ECOLOGY AND PHYSIOLOGY OF GREEN ROOF PLANT COMMUNITIES

A dissertation

submitted by

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ABSTRACT

Green roofs mitigate many negative environmental effects of urbanization, especially stormwater runoff and the urban heat island effect. There is also potential for green roofs to function as islands of biodiversity within urban and suburban environments. Historically most roofs have been planted with *Sedum*, a very stress-tolerant plant, but many people are promoting the planting of a more diverse set of plants, especially native plants. The performance of other species has been mixed and this necessitates greater focus on both patterns and mechanisms of plant growth and survival. In this dissertation, I began by reviewing and analyzing rationales for preferring native plants on green roofs. I identified 113 green roofs planted with native plants and 89 scholarly papers that promoted this practice. Scientific arguments were commonly used, but rarely tested experimentally. I then conducted a rooftop experiment to assess suitability of 19 native and non-native plant species. Summer water deficit resulted in high mortality of all but the most popular green roof species: *Sedum* (Crassulaceae). To determine if *Sedum*'s high performance was due to photosynthetic plasticity, I grew *Sedum* under wet and dry conditions in a greenhouse. There was variation in photosynthetic pathway among the eight species tested, including examples of C_3, CAM-cycling, and CAM-idling. Furthermore, several species exhibited rapid switching in photosynthetic pathway in response to short-term changes in water availability. Finally, I tested the hypothesis that *Sedum* species would reduce peak soil temperature and increase performance of neighboring plants during summer water deficit. During a three-year experiment on the Tisch Library Green Roof,

Sedum species decreased peak soil temperature by 5 - 7 °C. Overall, *Sedum* reduced neighbor growth during wet periods, but increased neighbor performance during summer water deficit. The results of this dissertation suggest that plant diversity on green roofs is constrained by abiotic stress, especially summertime water deficit and heat. Many *Sedum* species used on green roofs have high photosynthetic plasticity, which may explain their success as green roof plants. The palette of green roof plants can be expanded by using *Sedum* species as nurse plants.

ACKNOWLEDGMENTS

As a little girl, I dreamed of becoming a famous actress. I would sit in my room and practice my acceptance speech for when I won my first Academy Award. There I'd be in my sequin ballgown, smiling demurely when my name is called. I'd float up to the stage and graciously accept my award, rushing breathlessly through a heartfelt acceptance speech. I have come to terms with the fact that this will most likely never happen. My consolation prize is a Ph.D. and a big book with my name on the cover (it's a pretty sweet consolation prize). But it certainly is a terrible shame to waste all of that practice…so please consider this my heartfelt acceptance speech. For maximum effect, it should be read while listening to orchestral music, preferably a piece with soaring violins.

First, I would like to thank my thesis advisor, Dr. Colin Orians, for his continued guidance and support over the past five years. I am very grateful that he gave me so much freedom to develop a thesis project that is quite different from his own research. He helped me identify funding options and write grant proposals. He got me acquainted with everyone at Tufts and played a key role in the creation of the Tufts Green Roof Collaborative and the installation of the Tisch Library Green Roof. Dr. Orians also taught me valuable lessons in diplomacy.

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climbing the crumbling steps of a Mayan temple in Guatamala, dancing tango at a late night milonga in Buenos Aires, and scaling a glacier in New Zealand. You are my favorite.

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CHAPTER 1
Introduction

When Charles Darwin first set foot upon Chatham Island in the Galapagos, his response to the expansive field of jagged black lava was that "Nothing could be less inviting than the first appearance." I think it is safe to assume that Darwin did not spend much time on black tar roofs in the summer, although his description could easily be used to describe this environment. "The dry and parched surface, being heated by the noon-day sun, gave the air a close and sultry feeling, like that from a stove." Like the Galapagos lava fields, rooftops are harsh environments that are very hostile to life. In summer, temperatures can reach 60 – 70 °C. In winter, the roof is completely exposed to the elements. How could anything live in such an environment? And yet there is life. Rooftop biota may not be as exotic as marine iguanas or blue-footed boobies, but at the very least, we should respect/acknowledge their resilience. *Portulaca oleracea* can complete its entire life cycle in a small patch of soil blown into a corner of a roof (personal observation). *Sedum album* is so common on terra cotta roofs in Portugal that its common name there is *arroz-dos-telhados*, or "roof rice" (Smith and Figueiredo, 2010).

In this dissertation, I used ecological concepts I learned about in places like the Galapagos and applied these concepts to a seemingly mundane locale – a flat roof in suburban Boston. Why is the urban ecosystem worth studying? This simple question has resulted in heated debates at the annual meetings of the

Ecological Society of America. Historically, ecologists have sought to study nature in its purest, most unadulterated areas, viewing urban areas as ecological wastelands. Recently, this view has begun to shift, largely due to the persistent destruction and degradation of natural areas world-wide. By focusing on the urban environment, ecologists can also increase environmental awareness of residents of urban areas.

In this dissertation, I sought to identify species that would thrive in the roof top environment, traits that promote survival in this high-stress habitat and investigate interspecies facilitation as a method of increasing plant diversity and maximizing green roof performance. Each of the five data chapters of this dissertation functions as a stand-alone unit. Each of these chapters has either been published (Chapters 2 and 4) or is in review for publication (Chapters 3, 5, 6). This introduction provides a broader context for this research and also functions as a primer for many of the topics covered in subsequent chapters. I begin the introduction by discussing some of the negative effects of urbanization. I then review the design, history, and benefits of green roofs. Finally, I provide primers on native plant enthusiasm, interspecies facilitation, and photosynthetic plasticity.

