickness during the course of the study, most likely an adaptive strategy to protect the canopy in response to increasing levels of environmental stress factors.

There was also a strong relationship between the level of photosynthetic response or ʻsensitivity' of a species to changes in shading conditions (i.e. caused by variations in plant density, population size and species mixture) and species fitness and vitality. For example, photosynthetic performance did not have a significant effect on shrub mortality but it did significantly correlate with growth rate. The fact that growth rates slowed with increasing photosynthetic performance suggests that shrubs that are not able to adapt to surviving at lower levels of photosynthetic performance (i.e. have inefficient photosystems), like in the case of *Cistus*, could in the long-term see drastic reductions in their woody biomass in order to save energy and not die.

Finally, predicting mortality rates in species of woody shrubs must become a necessary part of plant selection for improving green roof functionality, because selecting unsuitable species resulted in very high mortality rates in the study species. In a real-life scenario, high mortality rates could have major performance and economic consequences. In this sense, leaf mass per area, or leaf thickness, was found to be a reliable predictor of shrub mortality and therefore could be applied to test the suitability of shrub species to rooftop environment. A species' photosynthetic response to change was also found to be an effective predictor of fitness and long-term survival. In fact, woody shrub species that were physiologically highly responsive to changes in plant density, population size and species mixture indicated greater levels of adaptability and long-term vigour and therefore greater suitability as green roof vegetation.

Appendix A: Description of experimental species

1. Land restoration plants (Competitors)

1.1 *Elaeagnus angustifolia*

Belonging to the same family and having similar ecological and morphological characteristics to the sea buckthorn (*Hippophaë rhamnoides*) is the deciduous *Elaeagnus angustifolia* L., known as the Russian Olive and one of the 45 species belonging to the genus *Elaeagnus* (Stannard et al. 2002). *Elaeagnus* sp. are large shrubs or small trees native to southern Europe, central Asia, and the western Himalayas, but are best represented in the steppe regions of this distribution (Graham 1964). The Russian Olive has been introduced as early as 1900 in semi-arid and saline environments of western United States because of its adaptability, for use as shelterbelts, food, wildlife cover, roadside reclamation, and soil stabilization (Knof and Olsen 1984). By the 1940s, *E. angustifolia* had naturalized in the Rocky Mountain region and become a common ornamental plant, and only a decade later was identified as a particularly difficult alien to eradicate (Stannard et al. 2002). Today, *E. angustifolia* is ranked as the fourth most dominant riparian tree species in western United States (Nagler et al. 2011). This and other species of the same genus (e.g., *E. umbellata*) occur across a range of environments with different light and moisture conditions, showing tolerance to drought, high pH soils, and pollutants (Stannard et al. 2002; Yates et al. 2004, Brym et al. 2011, Zinnert et al. 2011). These characteristics, combined with the ability to fix nitrogen, make *Elaeagnus* species successful invaders, capable of displacing co-occurring native species (Ahmad et al. 2005). The Russian olive is also invasive of wet-saline and certain riparian environments and tolerates infrequent fire, temporary flooding, browsing, and mechanical cutting (Stannard et al. 2002).

E. angustifolia is a large, spreading, multi-stemmed, spiny-branched, fast-growing shrub with a reddish shredding bark, often obtaining 3.5 to 5.5 m in height and the same in width, forming extensive, dense thickets (Dirr 1998, Katz and Shafroth 2003). The development of spiny branches is most pronounced in young plants and in individuals growing in dry, nutrient-poor environments (Graham 1964). The abaxial side of leaves (alternate, lanceolate, simple and entire), petioles, and current-year branches are covered in distinctive, silvery-gray peltate hairs (scales). Flowers are apetalous, 4-symmetrical, small, with a cylindrical to campanulate yellow calyx, clustered in axillary umbels produced in the spring (Graham 1964, Katz and Shafroth 2003). The drupe-like fruit, an excellent source of minerals, vitamins (A, C, and E), flavonoids, essential fatty acids and other bioactive components (Ahmad et al. 2005), is oval-shaped, 1-1.5 cm long, and has a fleshy pericarp containing a hard-coated achene primarily dispersed by birds (Graham 1964, Katz and Shafroth 2003). *Elaeagnus* sp. thrives in both disturbed areas and undisturbed habitats including the understory of pre-existing forests (Yates et al. 2004, Brym et al. 2011), and the Russian olive in particular readily propagates from vegetative structures. Stump sprouting commonly occurs after cutting down the shrub, and excavation of the entire stump can trigger root sprouting (Stannard et al. 2002).

Like the sea buckthorn, *E. angustifolia* forms an association with the nitrogen-fixing endosymbiont *Frankia* (Carro et al. 2013), which is thought to provide an advantage over co-occurring species in terms of nutrient acquisition, energy resources and stress tolerance (Yates et al. 2004). In fact, the Russian Olive is known to be drought tolerant (Zinnert et al. 2013), growing well in upland areas that receive 200 mm or less of mean annual precipitation (Gong et al. 2006). It also grows well in wet-saline soils and is generally described as tolerant to very tolerant of soil salinity and salt spray (Belcher 1977, Isermann et al. 2008), tolerating EC (Electrical conductivity) levels ranging 6000-12000 μS cm^{-1} in field situations (Stannard et al. 2002), which are about 4-8 times the maximum value of EC for freshwater (QTPA 2010). In desert regions of Northern China, *E. angustifolia* grows naturally on flat sands near inland rivers, where it was planted in the late 1970s for land reclamation. In a recent study, this species was found to have high water use efficiency despite high transpiration rates, compared to other three sand-binding desert species evaluated (Gong et al. 2006).

The Russian olive and other *Elaeagnus* species resemble the sea buckthorn and the Japanese rose (*Rosa rugosa*) in their highly invasive behaviors, representing a threat to the ecological functioning of coastal and semi-arid habitats once established (Katz and Shafroth, 2003, Yates et al. 2004). The Autumn Olive, *Elaeagnus umbellata*, is deemed highly invasive and difficult to control once established because of its ability to resprout vigorously when burned, cut, or mowed (Szafoni 1990). In a study on the behavior of non-native invasive species in a cold-temperate climate site (Illinois, USA), *E. umbellata* showed aggressive pioneering behaviors, like the ability to germinate under a variety of conditions, a preference for high light environments (shade intolerance), and the ability to withstand disturbance (Yates et al. 2004). In a study by Zinnert et al. (2013), the functional traits and resource strategies of *E. umbellata* were compared to those of two native, co-occuring species (*Vaccinium corymbosum* and *Clethra alnifolia*) in another temperate-climate site (Virginia, USA). In their study site, *E. umbellata* also grew in a variety of habitats, growing in thickets along roadsides, forest edges, in old fields, and even as understory shrubs. Zinnert et al. (2013) found that *E. umbellata* had a greater ability to capture light (i.e., horizontal leaf angle with respect to light interception) as well as a higher hydraulic capacity, water use efficiency, and nitrogen leaf content compared to the other species. The ability of *Elaeagnus* species to adapt to a wide range of conditions has also been related to their foliar architecture and anatomy: the smaller size, the greater thickness, and higher trichome and stomatal density of the upper sun-leaves compared to the less exposed lower shade-leaves are considered adaptations to environments that present strong variations in light, temperature, and humidity (Klich 2000).

Despite the controversies related to their past use in land restoration, *Elaeagnus angustifolia* shrubs, like the sea buckthorn and the Japanese rose, are undeniably hardy and prevent wind and water erosion of soils. Their high adaptability to a wide range of environmental conditions, together with strong root systems that provide them with a good anchorage against windthrow and the odd combination of both high WUE and hydraulic efficiency, make them potentially effective candidates for green roof vegetation (Yang et al. 2015).

2. Typical Mediterranean species (Drought-tolerators)

2.1 *Ceanothus thyrsiflorus* var. *thyrsiflorus*

Ceanothus thyrsiflorus Eschsch. var. *thyrsiflorus* (syn. *Ceanothus thyrsiflorus* var. *repens* McMinn, according to NBCI 2016 and Jepson eFlora 2016b) belongs to the cosmopolitan Buckthorn family (Rhamnaceae), which comprises approximately 50 genera and 950 species of mostly shrubs and trees, some climbers and a few herbs, often thorny, distributed and well-represented in both the tropical and subtropical climate regions. The many cultivated species are represented by the North American *Ceanothus* (California-lilac), the warm-temperate and Mediterranean *Frangula* (Coffee Berry), the generally temperate *Rhamnus* (Buckthorn), and the mostly tropical *Ziziphus* (Jujube), genera which together represent a third of the family in terms of species, *Rhamnus* being the largest and most widely distributed genus with 110 species (McMinn 1930, Jepson eFlora 2014, Richardson et al. 2004). However, species of Rhamnaceae have a tendency towards xeromorphism and favor drier habitats (Richardson et al., 2004), which is certainly the case for the genus *Ceanothus*, where species distribution ranges mainly from SW Canada to northern Mexico in western North America, between the Rocky Mountains and the Pacific Coast. Species are particularly concentrated in SW United States and Mexico, with more than 50 species found in California alone (72% of them endemic), where they are an important component of semiarid forest, oak woodland, and chaparral. Known generally as California-lilac, *Ceanothus* species are very common plants in California and may be called locally ‘buckbrush’ (*C. cuneatus*), ‘deerbrush’ (*C. integerrimus*), ‘blue blossom’ (*C. thyrsiflorus*), ‘mahala mats’ (*C. prostratus*) or ‘mountain lilac’ (*Ceanothus* ‘Concha’), the last of which is perhaps the oldest of hybrids. The climate of California’s coastal region is unique in North America due to its Mediterranean climate that, though progressively drier and more continental moving away from the coast, is influenced by a year-round oceanic cooling of temperatures from the Pacific Ocean. As a result, *Ceanothus* is adapted to growing in conditions that vary from warm and humid to hot and dry, often in relatively poor soils (McMinn 1930, Johnson 1977, Bell 2009, Burge et al. 2011).