Negative impacts of urbanization

In the past 40 years, the global human population has doubled to over 6.5 billion people, and the U.S. population alone exceeds 300 million (US Census Bureau, 2006). Urban areas, in particular, are growing rapidly with over 8% of the land area in the United States projected to be urban by the year 2050; this will be over double the amount measured in 2000 (Nowak and Walton, 2005). Pervious land cover, such as forest and grasslands, is being replaced with impervious surfaces like roads, rooftops and parking lots. Instead of infiltrating into the soil, precipitation flows over impervious surfaces transporting pollutants, such as oil, heavy metals, and fine particulates (Fig. 1.1). Often this surface runoff is routed directly into the nearest water body through the storm sewer system, thus bypassing potential infiltration areas and floodplain connections that are highly effective at pollutant removal (Kaushal, 2008).

Impervious surfaces also absorb and reradiate solar radiation creating the well-documented "urban heat island" effect, where average air temperatures in highly developed areas are consistently higher than the surrounding landscape (Rizwan et al., 2008). Additionally, creation of impervious surfaces reduces the amount of land in urban areas available for biological communities to develop. The cumulative environmental impacts of impervious surfaces in urban ecosystems have led to widespread interest in investigating how detrimental effects of impervious surfaces can be diminished.

Green roof design, history, and benefits

Nearly 50% of impervious surface in highly urbanized areas is unused roof space (Dunnett and Kingsbury, 2004). A green roof can be broadly defined as a roof that has been intentionally planted, but it is typically used to describe a specific type of planted roof, designed primarily for environmental reasons, which is made up of a thin layer of growing media and drought-tolerant herbaceous plants (Dunnett and Kingsbury, 2004; Weiler and Scholz-Barth, 2009).

The modern green roof has its origins in practically-minded Scandinavian turf roofs as well as decorative roof gardens of the urban elite. Historically, Scandinavian turf roofs served to keep rain out and insulate houses against cold weather (Dunnett and Kingsbury, 2004). In the 1800s, flat roofs began to be constructed in Europe and North America. Architects soon began to make use of this new space – the fifth façade. In 1914, Frank Lloyd Wright included a roof garden on his design of a Chicago restaurant (Dunnett and Kingsbury, 2004). In 1929, Le Corbusier designed the Villa Savoye, which included a roof garden (Howe). The modern green roof was developed primarily in Germany in the second half of the 20th century (Dunnett and Kingsbury, 2004). Green roofs have only recently arrived in North America, but their popularity has skyrocketed within the past decade, with over 800 built in North America since 2000 (Greenroofs.com project database).

Green roofs have multiple benefits, including stormwater retention (DeNardo et al., 2005; Mentens et al., 2006), insulation of the building (Kumar and Kaushik, 2005), acting as an amenity (Getter and Rowe, 2006; Loder et al., 2010), and providing habitat for urban wildlife (Bauman, 2006; Brenneisen, 2006; Coffman and Davis, 2005; Lundholm et al., 2009; MacIvor and Lundholm, 2010). In Europe, 121 experimental extensive green roofs retained, on average, 50% of total annual precipitation (Mentens et al., 2006). A green roof at the Ford Motor Plant in Michigan retained on average 45% of rain, ranging between 19 and 98%

for individual storm events (DeNardo et al., 2005). Research conducted in Pennsylvania (DeNardo et al., 2005), Japan (Onmura et al., 2001), and Massachusetts (Butler unpub., 2008) has shown that green roofs decrease the maximum roof membrane temperature by 20-30 °C. By reducing diel temperature fluctuations of the roof, green roofs can extend the life of the roof membrane (Leslie, 2005; Happe, 2005). A recent study found that office workers that had visual access to a green roof were better able to concentrate than those who did not (Loder, 2010). Data collected in Europe and the United States suggest that green roofs can provide habitat for birds, bees, spiders, mites, beetles, grasshoppers, and butterflies (Bauman, 2006; Brenneisen, 2006; Coffman and Davis, 2005; Lundholm et al., 2009; MacIvor and Lundholm, 2010). Green roofs may be especially effective as refuges for both domestic honey bees as well as wild hymenopteran pollinators, many of which are able to thrive in fragmented habitats typical of urban areas (Fetridge et al., 2008). However, the habitat potential of green roofs is likely not reaching its full potential because of the narrow plant palette used in these landscapes.

Because water and soil are heavy and it is not typically cost-effective to re-engineer a roof to increase its weight load, green roofs are designed with a thin layer (5-15 cm) of lightweight growing media, most commonly a mix of expanded clay or expanded shale, sand, and a small amount of organic matter (VanWoert et al., 2005). Plant diversity is constrained by the harsh environment of a green roof, especially summer water deficit (Carter and Butler, 2008), which is exacerbated by extreme heat (Martin and Hinckley, 2007) and high wind

(Retzlaff and Celik, 2010). In Chapter 2, I present results on a survey of the growth and survival of 19 plant species on an unirrigated green roof.