There are approximately 55 species in the genus *Ceanothus*, with evergreen (e.g., *C. cordulatus*, *C. velutinus*, *C. thyrsiflorus*, *C. cuneatus*, *C. prostratus*, *C. pumilis*, *C. arboreus*, *C. gloriosus* etc.) and deciduous plants (*C. integerrimus*, *C. sanguineus*, *C. americanus*) belonging to two subgenera, *Ceanothus* and *Cerastes*, whose distinct geographic distributions (more widespread throughout North America in *Ceanothus* or limited to the western part of the continent in *Cerastes*) reflect their primary reproductive strategies: seeder *and* (some) resprouting from root crown or obligate seeders, respectively (Conrad et al. 1985, Pugnaire et al. 2006). The latter more restricted distribution, known generally as the California Floristic Province, encompasses an impressive richness of *Ceanothus* and other species (Conrad et al. 1985, Jeong et al. 1997, Burge et al. 2011). The majority of *Ceanothus* species are sclerophyllous evergreen woody shrubs, ranging in habit from prostrate, like *C. gloriosus* (0.3 m), or sprawling, mound-forming and erect (*C. thyrsiflorus*), although some, like *C. arboreus* (4-8 m), may be found as small trees (McMinn 1930, Hardig et al. 2000, Pugnaire et al. 2006, Jepson eFlora 2016a). Some species are also spiny and many possess multicellular glandular trichomes, especially on leaf margins (Wollenweber et al. 2004). The natural diversity of this genus has made it attractive to horticulturists for over a century (Keeley and Keeley 1994) and, although native to North America, is widely planted as an ornamental garden plant in the United Kingdom (Denton et al. 2008). There are more than 80 cultivars of the genus *Ceanothus*, many of unknown origin and about a fourth consisting of hybrids (Keeley and Keeley 1994), as members of this group are prone to hybridization (Wollenweber et al. 2004). Moreover, their relative drought tolerance and conspicuous clustered inflorescences, ranging in color from white, pink, to cerulean or indigo blue, makes them increasingly valuable as landscape plants (Keeley and Keeley 1994, Jepson eFlora 2016a).

Ceanothus thyrsiflorus Eschsch. var. *thyrsiflorus* is one of two varieties (the other being *griseus*) of the species *C. thyrsiflorus* and classified under the more broad-ranging subgenus *Ceanothus*. Commonly known as Blue blossom, the plants of this variety are medium or large mat- to mound-like shrubs, generally < 1 m in height, with an open habit and subglabrous, flexible, and ascending to spreading stems. When in thickets in their native environment, individuals can be 1-4 m in height and have stems ascending to erect. Stipules are scale-like, thin and early deciduous. Branches are green, not spinose or papillate, angled distally and with ridged internodes. Leaves (0.5-4.5 × 0.3-2.5 cm, or at least < 2 × width) are alternate, evergreen, petioled (3-9 mm) and glandular, with stomata on lower epidermis and never encrypted. The leaf lamina is oblong-ovate to elliptic, firm, adaxially dark green, smooth, glossy and glabrous, abaxially paler and glabrous to minutely pubescent, with only a few coarse hairs along the prominent veins, which are 3-ribbed from the base. The tip of the leaf is obtuse to rounded and the margin slightly revolute, thick, and minutely gland-toothed, with teeth paler and glands dark. Inflorescences (1.5-7.0 cm) generally in subcompound racemes or panicles (termed 'thyrsoid'), axillary, with light to deep blue (rarely white) flowers (< 5 mm) and white to deep blue pedicels. Flowers are bisexual, radial, 5-stamened, with 5 hood-shaped petals and 5 lance-deltate and incurved persistent sepals, colored like petals. Ovary ½-inferior, 3-lobed and 3-chambered (each 1-ovuled). Fruit (2.5-4.0 mm) is a sticky, spherical, generally 3-lobed capsule, smooth and without horns but often with 3 ridges or crests, producing 3 seeds (2-5 mm). The growth of new leaves, flower buds, and branch elongation in this species are all observed to begin in February, while leave buds form at the end of June. Fruit development begins in April and maturation and dispersion occurs by June. Although evergreen, *Ceanothus thyrsiflorus* loses a major portion of its foliage during the summer, beginning in June and continuing until water stress persists. This variety *thyrsiflorus* can be found along bluffs, slopes and canyons as part of chaparral, coastal scrub and closed-cone pine forest vegetation of California's coastal range, at altitudes lower than 800 m. Its distribution outside California includes SW Oregon and northern Baja California, Mexico (Watson 1875, McMinn 1930, Jepson eFlora 2016b).

The common Blue blossom, *Ceanothus thyrsiflorus*, is veritably a native to northern California and a component of northern coastal scrub and prairie. This community is described as consisting of dense stands of shrubs and forbs, situated between coastal stand and redwood forest along the California coast north of Big Sur, from northern Santa Barbara County to the Oregon border and inland to the foothill of the Sierra Nevada, where the cooling influence of the Pacific Ocean moderates summer drought (Ford and Hayes 2007). This vegetation type is sometimes referred to as "soft" chaparral because of its flexible stems and foliage, herbaceous understory, intergradation with coastal prairie, and smoother appearance in the landscape compared to the stiff, leathery, and rough vegetation of the "hard" chaparral types in the more arid southern California (Axelrod 1978). One of the many components of the coastal scrub is in fact the Blue blossom scrub, composed of stands in which *Ceanothus thyrsiflorus* surpasses even the coyote brush (*Baccharis pilularis*) and other shrubs in land cover and, where these stands are dense, can shade out other shrubs and any understory. It occurs on ridges and upper slopes in scattered stands within a scrub landscape or in the understory of forests, reaching even 3 m in height in its southern limit. In the canopy, *C. thyrsiflorus* is however considered a temporary dominant as a result of the post-fire germination of dormant seeds found in the soil. After a long period free of burning or other disturbance, the dense patches of blue blossom become less frequent and post-fire sites then return to being dominated by other shrubs of the northern coastal scrub (Ford and Hayes 2007).

Ceanothus species are indeed known to be rapid pioneers of post-fire and degraded areas. This behavior is exemplified in the study by Harvey and Holzman (2014), which compared the vegetation community of a closed-cone pine ecosystem dominated by *Pinus muricata* (bishop pine) on the northern coast of California, before and 14 years after a devastating fire that occurred in 1995 (Holzman and Folger 2005). They found that before the fire, the study area was dominated by a mature, even-aged forest of *P. muricata* (85% of trees), with a high richness of scattered Mediterranean tree and shrub species, with low herbaceous cover and only a rare presence of *Ceanothus thyrsiflorus*. In the early- to mid-stages in the 14 years after the fire, the authors found that *P. muricata* and *C. thyrsiflorus* dominated the forest composition, with a prevalence in tree (91% composed of *P. muricata*) and shrub (46%) cover, with *C. thyrsiflorus* as the dominant post-fire shrub (78% of shrub population). These dense shrub patches of *C. thyrsiflorus* likely inhibited dominance of *P. muricata* at some point of the early post-fire stage, but they also set the scene for long-term structural and compositional diversity in tree and shrub species, because plants in the *Ceanothus* genus increase available nitrogen in the soil through symbiotic fixation (Delwiche et al. 1965), which improves site fertility compared to nearby stands dominated by pines (Johnson 1995) and the establishment of shade-tolerant species in pine-dominated stands after disturbance (Oakley et al. 2006).

Ceanothus is in fact known as being 'the primary nitrogen fixer in drier, mid-elevation ecosystems of the Pacific Northwest and Sierra Nevada range' (Conrad et al. 1985) and significantly contributes to ecosystem nitrogen budgets (Franklin et al. 1985). Because of their high leaf nitrogen content, *Ceanothus* species represent a very important food source for wildlife and *C. thyrsiflorus* in particular is considered one of the most important browse species. For the same reasons, the genus is also valuable for land restoration, as it can tolerate extreme conditions, contributes to soil amelioration, and prevents erosion, especially in the case of mat-forming species like *C. thyrsiflorus* and *C. prostratus* (Conrad et al. 1985). Like *Elaeagnus*, *Ceanothus* is a genus containing actinorhizal species, in which root nodules are infected by the actinomycetes *Frankia*. It is unclear exactly how many genera form relationships with this symbiont, possibly anywhere between 8 (Carro et al. 2013) and 24 woody dicotyledonous genera (Ritchie and Myrold 1999), six of which are notably *Alnus*, *Hyppophaë* (also of the Elaeagnaceae family), *Casuarina*, *Coriaria*, *Myrica*, and *Morella*. Research on the actinorhizal nodulation of this genus is comparably little compared to that of *Alnus* (alder), where nodulation has been reported to increase nursery production, improve seedling survival after replanting and enhance growth of non-nitrogen fixing species planted in close proximity to alders (Kennedy et al. 1999). Like alders, however, *Ceanothus* plants are able to increase soil nitrogen levels substantially and therefore have an important role in the revegetation of disturbed land (Krochmal and McCrain 1975), as demonstrated in the previous study by Harvey and Holzman (2014). A study that investigated the effect of nitrogen supply on nodulation in a *Ceanothus* cultivated variety, *Ceanothus griseus* var. *horizontalis*, found that nodulation was inversely correlated to nitrogen supply and it was greatly reduced or even suppressed when leaf N concentration was over 2% (Thomas and Berry 1989). The six-year study by Kennedy et al. (1999) confirmed this trend specifically in *Ceanothus thyrsiflorus*, where the effects of *Frankia* infection on the growth of nursery and field plants was investigated. The infection clearly improved growth, foliar N concentrations and survival rates in both scenarios, especially when a low N compost with slightly acidic soil was used (the latter favoring the growth of the fungi).

From what has transpired so far on their nitrogen-fixing capability, *Ceanothus* plants do not need fertilizing: not only because they fix nitrogen themselves, but also because this ability of theirs seems to wane when the soil already makes this micronutrient available. Therefore, *C. thyrsiflorus* var. *repens* investigated in the present study could potentially represent a successful candidate for growth on green roofs, where substrate is usually poor and shallow. However, it is not certain that this nursery-grown variety purchased in the United Kingdom is actually nitrogen-fixing. As *Ceanothus* species are native to North America, its *Frankia* symbiont is not naturally found in Europe and, at least 20 years ago (Kennedy et al. 1999), most *Ceanothus* plants produced commercially in the United Kingdom were thereby incapable of fixing nitrogen. This is a matter worth investigating because the same study by Kennedy et al. (1999), carried out in the United Kingdom on both uninfected and *Frankia*-inoculated plants, found that initially the two groups of plants did not show signs of having insufficient N (1.62% and 1.72%, respectively), while one year after planting in the field the foliar concentration in uninfected plants had fallen to a severely deficient level of 0.74% compared to a maintained acceptable level (1.66%) in the inoculated ones. Another problem that could potentially reduce the survival of this plant on green roofs could be that of contracting a fungus that causes leaf spotting followed by defoliation and dieback, a disease that has been carried over from North Americ and since 2001 observed on *Ceanothus* shrubs in several counties in the United Kingdom, confirmed specifically on *Ceanothus thyrsiflorus* and *C. arboreus* varieties and hybrids (Denton et al. 2008). Moreover, cold events in winter could potentially cause damages to this species. In a 4-year study in Oregon that evaluated the growth, flowering and cold hardiness of 38 species, cultivars and hybrid selections of *Ceanothus* (Bell 2009), including 7 varieties and hybrids of *Ceanothus thyrsiflorus*, reported that several cultivars showed dieback and leaf damage at temperatures lower than –5.5 °C, and among the most severely affected were the variety *C. thyrsiflorus* var. *griseus* and two of its two hybrids.