Native plants on green roofs

One taxon that seems especially well-suited to life in this environment is *Sedum* (Crassulaceae). *Sedum* species are low-growing succulent plants that can grow rapidly when water is available yet also survive long periods without water (Carter and Butler, 2008; Durhman et al., 2006; Monterusso et al., 2005). Recent attempts to grow non-*Sedum* plant species on roof tops have tended to focus on native plants (Bousselot et al., 2009; Butler et al., 2010; Licht and Lundholm, 2006; Martin and Hinckley, 2007; Schroll et al., 2009). In Chapter 3, I evaluate the widespread desire to use native plants on green roofs. Lundholm (2005) suggested a 'habitat template' approach, looking to natural ecosystems with physical characteristics similar to those on a roof to identify potential species. While this method is promising (Lundholm et al., 2009; Lundholm et al., 2010), it has yet to be widely adopted (Butler et al., 2010). As a consequence many studies have observed high mortality of non-*Sedum* species (Carter and Butler, 2008; Martin and Hinckley, 2007; Monterusso et al., 2005) unless irrigated (McIntyre, 2009; Schroll et al., 2009). The use of irrigation, however, is generally not encouraged because it goes against the goal of creating a self-sustaining community, wastes water, and requires a more complicated system. Perhaps the solution lies in using stress-tolerant plants to facilitate the performance of other plant species.

Habitat amelioration by nurse plants in harsh environments

In many stressful habitats, such as deserts, alpine tundras, and salt marshes, stress-tolerant ‘nurse plants’ reduce abiotic stress and increase performance and survival of neighboring plants (Bertness and Callaway, 1994; Callaway and Walker, 1997; Holmgren et al., 1997). The concept of nurse plants and interspecies facilitation can be traced back to an elegant field experiment by Turner and colleagues (1966). They found that in the Sonoran desert, shading by shrubs reduced peak soil temperature by 4-9 °C, dramatically increasing survival of seedlings of the saguaro cactus, *Carnegiea gigantea,* growing under these shrubs. Similar results have been found for the columnar cactus *Neobuxbumia tetetzo* growing in the Tehuacan Valley in central-southern Mexico (Valiente-Banuet and Ezcurra, 1991). In Chapters 4 and 5, I apply the concept of interspecies facilitation to a novel environment—a rooftop. I hypothesized that *Sedum* species would cool the soil, act as a competitor in wet conditions and a facilitator in dry conditions.

Photosynthetic plasticity in *Sedum*

This dissertation clearly demonstrates that the performance of *Sedum* is superior to other species (Chapter 2) and that *Sedum* is capable of facilitating the performance of other species (Chapters 4 and 5). This led me to examine the physiology of diverse *Sedum* species (Chapter 6). Specifically I wanted to examine whether the ability of *Sedum* to switch between C3 and CAM photosynthesis a possible mechanism for its success as a green roof plant. During photosynthesis plants use the sun's energy to convert carbon dioxide (CO_2) into sugar. CO_2 enters the leaves via stomata. As CO_2 diffuses in, water evaporates from the leaf. In the most common form of photosynthesis, C3, every gram of CO_2 absorbed from the atmosphere results in a loss of 400-500 g of water, which represents approximately 95% of the water taken up by roots (Taiz and Zeiger, 2006). In contrast to C3, where stomata are open during the day, in CAM photosynthesis stomata open at night, when there is a lower water gradient between the interior of the leaf and the atmosphere (Fig. 1.2). Although CAM photosynthesis is more water efficient (one gram of CO_2 gained results in 50-100 g water lost), it requires more energy because the plant must temporarily store the carbon as malic acid until the next day, when the Calvin Cycle converts this into sugar (Fig. 1.2). Many of the plant species used on green roofs, including *Sedum,* exhibit CAM photosynthesis, either constitutively or facultatively (Earnshaw et al., 1985; Gravatt and Martin, 1992; Castillo, 1996). The physiology of CAM-C3 intermediates, including *Sedum*, has been researched (reviewed by Luttge, 2004) but this has not been correlated with growth and survival under varying water availability. Photosynthetic plasticity could allow *Sedum* to grow quickly when water is available but also survive extended periods without water. In Chapter 6, I measure photosynthetic plasticity in eight species of *Sedum* under variable soil moisture.

Implications of this research

Results of these studies will be of value in expanding the range of plants available to green roof developers, and in extending application of green roofs to include pollinator habitat. Interspecies facilitation may provide an easy and low-cost method to reduce the abiotic stress of a green roof, which could expand the range of plants able to live in this habitat and consequently, increase the habitat value of this space for insects and other invertebrates. Thus, *Sedum* may have an important role in bio-diverse green roofs.