Studies performed on *Ceanothus* species to evaluate their freeze and drought tolerance, however, give more promising results. One by Langan et al. (1997) compared the different level of vulnerability to both water stress-induced and freezing-induced embolism in two evergreen sclerophylls, *Rhus laurina* (Anacardiaceae) and *Ceanothus megacarpus*, which are co-dominant shrub species in the mountainous coastal regions of southern California. Amazingly, *Ceanothus megacarpus* became 50% embolized at a water stress of –9 MPa (!!!) and 100% embolized by freeze-thaw events only at water potentials lower than –3 MPa. The reduction of thaw rates additionally and significantly lessened embolism occurrence (from 74 to 35%) in well-hydrated *Ceanothus* plants. The authors thus conclude that a combination of water stress- and freezing-induced embolism need to be included as possible factors limiting the growth, survival and distribution of this and other chaparral species and that, in the case of *Ceanothus* species, severe freezing-induced embolism results only when plants are already under extreme water stress. Another very similar study by Ewers et al. (2003) also had the aim of identifying which was the more vulnerable component, the living leaves (symplast) or the non-living water transport system (apoplast). The authors compared two co-occuring *Ceanothus* species in their response to 2-month long cooling experiments of winter-acclimated shoots and hypothesized that the more inland species *C. crassifolius* (evergreen and hairy) would be more tolerant of low temperatures than the coastal species *C. spinosus* (semi-deciduous and not hairy), both in terms of LT50 (temperature at which there is 50% loss of function or viability) and resistance to embolism. The LT50 for the coastal species was about –10°C while it was –18°C for the more continental one. Also, freeze-thaw cycles resulted in no change in embolism when the plants were well hydrated (–0.7 to –2.0 MPa), but at low dehydration (–5.0 MPa), the coastal species became 96% embolized with freeze-thaw while it was only 61% for the continental species, and the stems of the latter became 90% and 97% embolized at –6.6 MPa and –8.0 MPa, respectively. The authors conclude that the results are consistent with the species' relative ecological distributions (*C. crassifolius* in colder sites and *C. spinosus* in warmer sites) and both species show a relative symplastic tolerance to low temperatures and an apoplastic tolerance to freeze events in combination with drought stress (Ewers et al. 2003). Combined with the fact that *Ceanothus thyrsiflorus* is also moderately salt tolerant (Cassaniti et al. 2009), possibly an adaptation to coastal environments, the *thyrsiflorus* variety might not be doomed after all.

Another adaptation of *Ceanothus* species to coastal environments could be their shallow root systems (Poole and Miller 1975, Burk 1978, Langan et al. 1997), where root to shoot ration is almost 1 (Pugnaire et al. 2006) and root depth ranges from 0.6 m to 1.2 m, depending of soil conditions (Burk 1978). This could represent both a negative and a positive trait for survival on green roofs. On the one hand, a shallow root system is less of a threat to the root barrier of the green roof profile and roof deck, and intuitively a shallow-rooted plant would be better equipped to adapt to the typical green roof medium (≤ 15 cm). Shallow roots also respond more rapidly to changes in soil water availability (Burk 1978), taking advantage of the sporadic precipitation events in arid environments. The downside is that plant water status is highly dependent upon both transpiration rates of aboveground organs and absorption by the root structure, and plants with shallow roots are not able to absorb enough water to significantly modify their water status in conditions of aridity until deeper wetting of the profile occurs (Burk 1978). For example, in a study by Burk (1978) that compared diurnal and seasonal trends in stem water potential in the evergreen chaparral shrubs *Adenostoma fasciculatum*, *Quercus dumosa* and *Ceanothus crassifolius*, the first two being deep-rooted and *Ceanothus* obviously shallow-rooted, the *Ceanothus* species showed significantly greater seasonal changes in water potential and lower predawn water potentials but responded more quickly to winter precipitation compared to the other two. The authors concluded that deep-rooted species may have a longer vegetative season in conditions of aridity but that the early response to precipitation of a shallow-rooted species like *Ceanothus*, and its capacity to compensate for very negative xylem pressures by remaining metabolically active at greater levels of water stress, may in part offset the competitive advantage of a deeper root system.

In fact, *Ceanothus* species do not seem to adjust stomatal aperture in conditions of mild water stress, only showing increased stomatal resistance at potentials lower than –5.5 MPa (Poole and Miller 1975, Burke 1978). Among the three evergreen sclerophyllous and dominant co-occurring chaparral shrubs observed in a study by Baker et al. (1982), *Ceanothus cuneatus* reached significantly lower potentials compared to the other two species. For example, in the three study sites, cessation of branch elongation in *Ceanothus* occurred between –3.2 and –3.5 MPa, whereas minimum midday leaf water potentials ranged between –4.0 and –6.0 MPa throughout the drought period, and pre-dawn leaf water potential reached approximately –3.0 MPa. Even more impressive was the drop in predawn water potential in *Ceanothus megacarpus* and *Ceanothus crassifolius* in a study by Comstock and Mahall (1985), from –0.1 MPa at the beginning of the vegetative season in both species to lower than –6.5 MPa after a period of drought stress. Such high xylem pressures can only be sustained by having very narrow and redundant vessel elements and specialized xylem tissues, which this genus certainly has (Carlquist 1985; See Sect. 3.5). However, *Ceanothus thyrsiflorus* showed intermediate ecophysiological responses in terms of net photosynthesis (7.97±0.39 μmol m^{-2} s^{-1}), gas exchange rates (145.4±5.94 mmol m^{-2} s^{-1}), minimum leaf water potentials (–3.62±0.14 MPa) and WUE, and even had the lowest leaf area and leaf mass per area, LMA (1.33±0.04 cm^2 and 11.7±0.2 mg cm^{-2}), with respect to other two evergreen Mediterranean species (Abril and Hanano 1998). Yet, another study (Puganire et al. 2006) seemingly contradicts these values and claims that *C. thyrsiflorus* had values of relative growth rate (19.0 mg g^{-1} d^{-1}), net photosynthetic rate (58.5 mg

g^{-1} d^{-1}) and LMA (10.7 g cm^{-2}) that were higher compared to the mean values for all 10 species of *Ceanothus* investigated. While the values of leaf conductance to water vapor, g_L (110 mmol m^{-2} s^{-1}), leaf N content (2.1%), and photosynthetic nitrogen use efficiency, PNUE (0.60 mmol g^{-1} s^{-1}) for *C. thyrsiflorus* were very close to the average, water use efficiency (WUE) was much lower in *C. thyrsiflorus* (75 mmol mol^{-1}) than in the other *Ceanothus* species (≈120 mmol mol^{-1}).

In short, *C. thyrsiflorus* is a species with a shallow root system that can potentially reach very low negative water potentials in conditions of reduced soil moisture because it seemingly has high hydraulic safety but little control over stomatal closure, which in turn leads to this species having low WUE. However, some authors (Oechel et al. 1981) contradict this hypothesis and instead allege that various *Ceanothus* species are known to respond strongly in terms of leaf gas exchange regulation to reduced water availability, therefore regulating stomata. As this is a drought-tolerant species, it must employ mechanisms, including stomatal control, to withstand such high xylem tensions and avoid embolism during water stress. One such mechanism could be that of increasing xylematic levels of abscisic acid (ABA) concentrations in sap. The study by Tenhunen et al. (1994) observed that ABA concentrations in *Ceanothus thyrsiflorus* plants increased only when leaf water potentials were lower than –1.5 MPa, ABA concentrations reaching even 10,000 µmol L^{-1}. At less negative water potentials, ABA was lower and more variable (50-1000 µmol L^{-1}), inducing stomatal closure. Further increases in ABA concentration were associated with additional lowering of gas exchange rates, which probably contributed to improving WUE. The authors concluded that this species was able to sense even small changes in environmental conditions, probably due to initial drying of the uppermost soil and synthesis of ABA in the shallow roots. From the arguments exposed previously on shallow root systems, it could even be advanced that the extremely low water potentials reached by many *Ceanothus* species could be a means for allowing greater xylem tension, and therefore absorption capacity, in conditions in which relative water content at superficial depths in the soil is very low due to aridity. In other words, the plant would need to reach higher xylem tension without causing embolisms in order to extrapolate the little moisture that adheres to soil particles between pores.

Ceanothus thyrsiflorus may also exploit drought avoidance strategies to avoid the detrimental effects of high temperatures and irradiance and improve WUE. Comstock and Mahall (1985) found that the two evergreen *Ceanothus* species investigated (*C. megacarpus* and *C. crassifolius*) had steeper (more vertical with respect to incident solar radiation) leaf inclinations in their upper canopies, especially between May and August, during and following leaf loss from the lower canopy and when photosynthetic rates were rapidly declining due to reduced water availability. The authors also found that the increase in leaf inclination reduced the absorption of solar radiation by 6% and 20% in *C. megacarpus* and *C. crassifolius*, respectively. *C. crassifolius* has tomentum on both leaves and stem while *C. megacarpus* is glabrous, which would explain the differences in absorption reduction between the two species. Leaves of *C. megacarpus* exposed to high levels of irradiance were also found to have lower leaf conductance (transpiration), higher photosynthetic rates and required higher irradiances for photosynthetic saturation, resulting in greater WUE (Mahall and Schlesinger 1982). In fact, *Ceanothus* tends to shed branches and leaves of the lower canopy during the summer time drought, thus inducing natural pruning. Gas-exchange measurements performed by Mahall and Wilson (1986) on *C. megacarpus* indicate that the halting of new leaf production and the consequent natural pruning of the shaded branches would have small and probably negative effects on net carbon gain but would enhance overall WUE on a whole-plant basis.

Therefore, *C. thyrsiflorus* is a species that employs a vast number of adaptive strategies to both tolerate and avoid drought stress, including: nitrogen-fixing, seasonal self-pruning of foliage and branches, modifications in leaf inclination, stomatal control through heightened perception of soil moisture levels (i.e, higher root sensitivity via increase of ABA concentrations), and high hydraulic safety, all of which makes this a plant with great WUE, a very important trait for shrubs growing on green roofs during the summer.

2.2 *Cistus × hybridus*

As the scientific name suggests, *Cistus × hybridus* Pourr. (syn. *Cistus* x *corbariensis* var. *grandiflorus* Pau) is a spontaneous hybrid of the species *Cistus populifolius* L. and *Cistus salviifolius* L. (Martín Bolaños and Guinea López 1949, Tela Botanica 2016). It is a member of the Rockrose family (Cistaceae), which comprises about 180 species grouped in 8 accepted genera (Guzmán and Vargas 2005). While most genera of Cistaceae are native to the Mediterranean region and the warm-temperate parts of Europe (*Cistus*, *Fumana*, *Halimium*, *Helianthemum*, *Tuberaria*), a number of them are also distributed in the temperate zones of both North and South America (*Crocanthemum*, *Hudsonia*, *Lechea*). Rockroses are predominantly well-branched, perennial shrubs of small dimensions with characteristically showy flowers and covered in fine to dense pubescence (Martín Bolaños and Guinea López 1949). The genus *Cistus* is a typical component of the Mediterranean flora and includes 21 species (Amato and Sarnataro 2001, Guzmán et al. 2009), 16 of which are found in Europe and NW Africa (Warburg 1968), with the Iberian Peninsula, Morocco and the Canary Islands the richest in terms of both native and endemic species (Martín Bolaños and Guinea López 1949, Guzmán and Vargas 2005, Guzmán et al. 2009). *Cistus* species are highly thermophilous and xeric woody shrubs that range between 50 and 150 cm in height, with shallow and markedly planar root systems (Amato and Sarnataro 2001). They are commonly found in Mediterranean *maquis* and scrubland (*garigue*), usually as a result of the degradation of oak and pine scrubland (Bosch 1992, De Dato et al. 2013). In terms of pollination and reproduction, the genus includes species that are primarily self-incompatible (Bosch 1992, Amato and Sarnataro 2001) and as a result are particularly apt to producing spontaneous and artificial hybrids, which can originate from the crossing of even three or four different species (Martín Bolaños and Guinea López 1949). The identification of such hybrids in the field is relatively easy as they display characteristics that are intermediate between those of the nearby progenitors, especially if the latter are closely related (Guzmán and Vargas 2005).

The progenitors of *Cistus × hybridus* are in fact phylogenetically very close and are grouped in the monophyletic white-flowered *Cistus* lineage (Guzmán et al. 2009). The morphological traits of *Cistus × hybridus* are indeed intermediate between those of parents *C. populifolius* (tall, upright and very aromatic shrub with large glabrous, cordate, smooth-surface and flat-margined leaves) and *C. salviifolius* (small, sprawling and slightly aromatic shrub with small felted, ovate-lanceolate, rough-surfaced and crispate-margined leaves), both of which are highly branched, glabrous shrubs with slightly different ecologies and distributions (Guzmán et al. 2009, Abreu et al. 2012). Martín Bolaños and Guinea López (1949) describe *Cistus × hybridus* as being an erect shrub (0.5-1 m in height) with dark or blackish, elongated, glabrous and viscous stems. The leaves are petiolate, opposite, cordate to ovate at the base, elongated to oblong-lanceolate and slightly sharp or obtuse at the apex, generally rather small (20-30 mm × 10-20 mm up to 30-40 mm × 15-35 mm) but sometimes relatively large (70-80 mm × 25-40 mm) when mature. The leaf laminas are coriaceous on the adaxial surface and rough and reticulated on the abaxial side with prominent venation, partly stellate-hairy or subglabrous on both sides with tomentum only on younger leaves, and have a slightly undulate margin. The inflorescences appear at the tip of branches and carry 1 to 3 large (40-50 mm Ø), white, briefly pedunculated, axillary, 5-symmetry monoecious and many-stamened flowers that have one pair of ovate-lanceolate, tomentous bracts and 5 sepals characterized by a central bulge. The fruit is a pentagonal (5-valved) and slightly hairy dehiscent capsule about 8 mm long. Flowering occurs from May to the first week of June, while fructification begins immediately afterwards and maturation is completed by August, when seeds are released from the open capsule (Correia et al. 1992, De Lillis and Fontanella 1992). The hybrid's area of distribution is limited to the southern part of the Mediterranean Basin: Spain, S France, Italy (except for the NE region), the Balkans, Asia Minor and the coast of N Africa (Martín Bolaños and Guinea López 1949).

The genus is composed of pioneer species (De Dato et al. 2013) that not only colonize post-fire degraded scrubland (Bosch 1992, Schaffhauser et al. 2012), but also environments with extreme conditions like active geothermal sites (Bartoli et al. 2014) and contaminated mine wastelands (Abreu et al. 2012), showing tolerance to very acidic and infertile soil. In this regard, *Cistus* × *hybridus* and its progenitors have been found by Abreu et al. (2012) to successfully thrive in various Portuguese mining areas that presented high concentrations of various chemical elements and were thus considered seriously contaminated. For this reason, it was suggested by the authors that these species may be used for bioremediation, which in turn could prove beneficial to green roofs in potentially retaining organic and inorganic compounds found in polluted storm water. Additionally, Catoni et al. (2012) linked the high physiological plasticity found in leaves of three *Cistus* species to their distinct capacity to survive and grow in areas of potentially intense solar radiation, enabling them to colonize strongly degraded areas in conditions of full sun and contribute to the revegetation after fire (Gratani and Amadori 1991). *Cistus* species are in fact dependent upon this recurring ecological factor in the Mediterranean for reproduction and germination (De Dato et al. 2013), a trait that is characteristic of many ruderals and may contribute to their survival on a rooftop, where exposure to intense radiation and high temperatures can be significant.

A key feature of *Cistus* plants is their seasonal dimorphism (De Lillis and Fontanella 1992, Grammatikopoulos 1999, Gratani and Bombelli 2000, Catoni et al. 2012). As described previously in Sect. 2.3, *Cistus* species have evolved an adaptive strategy to withstand seasonal variations in water and nutrients through a series of phenological adjustments that result in the formation of two distinctive habits with considerable morphological, anatomical and physiological differences (Gratani and Bombelli 2000, Aronne and De Micco 2001, De Micco and Aronne 2009). *Cistus* species are in fact drought semi-deciduous plants, a sub-class of the drought-deciduous group that possesses intermediate characteristics between evergreen sclerophylls and drought-deciduous plants. These shrubs are relatively non-sclerophyllous but only semi-deciduous, in that they seasonally reduce a significant portion of their transpiring leaf surface area without completely shedding their foliage (Harley et al. 1987, Bombelli and Gratani 2003, De Micco and Aronne 2009). Their habit is therefore seemingly evergreen but only as a consequence of the alternation between two different leaf cohorts rather than by extended leaf longevity (Gratani and Bombelli 2000). The phenology of this unique habit is equally beguiling: autumn leaves are produced on shoots with long internodes, called dolichoblasts, in late autumn-early winter. These leaves, which are relatively large and thin (mesomorphic), last until May of the following spring when they are totally shed. At the same time, new spring leaves are produced between January and May on different shoots with shorter internodes, called brachyblasts, which grow at the insertion of autumn leaves, and are characterized by greater lamina thickness and smaller leaf area (xeromorphic). Spring leaves, which are partially shed during the summer, withstand summer aridity and are completely shed during the winter of the same year (Westman 1981, De Lillis and Fontanella 1992, Grammatikopoulos 1999, Aronne and De Micco, 2001, De Micco and Aronne 2009). In other words, during the spring season the contrasting cohorts of autumn and spring leaves coexist on the same plant (De Dato et al. 2013) and there is a continuous leaf and shoot growth throughout the year – only slightly lower during the cold and dry seasons (De Lillis and Fontanella 1992) – and a leaf lifespan ranges from four to eight months in spring and autumn leaves, respectively (Gratani and Bombelli 2000).

Morphologically and anatomically speaking, spring leaves differ from autumn ones in having a lower leaf area, less intercellular spaces in the mesophyll tissue and reduced chlorophyll content, while they are considerably thicker in palisade parenchyma and higher in tissue density, leaf mass per area (LMA) and trichome density. Spring leaves have encrypted stomata (Aronne and De Micco 2001) and can be up to 20% smaller, 21% thicker and 38% higher in LMA (Gratani and Bombelli 2000, Catoni et al. 2012). These traits, including anatomical differences in dolichoblast and brachyblast wood, are all veered toward greater water use efficiency and hydraulic safety during water shortage, through a combined reduction in transpiration and risk of cavitation. De Micco and Aronne (2009) studied the anatomy of branches in *Cistus* × *incanus*, a pink-flowered hybrid, and found that this species developed wood designed to protect from desiccation and regulate water transport by producing different types of seasonal wood. Brachyblast wood was found to be safer than dolichoblast wood and just as functional as "latewood" in mesophillous species because it had features that suggested the ability to remain active even when water availability is low, namely much narrower vessels and higher vessel frequency. This peculiar seasonal wood production, common in many other Mediterranean species, resulted in the formation of so-called "false" or seasonal rings in *C.* × *incanus*, in which two rings are produced annually after a dormancy period in summer (after the formation of brachyblast wood) and in winter (after the formation of dolichoblast wood), rather than the usual single annual ring developed after only one dormancy period in winter. In fact, the authors suggest that the anatomical evidence of seasonal dimorphism in *Cistus* wood lies in how cambial activity can have a double dormancy. However, most *Cistus* species have a single summer dormancy in cambial activity and thus generally form annual rings. Moreover, the occurrence of annual or seasonal rings in *Cistus* species may not only be species-related but also associated with the climatic conditions of the site (Cherubini et al. 2003).

Other characteristics of *Cistus* spring leaves include a lower chlorophyll content (by 14% in one case) compared to autumn leaves and the ability to fold under drought stress as a means of improving water use efficiency (WUE) and avoid photoinhibition, the folding aspect being prescribed to the less xeromorphic structure of *Cistus* leaves compared to evergreen sclerophylls (Gratani and Bombelli 2000, Catoni et al. 2012). Photoinhibition and transpiration are also reduced in *Cistus* through adjustments in the leaf inclination angle (up to 81° in angle difference between winter and summer foliage), whereas the thicker palisade layer, encrypted stomata and trichome density impede excessive water loss (Gratani and Bombelli 2000, Aronne and De Micco 2001, Bartoli et al. 2014), with pubescence potentially increasing reflectance and thus lowering leaf temperature as well (Gratani and Varone 2004). Closely linked to WUE are photosynthetic capacity and stomatal conductance, which are generally high in *Cistus* in autumn and spring-early summer but can fall in the winter and even by 54 to 80% in the hotter and drier periods in the summer due to water stress and leaf aging (Harley et al. 1987, Bombelli and Gratani 2003, Catoni et al. 2012). Generally, however, *Cistus* plants demonstrate turgor maintenance mechanisms that counterbalance these setbacks: a combination of elastic and osmotic adjustments that maintain leaf water potential between 11 and 33% higher compared to some evergreen sclerophylls (De Lillis and Fontanella 1992, Bombelli and Gratani 2003), despite having the highest relative water content (RWC) reduction, i.e. 20-40% (Grammatikopoulos 1999, Bombelli and Gratani 2003), a decrement in cellular water content that may have implications as a structural mechanism allowing leaf folding, again, as a protection against excessive exposure to radiation (Werner et al. 1999). Nevertheless, Grammatikopolous (1999) found that *Cistus creticus* in field conditions never reached values of water deficit that surpassed critical levels and associated this fact to its leaf dimorphism, where such phenological plasticity proved to help the species withstand dehydration and ultimately render *Cistus* more tolerant to drought.