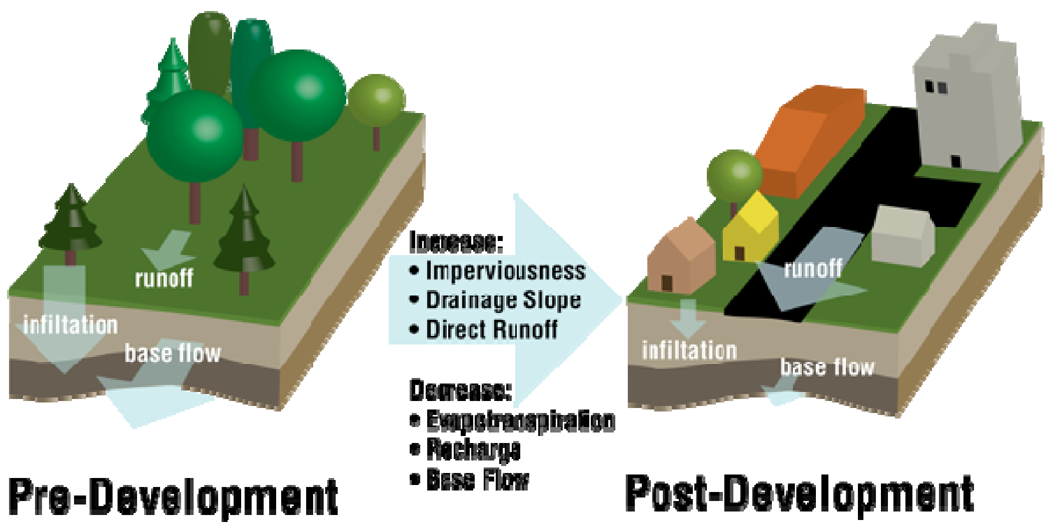


Figure 1.1 Effect of development on rain infiltration and runoff.
Figure from: www.invisiblestructures.com/stormwater.html

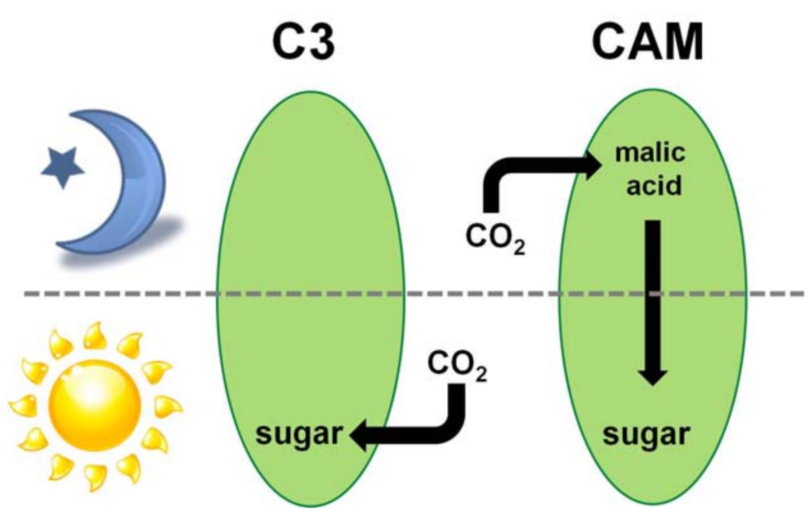


Figure 1.2 Simplified schematic of C3 and CAM photosynthesis

CHAPTER 2
Ecological impacts of replacing traditional roofs with green roofs in two urban areas

Note: This chapter is published in Cities and the Environment 1(2): Article 9. Research that occurred in Massachusetts is the work of C. Butler. Research that occurred in Georgia is the work of T. Carter.

Abstract

Urban land cover is dominated by impervious surface that degrades both terrestrial and aquatic ecosystems relative to predevelopment conditions. There are significant opportunities for designers of urban landscapes to use alternative land covers that have multiple functions, benefiting both human and nonhuman components of the urban ecosystem. Vegetated (green) roofs are one form of alternative land cover that has shown the potential to provide a variety of ecological benefits in urban areas. We evaluated how stormwater retention, building energy and temperature, and rooftop habitat are influenced by the use of green roofs using test plots in Georgia and Massachusetts. Green roofs were shown to recreate part of the predevelopment hydrology through increasing interception, stormwater storage, evaporation and transpiration on the rooftop and worked extremely well for small storm events. Temperature reductions were found on the green rooftop as compared to an asphalt surface, although other roof technologies that minimize temperatures, such as lighter colored membranes, provide similar benefits. Novel habitat was created on the rooftop, although the extent of this habitat was limited in part by plant survivability and the need for additional water inputs for diverse plant communities to survive. Despite the

challenges, the green roof benefits reported here suggest that green roofs can be used effectively as a multifunctional land cover in urban areas.

Introduction

In the past 40 years, the global human population has doubled to over 6.5 billion people, and the U.S. population alone exceeds 300 million (US Census Bureau, 2006). Urban areas, in particular, are growing rapidly with over 8% of the land area in the United States projected to be urban by the year 2050; this will be over double the amount measured in 2000 (Nowak and Walton, 2005). As cities are built, pervious land cover, such as forest and grasslands, is being replaced with impervious surfaces like roads, rooftops and parking lots. Instead of infiltrating into the soil, precipitation flows over impervious surfaces transporting pollutants, such as oil, heavy metals, and fine particulates. This altered hydrology in an urban area can generate five times as much surface runoff as an equivalent area in a forested condition (EPA, 2003). Often this surface runoff is routed directly into the nearest water body through the storm sewer system, thus bypassing potential infiltration areas and floodplain connections that are highly effective at pollutant removal (Kaushal, 2008).

Impervious surfaces also absorb and reradiate solar radiation creating the well-documented “urban heat island” (UHI) effect, where average air temperatures in highly developed areas are consistently higher than the surrounding landscape (Rizwan et al., 2008). This elevated temperature leads to increased building cooling costs, particularly in warmer areas of the United

States. Additionally, creation of impervious surfaces reduces the amount of land in urban areas available for biological communities to develop. While researchers have documented how some structures in the built environment create unique habitats (Larson et al., 2004), the conditions both in terrestrial and aquatic urban ecosystems tend to favor a limited number of generalist species adapted to the harsh ecological conditions of the city (McKinney, 2006). The cumulative environmental impacts of impervious surfaces in urban ecosystems have led to widespread interest in investigating how detrimental effects of impervious surfaces can be diminished.