Taking into consideration all the singular characteristics of *Cistus* shrubs, the question that ultimately arises is the following: are *Cistus* plants drought-avoidant or drought-tolerant? In other words, as they are an intermediate form between evergreen sclerophylls (drought-tolerants that do not shed their leaves and continue to grow during the dry season) and drought-deciduous plants (drought-avoidants who completely shed their leaves in the winter and stop growing during the dry season), what is then their main adaptive strategy to survive the unfavorable conditions of summer aridity? The authors that considered this aspect are somewhat divided. De Lillis and Fontanella (1992), based on comparisons between the growth activity of species with different adaptive strategies, concluded that semi-deciduous species like *Cistus* adopt a perfectly intermediate strategy between evergreen sclerophylls and drought-deciduous plants, because they were found to grow even during the dry and cold seasons, whereas De Micco and Aronne (2009) claim that the safety of brachyblast wood sustains leaves during summer drought, allowing them to maintain an almost evergreen habit that is more drought-tolerant than avoidant. Harley et al. (1987) are the only ones that found *Cistus* to have considerable stomatal control, typical of sclerophylls. However, most authors (Grammatikopolous 1999, Sánchez-Blanco et al. 2002, Bombelli and Gratani 2003, Catoni et al. 2012, De Dato et al. 2013) interpret the decrease in overall leaf evaporative surface in summer (i.e. reduction in leaf size and intercellular air spaces), as well as the increase in high trichome density and leaf rolling, as drought avoidance mechanisms to conserve water and prevent dehydration and embolism. In favor of the ‘intermediate form’ theory, Carlquist (1988) explains how many Mediterranean shrub species have a rather special safety-efficiency tradeoff, in which wood is produced with traits (i.e., large vessels) that allow high conductivity when water is available (in *Cistus* this would correspond to brachyblast wood) but also for safety during drought periods (narrow vessels, equivalent to dolichoblast wood). The seasonality of its foliage and wood and the unique ensemble of other exceptional features of *Cistus* points to the overwhelming possibility that this, and likely other semi-deciduous Mediterranean species, may not fit in either grouping, simply because it possesses a series of intermediate characteristics between the xeric and mesic extremes.

2.3 *Cotinus coggygria*

Cotinus coggygria Scop. belongs to the Anacardiaceae, a virtually cosmopolitan family comprising anywhere between 60 and 75 genera with 400 to 600 species. A few of its tropical (e.g., *Anacardium*, *Mangifera*) and temperate (*Rhus*, *Cotinus*, *Pistacia*, *Schinus*) genera are notorious for yielding economically important drupes, like cashew nuts (*Anacardium occidentale*), mangos (*Mangifera indica*) and pistachios (*Pistacia vera*), as well as other local, less renowned tropical fruits (e.g., makok or yellow mombin, marula, pink peppercorn), while some species infamously cause violent allergic skin reactions (e.g., poison ivy, *Toxicodendron radicans*) (Mitchell and Mori 1987, Wannan and Quinn 1991, Bezerra et al. 2007, Bachelier and Endress 2009). This family is characterized by the presence of resinous conduits in the cortex and wood that produce an exudate (resin), which also occurs in leaves, flowers and fruits (Mitchell and Mori 1987) and almost certainly contains the biflavonoid agathisflavone (Wannan and Quinn 1991). The genus *Cotinus* P. Mill is closely related to that of *Pistacia* (Xie et al. 2014) and *Rhus* (Pijut 2008), the latter encompassing species commonly known as the sumacs. However, unlike these and most other members of the Anacardiaceae (46 genera) and all other families of its order (Sapindales), *Cotinus* is not characterized by pinnate (compound) leaves but by simple leaves (Wannan and Quinn 1991). *Cotinus* is a very small genus of deciduous small trees or shrubs commonly known as “smoketrees” because of the wispy, plumose inflorescences that, after flowering, produce elongated pedicels and peduncles finely covered in plumose-villous hairs, creating a showy smoke-cloud effect. They are widely distributed through C and S Europe to the Himalayas and SW China, like the Common Smoketree (*C. coggygria*), as well as in the SE United States, as is the case for the American Smoketree, *C. obovatus* (Tzakou et al. 2005, Pijut 2008, Gilman and Watson 2014).

C. coggygria is an upright, spreading and multi-stemmed tall shrub (30-70 cm), rarely small tree (1-4 m), with smooth, grayish bark that smells of sap due to its production of resins and tannins (Pignatti 1982). A characteristic terpene-like fragrance can also be detected in leaves and inflorescences, which produce essential oils composed of limonene, α-pinene, terpinolene, various monoterpenes and many other organic compounds (Tzakou et al. 2005). Leaves are opposite, simple, entire, glabrous, glaucous and without stipules; those found near the base of the plant have rounded laminas (5-7 cm ø) and long petioles (3-7 cm), while the leaves near the apex become progressively more ovate (22-35×35-60 cm), with a maximum width at one-third of the lamina and a pointy base. In its venation architecture one may distinguish 8-10 veins diverging at almost 90°, becoming dichotomous at the apex. Flowers are usually infertile and monoecious, radially pentamerous, free and reduced, with 5 stamens, long peduncles and pale yellow to yellowish-green petals, borne in polygamous, erect, loose, terminal, and plume-like panicles (10-20 cm) that bloom between May and July and often persist through September. The fruit is a dry, one-seeded, reticulate, sclerenchymous and pseudomonomerous drupe (3-4 mm), light-reddish brown in color and ripening to near black between August and October (Pignatti 1982; Greuter et al. 1984, 1986, 1989; Diamantoglou et al. 1989; Wannan and Quinn 1991; Dirr 1998; Tzakou et al. 2005; Pijut 2008; Gilman and Watson 2014; Schönfelder and Schönfelder 2014). Leaves are produced in March and undergo growth and a natural defoliation process until about 25% of its foliage is dropped by June, leaf senescence starting late August and persisting until September and October when leaves turn a vivid yellow-orange and are completely shed (Diamantoglou et al. 1989). The western distribution area of *C. coggygria* extends mostly to the southern part of Europe, including Spain, France, Italy, the Balkan Peninsula, Lebanon, Syria and Crimea (Greuter et al. 1984, 1986, 1989), growing in thickets especially on dry, rocky limestone soil in brush and cliffs (0-900 m) (Pignatti 1982, Tzakou et al. 2005, Gilman and Watson 2014).

Not unlike *Cistus* plants, *C. coggygria* is among the typical pioneer species that develop during the natural encroachment of abandoned rural and degraded areas, a tendency briefly mentioned in Sect. 2.8. This behaviour is ascribed to the species' high hydraulic efficiency, based not only on its low root resistance, which translates into efficient water absorption and transport (Nardini et al. 2003), but also on its active stomatal control (Li et al. 2015), osmotic regulation (Diamantoglou et al. 1989), greater WUE and photosynthetic rates under conditions of high light intensity (Li et al. 2010), and the ability to alter its root morphology (i.e., increase root surface area, diameter and number and type of roots) in conditions of moderate to severe drought stress (Li et al. 2014). When used as green roof vegetation, this species was found to be resistant to drought and heat stress and showed a low mortality rate (<20%) one year after planting on very shallow substrate (10-13 cm) and in a sub-Mediterranean climate context (Savi et al. 2015). Nardini et al. (2012) also found that green roof modules densely vegetated (7 plants per m^{-2}) with two-year old *C. coggygria* plants and another typical Mediterranean shrub (*Prunus mahaleb*) reduced storm water runoff by more than 90%, despite *C. coggygria* (and probably *P. mahaleb*) being a shrub that maintains water status stability in the deciduous leaves for the entire dry period up until senescence (Diamantoglou et al. 1989, Nardini et al. 2003) and is able to lower its stomatal conductance under severe water stress to as little as 50% of that of control (Li et al. 2015). What was just described were clear consequences of prolonged stomatal closure, a condition that would usually (like many CAM-photosynthesizing plants) preclude an intense substrate water depletion through transpiration. In fact, net photosynthetic and transpiration rates in three-year old individuals declined significantly as drought stress increased and was prolonged (Liu et al. 2010, Li et al. 2015).

Although drought-deciduous species – and in general all deciduous plants – *avoid* unfavorable conditions through the shedding of leaves (Kozlowski 1991) and a variety of other morphological and physiological adjustments (See Sect. 2.6), *C. coggygria* is considered to be highly drought-tolerant (Nardini et al. 2003). Leaves may display symptoms of water stress (i.e., wilting, chlorosis, partial desiccation) – which are also signs of low sclerophylly – due to reduced water availability and high temperatures, but plants tend to replace them by sprouting new ones (Savi et al. 2015) and decrease leaf size during the summer (Nardini et al. 2012) in order to tolerate these conditions. In fact, Diamantoglou et al. (1989) found that leaves of this and another deciduous and closely-related species (*Pistacia terebinthus*) were surprisingly more sclerophyllous than those of *Cistus* sp. (semi-deciduous shrubs with a seemingly evergreen habit). However, in a recent study by Savi et al. (2017) morpho-anatomical and physiological traits of both *Cotinus coggygria* and a *Cistus* species (*C. salviifolius*), amongst other typical Mediterranean plants, were measured and compared, and *C. coggygria* actually presented a slightly lower LMA (10.0±0.3 mg cm^{-2}) in comparison to that of *Cistus* species (12.9±0.8 mg cm^{-2}), where high LMA is considered a characteristic of sclerophyllous leaves (See Sect. 2.6). Taking into consideration other traits measured in the same study, the two species showed relatively high cell wall elasticity (low values of bulk elastic modulus, ε), with *Cotinus* having a slightly lower elasticity (6.6±1.3 MPa) compared to *Cistus* (5.4±0.8 MPa), but leaf area was much higher and variable in *Cotinus* (19.5±1.6 cm^2) than in *Cistus* (5.7±0.7 cm^2). Therefore, a smaller leaf with more elastic cell walls and greater amounts of xeromorphic tissue (higher LMA) would probably indicate the *Cistus* leaves as being the more sclerophyllous ones.