Strategies to mitigate the negative impacts of impervious surfaces in urban areas take three general forms. The first and most common practice is to treat the symptoms of impervious surface through engineered practices. Since altered hydrology is a trademark of urban systems, much effort has been invested in engineering ways to manage and treat stormwater runoff. Structural stormwater best management practices (BMPs) are designed and constructed to retain stormwater volume, filter pollutants through growing media and remove pollutants through biological uptake. Commonly used structural practices include stormwater ponds, constructed wetlands, bioretention areas, and sand filters. Governmental regulation such as the Clean Water Act's National Pollutant Discharge Elimination System (NPDES) Phase I and II requirements have accelerated the installation of these post-construction stormwater management practices in urban areas to diminish impervious surface impacts (White and Boswell, 2005; EPA, 2005).

A second strategy for mitigating impervious surface ecological impacts is to identify areas containing high ecological value in the landscape and prevent conversion of additional areas of the landscape to impervious surface. This may be accomplished through the creation of parks or wildlife corridors through a variety of policy instruments such as conservation easements and greenspace requirements (Arendt, 1999). Often, riparian areas are targeted and incorporated into a community's greenspace plan with regulatory protection guaranteeing that the land cover will remain in an undeveloped condition. This use of "green infrastructure" (Benedict and McMahon, 2006) to protect functional landscapes can also be applied to areas experiencing urban growth. For example, new residential subdivisions may use cluster development and other low impact development (LID) techniques to minimize impervious surface cover of the site (Arendt, 2004). While this strategy is effective for areas experiencing urban growth, it is not always practical in urban areas that are already highly developed.

A third strategy involves the conversion of impervious surfaces in urban areas into a multifunctional land cover that serves both human demands such as transportation and housing, as well as ecological functions such as stormwater retention, energy conversion resulting in primary production, and habitat creation. The transportation network, for example, can use porous pavements to permit both traffic flow on the surface and water flow through the pore spaces, allowing infiltration into the soil. While porous paving strategies create an additional and important function in providing infiltration capacity in urban areas, they are limited in their ability to fully replicate predevelopment conditions. An obvious limitation is that the opportunities to grow vegetation in porous pavement systems are typically relegated to turf grass used in a grass paver application (Ferguson 2005).

Vegetated (green) roofs are another example of this third strategy. Nearly 50% of impervious surface in highly urbanized areas is unused roof space (Dunnett and Kingsbury, 2004). Green roofs convert the impervious surface of a rooftop into multifunctional spaces in urban areas using vegetation, growing media and specialized roofing materials. This practice has been used expansively in Germany for over 30 years. In 2002, over 12% of the flat rooftops in Germany had some type of a planted roof (Harzmann, 2002). Both flat and sloped roofs of new commercial and residential buildings can be converted into green roofs. Green roof retrofitting onto existing structures is also a common practice, particularly with lightweight green roofs and structures that can support the weight of the vegetated system (Gedge et al., 2006).

Green roofs are typically divided into two categories: extensive and intensive. Extensive green roofs have thin substrates (5-15cm), limited plant palates, relatively low costs, and minimal weight requirements. In Germany, extensive systems are by far the most common application, representing over 80% of all green roofs (Harzmann, 2002). In contrast, intensive green roofs, sometimes referred to as "rooftop gardens," have deeper substrates (>15 cm) which allow for higher potential for increased plant diversity, but also come with increased weight and higher cost and maintenance requirements. Following the German example and with current market conditions that emphasize maximum cost-effectiveness, it is likely that the majority of new green roof installations in North America will be extensive systems.

Many factors influence how green roofs perform ecologically in urban areas with green roof functions limited by the unique conditions found on the rooftop. One example is green roof habitat. Data collected in Europe and the United States suggest that green roofs can provide habitat for spiders, mites, beetles, grasshoppers, butterflies, and birds (Brenneisen, 2003; Getter and Rowe, 2006; Coffman and Davis, 2005). With this paradigm shift toward a focus on habitat and biodiversity has come a rejection of traditionally used green roof species, such as *Sedum,* in favor of a more diverse palette of plants, especially plants native to the region where the green roof is located. Unfortunately, this strategy has achieved limited success with high mortality of non-*Sedum* species due to extreme rooftop climatic conditions (Monterusso et al., 2005; Rowe et al., 2006). Because green roofs are by definition uniquely human created and engineered habitats, rooftop plant nativity may need to be reconsidered and using regionally native plants on green roofs may not be a feasible or useful goal. However, increasing the diversity of green roof plants may help to increase a roof's value as habitat for other species. Research has also demonstrated that diversity increases productivity of an ecosystem (Tilman, 1997), increases stability of that ecosystem (Tilman, 1994), and increases retention of soil nutrients (Ewel, 1991).

This paper will evaluate the potential for extensive green roofs to provide increased ecological function in urban areas as compared to impervious surface rooftops by discussing two green roof case studies from the Southeastern and Northeastern United States as well as previously published data. We will focus on three benefits--stormwater retention, temperature mitigation and habitat creation-- and qualitatively and quantitatively compare a green roof's function with the functions created by typical impervious surface roofs. In addition, we will discuss limitations of the current technology in replicating predevelopment land cover functions.

Methods

Two green roof case studies. Data from two green roof field sites were evaluated in this study. The first study site was constructed on the Boyd Graduate Studies building on the campus of the University of Georgia (UGA) in Athens, GA in October, 2003. This green roof site contained two types of extensive green roof systems (Figs. 2.1 and 2.2). One system, approximately 42 m^2 in area, was integrated into the roof membrane using a variety of synthetic green roofing material for drainage and water retention; this design is called the "Extensive Garden Roof" assembly (American Hydrotech 2002). This green roof system's growing media contained a 55:30:15 mix of expanded slate, USDA sand, and organic matter, respectively. Plant material was a mixture of *Sedum* and *Delosperma* species (Table 2.1). Additional details of the integrated UGA green roof system can be found in Carter (2006). An identically sized gravel roof section was constructed adjacent to the integrated green roof as a control plot. A modular extensive green roof system was also installed at the UGA site. This system, produced by St. Louis Metalworks and called Green Roof Blocks™, was approximately 37 m^2 and used a 61 x 61 cm aluminum container with 10.16 cm of growing media. No other specialized green roofing material was used. The growing media in the modular systems contained 80:20 mix of expanded slate and organic matter, respectively. The modular system used a randomized complete block design with 12 Green Roof Blocks™ containing three treatments (empty block, non-vegetated block, and vegetated block) replicated four times (Fig. 2.3). Additional details of the modular UGA green roof system can be found in Hilten (2005) and Prowell (2006).

The second case study green roof was located on the Tisch Library at Tufts University in Medford, Massachusetts, 8 km northwest of Boston (Fig. 2.4). This extensive green roof used a modular system to allow for independent replication of experimental treatments. Modules were made of black plastic with the dimensions 38.1 x 38.1 x 15.24 cm. Before the addition of substrate, each Module received a drainage fabric layer (fused, entangled filaments and nonwoven geotextile Colbond Enkadrain® 9611) to prevent waterlogging and a filter layer (Easy Gardener WeedBlock ®) to minimize soil loss. Each Module was filled with an industry-standard green roof substrate (55:30:15 expanded shale aggregate, USGA sand, leaf compost). Substrate was 13 cm deep with a dry weight of 1.08 g / ml, saturated weight of 1.42 g / ml, and field capacity of 0.35 cm^3 water / 1 cm^3 substrate. At the start of the experiment, controlled release fertilizer was mixed into the substrate at a concentration of 3.6 g fertilizer per liter (Scott's Osmocote® Plus 15-9-12, 3-4 months at 70 ° F).

At the Georgia site, annual rainfall averages approximately 123.2 cm/year with March typically having the highest rainfall total. Average annual temperatures range from 30° C in the summer to 3° C in the winter (www.ncdc.noaa.gov). The Massachusetts site receives 130 cm annual precipitation, has an average summer temperature of 21°C and an average winter temperature of -2°C.

For both studies, a number of environmental parameters were measured to determine how an alternative land cover like green roofs would function differently from impervious surfaces in the urban landscape. However, the green roof study sites were constructed with different research objectives in mind. The Georgia study site was monitored for stormwater retention and temperature mitigation while the Massachusetts site was designed to test for plant growth and habitat creation. The measurements for each case study are described below.

Stormwater. At the UGA site stormwater runoff was monitored from both the integrated and modular green roof assemblies. From November 2003 – November 2004, runoff flow and volume were measured using a two stage weir, pressure transducers, and data logger which were linked to an on-site tipping bucket rain gauge to collect detailed rainfall-runoff relationships from the green and conventional roofs. Details of the monitoring set up can be found in Carter and Rasmussen (2006). The modular green roof system was monitored from October 2004 – September 2005 and tested both total stormwater retention and the effect of plants and growing media on stormwater retention performance. Details of the modular monitoring setup can be found in Prowell (2006). Stormwater runoff was not collected from the Massachusetts green roof site.

Energy and temperature. At the UGA site the modular green roof system was monitored from January to August of 2005 for physical parameters including: humidity, air temperature, wind speed, radiation, soil temperature, volumetric moisture content and heat flux. Measurements were taken every 15 minutes. These data were used to inform a HYDRUS 1D moisture transport model and describe the thermal conductivity of the engineered green roof soil. Building energy loads were calculated using eQuest. More descriptions from this study can be found in Hilten (2005). Temperature and energy data were not collected at the Massachusetts site.

Habitat creation. The goal of the experiment at the Massachusetts study site was to measure survivorship of potential green roof plant species. The Massachusetts green roof contained 19 plant species, representing 12 families. Plants were sampled broadly across angiosperm phylogeny to determine if there are non-*Sedum* drought-tolerant plants that can survive on an extensive green roof in New England. Plants were chosen based on their drought tolerance and growth habit (low-growing herbaceous perennials) (Table 2.1). In contrast to many previous green roof experiments, it was not assumed that native plants would show higher growth and survival than non-native plants. Although not all of the species were native to New England or North America, none of the species had a record of being invasive (USDA, 2008).

Plugs were planted during the first two weeks of June 2007. Due to infrastructure reasons, modules were planted elsewhere on campus and were subsequently moved to the Tisch Library roof on July 5, 2007. Ten replicate modules were created for each of the 19 species. Each replicate module contained 9 plugs of a single species. Due to limited number of plants, the following species contained 5 plugs per module: *Armeria maritima*, *Dianthus petraeus*, *Festuca glauca*, and *Veronica oltensis*. Plants were watered to saturation daily until July 5, 2007. After this, planted received no supplemental water except on August 28, 2007 when all plants were watered after an unseasonably long drought of 20 days without rain. Limited weeding took place throughout the growing season. Weekly overhead photos of each module were analyzed with Image J (available at http://rsb.info.nih.gov/ij/) to obtain a value of percent plant coverage per module. Percent cover was used as an approximation of growth. A formal analysis of plant growth was not performed at the UGA site.