Despite previous statements about *C. coggygria* being drought-tolerant, Diamantaglou et al. (1989) found that the distinct accumulation of soluble sugars and the consequently lower (less negative) values of osmotic potential in leaves of *C. coggygria* during the summer drought period was an important drought avoidance mechanism employed by this species, leading them to suggest that

Cotinus spp., as was the case for *Cistus* (See Sect. 3.2.2), may have intermediate characteristics between evergreen sclerophyllous drought-tolerators and deciduous drought-avoiders. The species' constant water status can immediately be associated to the following: strict stomatal control (Lambers et al. 2008), a high WUE (Sperry et al. 2002, Nardini et al. 2014) and a high cell wall elasticity, all of which would allow a large water potential gradient with little change in RWC, in turn increasing the plant's ability to extract moisture from an increasingly arid soil (Lambers et al. 2008), an action aided by the previously mentioned low root resistance found in *Cotinus* (Nardini et al. 2003). Additionally, the relatively high hydraulic efficiency (quantified here as the maximum stem conductivity, K_s) in *Cotinus* (0.52 kg m^{-1} MPa^{-1} g^{-1}, compared to 0.35 for *Cistus*) and its rather low safety (–3.88 MPa, quantified as the potential at which 50% of conductivity is lost, P_{50}) compared to *Cistus* and the evergreen sclerophylls *Rhamnus* and *Arbutus* (–4.40, –4.50 and –5.43 MPa, respectively), for example (Savi et al. 2017), lead to the support of the hydraulic safety-efficiency tradeoff: *Cotinus* is a species with relatively high efficiency but low safety, whereas *Cistus* has lower efficiency but higher safety. The fact that *Cotinus* enjoys high hydraulic efficiency in spite of tight stomatal control and stable water status in adverse conditions makes this a rather bizarre combination to have in a deciduous species, which would generally have a greater capacity for water transport but also higher photosynthesis rates and lower drought tolerance (Waring 1991, Aerts 1995, Tyree and Cochard 1996, Baldocchi et al. 2010). As this is not the case, it may be concluded that *C. coggygria* is not the typical drought-deciduous plant and may prove a successful shrub candidate for green roof vegetation cover.

3 Invasive species (Ruderals)

3.1 *Buddleja davidii*

Buddleja is a cosmopolitan genus belonging to the family Scrophulariaceae (EOL 2015) and includes 100 species widely distributed in temperate, subtropical and tropical regions of the world (Leeuwenberg 1979). Extensive natural hybridization occurs among *Buddleja* species – allegedly, there are around 19 natural hybrids among neotropical *Buddleja* species, involving 24 species, and polyploidy exists in over half of *Buddleja* species, especially in the Sino-Himalayan region (Zhang et al., 2014). Leeuwenberg (1979) described the natural distribution of *Buddleja* in North and South America, Africa, and Asia, with more than 20 species only in China. While this genus is not native to Europe, Australia, and New Zealand (Stuart 2006), some species, mainly *Buddleja davidii* Franchet, have naturalized and become successful invaders in both the European (Ebeling et al. 2008, Wittig 2012) and Australian (Smale 1990, Bellingham et al. 2005) continents. *Buddleja davidii* is native to central and southwestern China up to 3500 m and was introduced to Europe as an ornamental in the late 19th century (Owen and Whiteway 1980). Since 1920, seven subspecies of *B. davidii* have been described and 90 different cultivars have been bred (Stuart 2006). These have long escaped cultivation and in the United Kingdom has spread to every angle of the British Isles (Owen and Whiteway 1980). The same has happened for other parts of Europe, *B. davidii* extending from the southernmost parts of the Mediterranean Basin to southern Norway, and from Spain to Bulgaria in the east (Kriticos et al. 2010). The invasiveness and expansion of *B. davidii* to such a wide range of climates is certainly related to its high adaptability and tolerance of many different types of soils and environmental conditions. However, *B. davidii* seems to prefer open dry, disturbed sites, like roadsides, abandoned areas, quarries, pastures, scree slopes, open woodlands, riverbanks, and forestry plantations (Binggeli 1998, Ebeling et al. 2012).

Known as the Orange Eye Butterflybush (EOL 2015), *Buddleja davidii* is a semi-deciduous, fast-growing, multi-stemmed shrub that forms canopies of dense foliage and fragrant, showy flowers (Leeuwenberg 1979). The habit of *B. davidii* is unique in that it has no main trunk: the main meristem (four-angled) grows underground, while the aboveground biomass is comprised of several stems that originate from the main meristem (Tallent-Halsell and Watt 2009). Leaves (5-20 cm × 1-7 cm) are usually ovate (less commonly lanceolate), serrated, wedge-shaped, and shortly petiolate, with the adaxial surface dark green and glabrous and the abaxial side whitish to greyish tomentose with stellate and glanduliferous hairs that extrude crystals, giving them a characteristic sheen (Leeuwenberg 1979, Webb et al. 1988, Tallent-Halsell and Watt 2009). Leaves are described as 'semi-deciduous' in that they are shed in the autumn and immediately replaced with a set of new, smaller leaves covered in downy hairs that persist until the following spring. Both spring shoots and leaves are pubescent but become glabrous as the year progresses (Tallent-Halsell and Watt 2009). Flowers (5-8 mm) are zygomorphic, four-symmetrical, with petals fused into a lilac or purple corolla tube that opens at the top to form four separate petals and has an orange interior with a series of yellow nectar guides (Leeuwenberg 1979). Flowers, borne in long corymbose panicles that can extend up to 30 cm in length, mature from late spring to mid-summer from the base to the top of the inflorescence (Findley et al. 1997). The fruit is a brown, narrowly ellipsoid to ovoid cylindrical, two-valved capsule (5-9 × 1.5-2 mm) with an acute apex, an impressed line along the dehiscence zone, and containing many small (3-4 × 0.5 mm), thread-like and long-winged seeds that disperse with wind (Leeuwenberg 1979, Norman 2000). *B. davidii* depends on insects and other wildlife for pollination (Norman 2000), attracting many species of butterflies, moths, bees, wasps, hornets, hoverflies, beetles and even hummingbirds in the New World (Stuart 2006, Chen et al. 2011) with both the scent and nectar it produces in abundance (Houghton et al. 2003). A recent study by Chen et al. (2014) identified terpenoids as being the most important group of organic compounds (floral scents) produced by *B. davidii*, in particular 4-oxoisophorone, a well-known moth attractant and stimulator of antennal responses in butterflies and bees.

In their study, Feng et al. (2007) compared various ecophysiological traits of *B. davidii* with those of five co-occurring native woody shrubs of nitrophilous ruderal, dry scrub, or river bank communities growing in Germany: *Berberis vulgaris* (Berberidaceae), *Cornus sanguinea* (Cornaceae), *Sambucus nigra* (Caprifoliaceae), *Crataegus monogyna* (Rosaceae), and *Betula pendula* (Betulaceae). The authors found that *B. davidii* had significantly higher electron transport rates, maximum carboxylation rates, carboxylation efficiency, light-saturated photosynthetic rates, and photosynthetic nitrogen utilization efficiency (PNUE) compared to native species. The leaf nitrogen content was not significantly different among the six species, but *B. davidii* allocated more nitrogen to photosynthetic activity and, thus, to growth. However, Feng et al. (2007) observed that, as *B. davidii* had also higher values of stomatal conductance, the individuals studied did not increase leaf mass per area (LMA) or reduce leaf construction costs to compensate for its lower water use efficiency (WUE). Therefore, its nitrogen use efficiency, together with high growth rates, early maturity, high reproductive output of easily distributed seeds and its tolerance to a broad range of environmental conditions (Webb et al. 1988) makes *B. davidii* highly invasive (Ebeling et al. 2008, Kriticos et al. 2010) and one of the top twenty invasive species of Western Europe (Sheppard et al. 2006). *B. davidii* also tolerates severe cold (Stuart 2006), and its range only excludes northern parts of Scandinavia, most of Canada and inland parts of northern USA (Kriticos et al. 2010). However, the distribution model developed by Kriticos et al. (2010) found that heat and water stress are limiting factors for this species, which reflect both its native and introduced range. For example, *B. davidii* does not extend to the lowlands of most tropical regions and is excluded from arid and semi-arid regions of South America, Africa, Australia, and Asia. The butterfly bush is, however, naturalized in the western coast of New Zealand, where mean annual rainfall is over 5000 mm (Bellingham et al. 2005). From observing distribution and adaptive strategies, it is clear that *B. davidii* is not a xerophyte and may suffer from periods of drought, as it chooses to allocate more resources to promote growth rather than to reduce water loss.

4. Typical understory plants of temperate-climate regions (Shade-tolerators)

4.1 *Viburnum tinus*

The genus *Viburnum* is the largest member of the Adoxaceae family and contains approximately 75 species of shrubs and small trees, mostly distributed in the Northern Hemisphere (Winkworth and Donoghue 2004). The Laurustinus (*Viburnum tinus* L.) belongs to genus *Viburnum* and is distributed throughout southern Europe and North Africa in the Mediterranean-climate region. It is a constituent of *garrigue*-type scrub and forest fringes, often in association with *Laurus nobilis* and *Myrtus communis* as understory components of woodland *maquis* (Clennett 2004). *V. tinus* is therefore well adapted to semi-arid environments that experience summer drought and high temperatures (Nardini 2002), but that also have high winter rainfall and little frost (Clennett 2004). The Laurustinus was introduced to the British Isles for cultivation in the late 16th century and is today observed to perform well in southern and western parts of Britain, being frost hardy in all but the worst conditions and tolerant of a variety of soil types. Mortality or loss of young shoots can occur, however, under conditions of hard frost. Therefore, *V. viburnum* in Britain is considered best suited to sheltered spots if grown in gardens in northern England and eastern Scotland (Clennett 2004).

V. tinus is an evergreen shrub with a dense growth form (multi-stemmed base) reaching 1.5-2.5 m in height, occasionally more (Clennett 2004). Shoots are adventitious, pubescent when young, becoming glabrous, smooth, with a reddish bark at maturity (Kollman and Grubb 2002). Leaves are sclerophyllous or coriaceous to the touch (Salleo et al., 1997), opposite (Kollman and Grubb 2002), shortly petiolated, narrowly ovate to oblong (3-10 cm long), acute at both ends, entire, dark green and glossy above but lighter beneath with some axillary pubescence (Clennett 2004). Flowers have a white to pinkish funnel-shaped corolla with five lobes (Kollman and Grubb 2002), are somewhat fragrant, and are borne in convex terminal umbel-like cymes (5-7 cm wide). Fruits (single-seeded drupes) are ovate, deep blue and turn black at maturity in early autumn. *V.* tinus has a long, winter flowering period that goes from November to April both in the wild and in cultivation (Clennett 2004).

The distributional range of *V. tinus* reflects the adaptation of this species to living under two different types of light condition: under high irradiance as a part of the Mediterranean *maquis* and in the partially shaded environments of the understory (Fini et al. 2010). In their study, Fini et al. (2010) determined the long-term response of growth (whole-plant biomass), leaf morphology (including LAI, leaf area, and leaf thickness), and gas exchange of three common evergreen shrubs used in landscaping (*Viburnum tinus*, *Camellia* x *williamsii*, *Photina* x *fraseri*) at different levels of irradiance (100%, 60% and 30%). The authors observed that *V. tinus* increased leaf and stem biomass as well as net photosynthesis and water use efficiency with increasingly lower irradiance. Therefore, though adapted to variable light conditions, *V. tinus* tends to perform better under conditions of shade. The importance of light environment for this species is shown in a study by Nardini (2002), in which shoot hydraulic conductance and shoot and leaf growth rates were measured and compared on three evergreen (including *Viburnum tinus*) and three deciduous shrubs growing in the same water, soil, and light conditions. Nardini (2002) observed low shoot and leaf growth rates and low shoot hydraulic conductance per unit leaf area in both *Viburnum tinus* and *Corylus avellana*, the latter being a water-demanding shrub typical of temperate forest understories. Clearly, as *V. tinus* is a typical understory shrub adapted to drought, the factor that associates these two species in their similar growth rates and hydraulic conductances seems more related to their genotype, which allows them to adapt to conditions found in their natural habitats (shading), than to their water use efficiency.