Results and Discussion

Stormwater. Green roofs have been shown to change the hydrologic characteristics relative to impervious surface cover. Mentens et al. (2006) used data from 121 experimental extensive green roofs throughout Europe and found that on average, these roofs retained 50% of total annual precipitation. Moran (2004) evaluated green roof field sites in North Carolina finding over 60%

reduction in stormwater volumes and large peak flow reductions from storm events sampled throughout the year.

Results from the monitored green roof sites in Georgia demonstrated clear benefits from both the integrated and modular systems relative to traditional impervious roofing. The first documented benefit is additional stormwater storage provided by the roof system. This is measured by the total amount of rainfall retained during the study period at the site. In the case of the integrated roof system, nearly 78% of the rainfall was held on the roof surface (Carter and Rasmussen, 2006). The modular roof system provided slightly less retention with approximately 67% of the average rain event throughout the course of the year held on-site. The overall annual retention was approximately 43% due to the distribution of the rainfall as 23 of the 70 rain events throughout the year contributed more than 73% of the total annual precipitation (Fig. 2.5). Additionally, as tested in the modular system, vegetation provided negligible stormwater retention (Fig. 2.5). The total amount of stormwater retained on a traditional roof is negligible with surface runoff commencing upon initiation of rainfall and green roof runoff hydrographs behaving similarly to the traditional roof only after reaching saturation (Fig. 2.6).

This storage provided by green roofs replicates the evaporation, transpiration, and interception component of the water budget which tends to be lost from the land once it is covered with a building footprint (Wang et al., 2008). This storage is also particularly important for small storm events, which green roofs do a particularly good job of retaining on-site (Fig. 2.7). In urban areas, the increased frequency of surface runoff from small storms has been implicated as a likely cause of degradation to stream biotic communities (Walsh et al., 2005). As an alternative land cover, green roofs can function as part of stream restoration efforts through re-establishing part of the predevelopment hydrology in urban catchments.

Energy and temperature. A number of studies have attempted to model how green roofs may mitigate the effect of the UHI. Alexandri and Jones (2008) modeled the thermal effect of both green roofs and green walls in nine cities around the world concluding that the practices had the greatest effect in hot, dry climates. Takebayashi and Moriyama (2007) determined that green roofs accounted for reduced heat flux into the building because of the large latent heat flux generated by evaporation. Other studies have focused on the evaporative cooling effect provided by a variety of green roof systems (Lazzarin et al., 2005; Onmura et al., 2001; Saiz et al., 2006). Energy studies have also demonstrated how green roofs can act as an additional layer of insulation for the building (DeNardo et al., 2005; Niachou et al., 2001; Kumar and Kaushik, 2005).

Data from the UGA modular roof system support the conclusions that green roofs provide an insulative barrier for the roof surface. Hilten (2005) studied the UGA test site and found the UGA modular roof to provide insulation equivalent to preformed cellular glass at a 25 mm depth. The eQuest energy model also demonstrated increased performance of the rooftop as it relates to energy savings for the building. For Athens, GA, the model demonstrated that the modular green roof reduced the amount of energy needed to heat or cool a typical office building by 0.3 – 5.0% depending on the build type and configuration (Table 2.2). Additionally, the energy data from UGA's modular green roof was modeled for a one-story "big box" store of 14,000 m^2. In this case, the ratio of rooftop to internal volume of the building is higher than a commercial building and the reduction in cooling energy loads increased to 12.1% and reductions in heating energy loads increased to 31.7% for Atlanta's climate (Table 2.2).

Green roofs clearly provide additional temperature mitigation for individual rooftops. This provides benefit for the private building owner through reduced energy costs (Carter and Keeler, 2007) as well as decreasing the temperature of the stormwater runoff which improves conditions for receiving water bodies. What is not clear is the effect that green roofs would have on the UHI phenomenon since rooftop temperature is only one of UHI's causes. Bass et al. (2003) modeled the effects that green roofs would have on Toronto's UHI and projected that roof greening would lower temperatures city-wide by 0.1 – 0.8 ° C. This reduction was considered insignificant due to uncertainty in the model predictions. Regardless of the extent of effect, however, the UGA energy modeling study demonstrates that improvements in rooftop performance from an energy and temperature perspective can be realized using relatively simple, modular green roof systems.

Habitat creation. The results of the Massachusetts green roof experiment underscore the importance of conservative plant choice. While the 2007 summer weather in eastern Massachusetts was highly unusual—August 2007 was the driest August in Boston since 1883—results from the experiment added to the wealth of data on the extreme drought tolerance of *Sedum* species. With the exception of two large storm events on July 28 and 30, the precipitation for July was typical of New England summers (Table 2.3). August showed greatly decreased precipitation, only 1.65 cm. These novel weather patterns allowed us to examine plant growth and survival in two distinct precipitation scenarios: normal and extreme drought.