García-Navarro et al. (2004) estimated the relative water use among four ornamental landscape species (*Viburnum tinus*, *Spiraea vanhouteii*, *Arctostaphylos densiflora* and *Leucophyllum frutescens*) grown in 4L containers or in drainage lysimeters, in order to compare water use and growth in nursery and landscape conditions, respectively. The authors found that in both container and lysimeter experiments, *V. tinus* and *A. densiflora* (both evergreen sclerophylls) showed the lowest water use and the slowest response to water stress with water use reduction compared to the other two species, and *V. tinus* in particular showed the highest decrease in water use (45%) under conditions of water stress in lysimeter experiments. However, reduced irrigation affected growth in all species tested, especially *V. tinus*. Its leaves did not senesce but those more exposed to light suffered sunburn and growth was limited during the experiment. On the other hand, despite the higher water use, deciduous shrub *S. vanhouteii* responded to the most severe water stress by shedding most of its foliage and maintaining only its perennial structures (roots and stems), resprouting leaves only when conditions were again favorable. This behavior is reminiscent of that of *Cotinus*, described previously in Section 3.2.3. García-Navarro et al. (2004) concluded that, despite its enduring evergreen habit and water use efficiency, long periods of drought might render individuals of *V. tinus* unable to recover after irrigation, while deciduous species like *S. vanhouteii* might perform better in conditions of prolonged water stress by being able to shed its foliage and maintain basic metabolic activity. This result clearly demonstrates the different adaptive strategies adopted by species with evergreen and deciduous habits, as discussed previously in Section 2.5.

Salleo et al. (1997) in their study also found *V. tinus* to have a slow response to water stress. The authors compared the control of leaf dehydration and rehydration in two sclerophylls (*Viburnum tinus* and *Ilex aquifolium*) with that of two non-sclerophylls (*Hedera helix* and *Sambucus nigra*) to assess the potential role of sclerophylly in this process. The authors found that the two sclerophyllous species did not recover from leaf water loss more rapidly than the non-sclerophylls, but that the increase in leaf water potential (more positive) after dehydration was much larger compared to that of non-sclerophylls, thus suggesting that sclerophylls, because of the greater amounts of fibers and mechanical tissues, can recover from xylem cavitation more completely compared to non-sclerophylls. This was interpreted by Salleo et al. (1997) as an advantage to plants subjected to large diurnal drops in leaf water potential followed by nocturnal recovery, which is the case for Mediterranean sclerophylls growing in areas characterized by high air humidity that condenses at night on the soil.

The work by Sack et al. (2003) is particularly enlightening, in that it emphasizes a very important aspect of *Viburnum tinus*: its ability to cope with shade and drought simultaneously. In this study, the authors summarize the theories behind the hypothesis that plants cannot tolerate combined shade and drought as a result of morphological and ecophysiological tradeoffs (Smith and Huston 1989). However, Sack et al. (2003) underline the fact that many plant species are widespread in shaded forest understories in drought-prone areas, and again give a synopsis of results from different studies, specifically that understory plants of sclerophyll-dominated, seasonally-dry forests in the Mediterranean Basin face extreme conditions related to heavy shade and severe drought: shade as low as 3% incoming irradiance throughout the year and pre-dawn water potentials below –2 MPa in leaves of deep-rooting canopy trees during summer. In their study, Sack et al. (2003) measured functional traits of juveniles and mature individuals belonging to six species (including *Viburnum tinus*) that cope with severe summer drought in understories of mixed *Quercus* forests in southern Spain. The authors found that all species had features conferring combined tolerance to shade and drought, which converged in the reduction of resource demand. Specifically, demand for water was reduced through changes in belowground biomass (moderate to high) and specific leaf area (low to moderate), while demand for both irradiance and water was reduced through variations in foliar nitrogen concentration (low to moderate) and lengthening of leaf lifespan. The species also showed specific adaptations to either shade or drought, the ones not excluding the others. These included deeper roots compared to shoot size, moderately high specific leaf area in shade, and higher chlorophyll to nitrogen ratio in shade. In contrast, nitrogen content in leaves was higher in sun leaves independent of specific leaf area. These findings are in accordance with results from previous studies, which indicate that the promotion of plant organs with longer lifespan (needing less resources to replace) is a mechanism that reduces the simultaneous demand for irradiance, water, and other resources (Lusk and Reich 2000).

In conclusion, *Viburnum tinus* is both a drought- and shade-tolerant species, characterized by a unique set of functional traits that allow plasticity in response to variable environmental conditions: slow growth rate, low hydraulic conductance, evergreen and sclerophyllous foliage (longer lifespan), high recovery from cavitation, and high water and nutrient use efficiency. We once again come across a species that leaps over conventional tenets on ecophysiological tradeoffs and enters the field of those that instead are benefited with a unique combination of traits, as was also the case for *Cistus* and *Cotinus*. The singular (or better, compromising) attributes of these species will likely render them both difficult to predict and dynamic in their responses to green roof conditions.

5. A special note on wood anatomy: true, vascular and vasicentric tracheids

Having related the main morpho-anatomical and physiological characteristics of the six experimental species and reviewed their different adaptive strategies, it may have come to the reader's attention that all of these species depend heavily upon varying degrees of hydraulic efficiency and safety, some of which have evolved unusual medleys of traits to endure the variable conditions in temperate and sub-tropical climate. One, for example, is simultaneously shade- and drought-tolerant (*Viburnum tinus*); another is hydraulically efficient and withstands aridity at the same time (*Cotinus coggygria*); yet another is an invader of wet, arid and even saline environments with both high hydraulic capacity and WUE (*Elaeagnus angustifolia*), and there's even a species that changes habit with the different seasons (*Cistus* × *hybridus*), like a superhero, transforming to face the challenges of an unpredictable and capricious climate. What ultimately sustains the evolution and adaptation of these and all other plant species to the ever-changing conditions on Earth is the modification of xylem anatomy, in particular the water-conducting and support elements of the xylem tissues, namely the tracheary elements: the vessel element in angiosperms and the tracheid in gymnosperms.

Anyone with a basic knowledge in plant anatomy can say that the shrub species described previously are all dicotyledonous angiosperms forming secondary xylem tissues (wood), and therefore their principle water-conducting tissue will obviously be composed of vessel elements. Vessels are lignified cells of varying length that form longitudinal structures (conductive tissue), surrounded by parenchyma and other mechanical tissue (i.e., fibers) and connected to each other through perforated, tube-like structures called perforated plates, unlike tracheids that are long, unperforated tracheary elements. Tracheids, having evolved in gymnosperms and thus before the appearance of angiosperms, are sometimes found alongside vessel elements in flowering plants but the same is not true for gymnosperms, where the only tracheary element is the tracheid (Sperry 2003). The purpose of this 'lecture' on plant anatomy was not to pointlessly meander into the complex subject of the xylem system (of which I am not an expert), but to give a superficial introduction before discussing a rather interesting study by Carlquist (1985). This work by the famous American botanist and wood anatomist deserves notice for its insight into the ecophysiology of a certain group of plants, in the attempt to explain the experimental shrubs' curious adaptations and to use this information as a potential predicting factor of the shrubs' performance on a green roof.

Carlquist's study (1985) is a monograph on a particular group of tracheids that are intermixed with vessel elements and that have been found in a relatively small number of families of dicotyledonous angiosperms. The author describes two types of tracheids that can be found in this group of plants, alongside vessels: 'vasicentric tracheids' and 'vascular tracheids'. 'Vasicentric tracheids' are defined as imperforate tracheary elements (tracheids) present adjacent vessels in a wood which also possesses libriform fibers or fiber-tracheids (mechanical tissue), which occur throughout the growth ring in wood of diffuse-porous species. The 'vascular tracheids' would be defined in the same way as vasicentric tracheids, except that these occur only in latewood; in fact, they are extremely narrow latewood elements which lack perforation plates. Vasicentric and vascular tracheids are to be distinguished from what the author calls 'true tracheids', which are present as the sole imperforate tracheary element in the xylem and thus are found in all gymnosperms and rarely in angiosperms. In fact, true tracheids are found in wood too primitive for to have ever evolved mechanically significant cells like libriform fibers or fiber-tracheids.

All three types ('vasicentric', 'vascular' and 'true') are alike in being imperforate tracheary elements with relatively large bordered pits, about as large and as dense as those on vessel elements. The distinctions between the three types of tracheids is important because they reflects the different adaptive strategies of the species that possess these particular elements. For example, vasicentric tracheids represent an alternative transport system that can supply water to stems and leaves (at a slower pace) when the adjacent vessels fail because of air embolisms. Vascular tracheids also maintain water columns in stems which thereby persist through dry seasons, but, as they are produced only in latewood, may not adequately supply leaves, which may wilt as drought progresses. The presence of both vascular or vasicentric tracheids would be advantageous to plants living, for example, in regions where the dry season can be highly unpredictable, like those with a Mediterranean-type climate. However, species with vasicentric tracheids might be expected (with only a few exceptions) to be evergreen, whereas species with vascular tracheids tend to have drought-deciduous or seasonally deciduous foliage.

The author relates the presence of vasicentric tracheids in particular to the evergreen habit because of the redundancy of this element in genera pertaining to floras of areas in which evergreen drought-tolerant shrubs are adaptive, namely Mediterranean-type climate regions. Though not common in dicotyledons at large, vasicentric tracheids are found, to date, in 68 different families, 26 of which in southern California's chaparral vegetation alone. The genera of chaparral plants with the highest number of species with these elements are *Arctostaphylos*, *Ceanothus*, *Prunus*, *Quercus* and *Salvia*. Other regions with a Mediterranean climate (Chile, S Australia, Mediterranean Basin, S Africa) also have genera with vasicentric tracheids, the most notable ones being *Banksia*, *Carissa*, *Eucalyptus*, *Grevillea*, *Hakea*, *Protea*, *Quercus* and *Rosmarinus*. It strikes as very interesting that *Ceanothus* (as well as *Rhamnus*, another Rhamnaceae of the European Mediterranean flora) are thought to have vasicentric tracheids. The description of a typical plant with vasicentric tracheids fits with *Ceanothus*, as it is a typical evergreen component of California's chaparral vegetation. Most surprising is instead the fact that vasicentric tracheids have been found in the genus *Buddleja*, which is a family of mostly semi-deciduous plants that have a wide distribution but that are native to mainly mesic habitats, being a genus of species that are not drought tolerant. Carlquist (1985) in fact identifies vasicentric tracheids in a species native of SW United States (*Buddleja utahensis*), undoubtedly adapted to dry climate. Whether the tracheids have been analyzed in other *Buddleja* species is not clear. It is more probable that common and more wide ranging species like *Buddleja davidii* have vascular tracheids, if any, as this species typically has low WUE and fast growth rate and therefore would not be expected to have specialized means of preserving hydraulic safety.

Carlquist (1985) provides a list of species that either have vasicentric or true tracheids intermixed to vessel elements, but not species with vascular tracheids. By the description provided previously, it is highly possible that the genus *Cotinus* is provided with vascular tracheids. Although its distribution extends slightly beyond that of the Mediterranean Basin, *Cotinus coggygria* is a drought-deciduous species that most likely only produces latewood (being deciduous), maintaining conductivity throughout the dry season with rather high hydraulic capacity but that may experience wilting and loss of leaves in order to prevent xylem cavitation when levels of soil availability reaches critical level. *C. coggygria* also uses strict stomatal control and osmotic adjustment as mechanisms to maintain leaf turgor and water potentials before wilting and leaf drop. The ability of *C. coggygria* to withstand periods of intense and prolonged drought makes this plausible, in that only a xylem system with mechanical tissue (i.e, libriform fibers, sclereids) and a safety-guarding mechanism (i.e., vascular tracheids) could allow a deciduous shrub species to survive in a Mediterranean-climate region.

By contrast, true tracheids are found in flora of wetter climates, like that of Japan or New Zealand, and are relatively few in dicotyledons, apparently only in those that were able to make the transition from areas with wet climates, where they originally evolved, to those with dry climates. In fact, true tracheids have much the same physiological effect of vasicentric tracheids, maximizing potential safety in conduction, and an appreciable number of these can even be found in a small number of chaparral and desert species. However, dicotyledons with true tracheids have evolved many morphological and physiological adaptations (including smaller leaf size) in order to sustain unfavorable environmental conditions. Among these is none other than genera *Cistus* (and *Helianthemum*), belonging to the Cistaceae. It comes as a surprise to find the genus *Cistus* among those rare dicotyledons that have true tracheids, because the author describes true tracheids as evolving in wood 'too primitive' to have mechanical tissue, while *Cistus* is thought to have evolved fairly recently, with an adaptive radiation that occurred a little after the establishment of a Mediterranean climate in Europe (c. 2.8 Ma) (Guzmán et al. 2009). However, the wood anatomy in *Cistus* is quite unique: not only is the foliage of this species seasonally dimorphic, leaf traits varying both morphologically and physiologically between spring and summer, but also the xylem tissue produced is seasonally different. Brachyblast branches, which have narrow and redundant vessels, are produced in spring and remain active throughout the summer, whereas dolichoblast branches are produced in the autumn and persist until early spring, with larger vessels and a lower vessel frequency. The fact that *Cistus* should not present the typical ring-porous wood, typical of plants that experience seasonal variations in precipitation, but instead shows a complete and distinct alternation of wood production type between seasons (and, in the spring, the two branch types are even present at the same time) helps to explain how *Cistus* species can present such a strange mix of drought tolerance and avoidance mechanisms. The author also reports that true tracheids are found in plants with a distribution in cooler and wetter climates compared to the Mediterranean one, and *Cistus* is a typical component of Mediterranean flora. Again, the conundrum is easily resolved – *Helianthemum*, also a Cistaceae with true tracheids, is a genus commonly found amongst the coastal sage vegetation of California, and Carlquist and Hoekman (1985), after an extensive study into wood anatomy of southern California plants, are here stated as concluding that "for taxa in southern California in which true tracheids have been retained, xeromorphy can be achieved in terms of loss of bars (where present) on perforation plates, increase in number of vessels per unit area, decrease in vessel diameter, increase in vessel wall thickness, decrease in vessel-element length (to a limited extent), development of helical sculpture on vessels, and the development of growth rings." In other words, the retention of primitive structures like true tracheids in plants adapted to hot and dry climates is possible, but after major modifications to the xylem system. For example, some *Cistus* species produce seasonal not annual rings, growth occurring in both spring and fall; this together with the wood dimorphism would suite the prerequisites described. Therefore, it seems fitting that the dicotyledonous *Cistus* species, of all plants, should present rare and unique tracheary elements like true tracheids in their xylem system.

The two remaining experimental shrubs, *Viburnum tinus* and *Elaeagnus*, are harder to place. It must be reminded that only a small number of plant species actually have vasicientric, vascular or true tracheids and it is probable that these two species do not have tracheids in their conductive tissue at all. Carlquist (1985) in fact does not include the Adoxaceae as having any form of imperforated tracheary elements. However, the author does comment that the absence of a family or genus may be due to the difficulty of spotting vasicentric tracheids in microscope sections. *V. tinus* is an evergreen sclerophyll and typical element of the Mediterranean flora that shows both shade and drought, so it is not excluded that this species may have vasicentric tracheids. On the other hand, the family Elaeagnacea (in the genus *Shepherdia*) was found to have true tracheids. *E. angustifolia* belongs to the Elaeagnaceae but may not have them. However, *E. angustifolia* is a typical riparian species that is tolerant to a wide range of conditions (flooding, aridity, salinity, fire, mechanical damage), owing mostly to its association with a nitrogen-fixing fungi, and it would seem fitting for this species to have tracheary elements that serve as a subsidiary transport mechanism in case of embolism, since *E. angustifolia* has both high hydraulic and water use efficiency and is fast-growing. Even its foliar architecture and anatomy is curiously reminiscent of *Cistus*, another "true tracheidian": the smaller leaf size, greater thickness, and higher trichome and stomatal density of the sun-leaves found on the upper part of the canopy compared to the less exposed lower shade-leaves.

In conclusion, *Ceanothus thyrsiflorus* var. *repens* and *Cistus* × *hybridus* are species belonging to genera that are known to have specialized xylem tissues that ensure hydraulic safety, providing an alternative water transport pathway in case of embolism in the main vessel elements. Alongside vessel elements and mechanical tissue (i.e, fibers and sclereids), *C. thyrsiflorus* var. *repens* also presents vasicentric tracheids, while *C.* × *hybridus* has true tracheids. It might be possible that even *Viburnum tinus* and *Elaeagnus angustifolia* have vasicentric and true tracheids, respectively, based on the descriptions of typical habits and physiological responses in plants with these tracheary elements. It is instead more likely that *Cotinus coggygria*, a drought-deciduous species, should have vascular tracheids. Finally, vasicentric tracheids have been found in one or possibly more species belonging to the genus *Buddleja*, but it is more likely that the mesophyllous *Buddleja davidii* does not have tracheids in its xylem tissues.

Appendix B: Tables of correlations

Table A. P-values for Pearson's correlations between different morphological parameters.

Parameter	M	G/RGR	LMA$_T$	LMA$_B$	CD	B_L	A_L	B_L*	A_L*	A_W	Branch length	Ramifi-cation	ADI	B_W	LAI
M	---	0.557	0.909	0.542	0.648	0.592	0.437	0.668	0.735	0.064	0.677	0.578	0.839	0.887	0.473
G/RGR		---	0.148	0.348	0.299	**0.007**	0.116	0.416	0.810	0.511	0.704	0.180	0.466	0.161	0.134
LMA$_T$			---	**0.049**	0.338	0.166	0.843	0.934	0.552	0.394	0.290	0.578	0.814	0.405	0.909
LMA$_B$				---	0.102	0.218	0.935	0.523	0.232	0.225	**0.033**	0.572	0.460	0.875	0.976
CD					---	0.086	0.357	0.721	0.512	0.886	**0.034**	0.652	0.336	0.618	0.390
B_L						---	0.060	0.472	0.830	0.563	0.322	0.147	0.765	0.679	0.075
A_L							---	0.130	0.199	0.916	0.793	0.093	0.372	0.679	**<0.001**
B_L*								---	**0.006**	0.988	0.562	0.185	0.120	0.451	0.131
A_L*									---	0.810	0.402	0.297	0.126	0.732	0.185
A_W										---	0.569	0.142	0.465	0.292	0.890
Branch length											---	0.681	0.203	0.424	0.829
Ramification												---	0.169	0.344	0.085
ADI													---	0.083	0.338
B_W														---	0.677
LAI															---

*Relating to data acquired throughout the study and not after harvesting

Table B. *P*-values for Pearson's correlations between different physiological parameters.

Parameter	**QY**	**RWC_L**	**T_L**	**g_S**	**A**	**E**	**WUE_P**	**Ψ_L**
QY	**---**	0.092	0.978	0.318	0.530	0.472	0.956	0.772
RWC_L		---	0.391	0.772	0.775	0.618	0.856	0.076
T_L			**---**	0.283	**0.012**	**0.038**	0.150	0.314
g_S				---	0.095	**0.014**	0.871	0.162
A					---	**<0.001**	0.167	0.413
E						---	0.443	0.170
WUE_P							---	0.593
Ψ_L								---

Table C. P-values for Pearson's correlations between morphological and physiological parameters.

Parameter	**QY**	**RWC$_L$**	**T_L**	**g_S**	**A**	**E**	**WUE$_P$**	**Ψ_L**
M	0.273	0.505	0.317	0.367	0.700	0.937	0.307	0.913
G/RGR	**0.017**	0.313	0.492	0.208	0.238	0.189	0.607	0.662
LMA$_T$	0.326	0.268	0.541	0.852	0.441	0.614	0.091	0.335
LMA$_B$	0.531	0.477	0.245	0.731	0.146	0.411	**0.004**	0.460
CD	0.166	0.225	0.704	0.381	0.256	0.436	0.306	0.559
B_L	**0.005**	0.132	0.630	0.305	0.255	0.303	0.522	0.746
A_L	**0.021**	0.209	0.881	0.449	0.680	0.609	0.635	0.985
B_L*	0.276	0.278	0.394	0.706	0.472	0.597	0.307	0.715
A_L*	0.546	0.519	0.284	0.591	0.312	0.442	0.110	0.909
A_W	0.968	0.829	0.064	0.961	0.181	0.379	0.160	0.870
Branch length	0.573	0.279	0.699	0.972	0.425	0.851	0.104	0.228
Ramification	0.233	0.448	0.545	0.858	0.457	0.581	0.792	0.959
ADI	0.681	0.793	0.752	0.835	0.935	0.700	0.446	0.366
B_W	0.555	0.832	0.323	0.502	0.471	0.300	0.828	0.455
LAI	**0.031**	0.250	0.906	0.450	0.672	0.599	0.607	0.926

*Relating to data acquired throughout the study and not after harvesting

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