As previously shown (Monterusso et al., 2005; Durhman et al., 2006), *Sedum* can withstand extreme water stress. All *Sedum* species showed rapid growth (as seen by increased percent plant cover) between July 18 and August 2, then showed a slight decrease in percent cover between August 2 and August 31 (Figs. 2.8a-c, 2.9). We found that in periods of the growth season with average rainfall, several non-*Sedum* plants grew and some showed rapid growth (such as *Asclepias verticillata* and *Agastache rupestris*) (Figs. 2.8a-c, 2.9). However, only *Sedum spp*. had any living aboveground biomass after the August drought. In the spring of 2008, *Festuca glauca* began to re-grow and kept aboveground living biomass throughout the winter, spring, and now summer. Several individuals of *Armeria maritima*, *Eryngium yuccifolium*, *Fragaria vesca*, and *Salvia nemorosa* have since grown back and have been growing without supplemental irrigation. Interestingly, the surviving plants (excluding *Festuca glauca* and *Sedum* spp.) were all located in low spots on the roof where water pools after rain (up to 0.5 cm deep). These oases dry up within a few days and consequently, do not represent a continued increase in water availability. This seemingly negligible volume of water seems to have allowed survival of these plants. The results from this experiment are consistent with previous studies examining the efficacy of non-*Sedum* plants on green roofs. Rowe et al. (2006) grew 2 species of *Sedum* and 6 species of Midwestern US prairie species under varying substrate and nutrient regimes. The non-*Sedum* species showed high mortality in all treatments. Monterusso et al. (2005) tested 18 Michigan native plants and found that only 4 were suitable for non-irrigated extensive green roofs. In a study by Licht and Lundholm (2006), 15 Northeast coastal native plants and 3 *Sedum* species were tested for survival on a non-irrigated extensive green roof in Massachusetts. After a summer without irrigation, only 2 of the 15 native plants survived in comparison to 100% survival of the 3 *Sedum* species. Together, these data suggest that non-*Sedum* plants can only be used on extensive green roofs if supplemental irrigation is available during droughts.

Future opportunities for green roof study

This study focused on the additional functions provided by extensive green roof systems when compared with traditional roofing systems. As the land consumed by urbanization continues to outpace population growth (Benedict and McMahon, 2006), efforts must be made to create multi-functional land cover if some predevelopment ecological function is to be preserved. While complete preservation of these predevelopment functions may not necessarily be achievable or even appropriate, there is often institutional and regulatory considerations that would drive environmental concerns in urban areas in addition to public demand for ecological services (Grimm et al., 2008).

The extent of the above analyses was limited to three major benefits of green roofs including stormwater retention, temperature reduction and habitat creation through vegetation establishment. Green roofs recreate part of the predevelopment hydrologic cycle through storing rainfall in the pore spaces of the growing media and specialized roofing materials and allowing evaporation, transpiration, and interception functions to remove water from the roof surface. On a non-vegetated roof this water would quickly enter the storm drain system and often a receiving water body as surface runoff. In parcels that contain large amounts of rooftop relative to the total amount of parcel area, green roofs offer an attractive and economically viable option for parcel owners looking to provide stormwater management on their site (Carter and Jackson, 2007). A future research direction relating stormwater management and green roofs is to investigate how the complete predevelopment hydrology of a site may be replicated using green roofs as one component of the stormwater management system. To date, stormwater management is primarily focused on water quality or peak flow controls, but researchers have begun to investigate how to replicate a predevelopment hydrograph (Echols, 2008). In this case the evapotranspiration of green roofs could be integrated with infiltration, subsurface flow path creation, and groundwater recharge of other engineered systems to recreate predevelopment hydrologic conditions.

The temperature reduction provided by green roofs is a benefit relative to conventional asphalt or built up roof. This benefit may be tempered somewhat, however, by the number of other options available to a building owner interested in reducing rooftop temperatures and building energy costs. For example, highly reflective Thermoplastic Polyolefin (TPO) and ethylene propylene (EP) roofs are becoming a common way for building owners to mitigate rooftop temperatures with EPA's Energy Star program recognizing these and many other types of roof materials and coatings that increase reflectivity and insulation (www.energystar.gov). When energy savings are taken in isolation, green roofs are not economically viable when compared with potentially less expensive practices to mitigate rooftop temperatures. When combined with the stormwater management potential, however, green roofs may overcome the competitive advantage of selecting other roof systems strictly for the temperature and energy savings.

Another important consideration for green roof energy savings is the type of building itself. The green roof energy model demonstrated that energy savings were most pronounced on "big box" types of buildings that contain a large rooftop area relative to the internal heated/cooled space of the building while typical commercial buildings have relatively small energy benefits associated with modular green roof applications (Hilten, pers. comm.). Existing and future urban and suburban development forms that contain large one-story structures may be well-poised to capitalize on the energy benefits green roofs provide. These building forms, however, are often found in "strip type" developments that may not be desirable from a planning perspective due to ecological impacts (Arnold and Gibbons, 1996). These findings illustrate how more investigation is needed to determine which building designs may maximize particular green roof benefits such as energy savings while different environmental goals may be met within a different built context.

While there is potential for habitat creation on green roofs using non-*Sedum* plants, it is clear from this study that these diverse systems will require more water input to survive. This could be accomplished through the use of a water recycling system within a building to allow for both responsible stormwater management and habitat creation. Additionally, the exclusive use of *Sedum* species still provides habitat opportunities for macroinvertebrates. Coffman and Davis (2005) found a wide variety of insects on the Ford Motor Company's green roof which is dominated by *Sedum.* A future area of study may be to evaluate how variation within the *Sedum* genera may be used to encourage specific biotic assemblages. Since extensive green roofs are designed to involve minimal maintenance, another research project would be a long term study of the plant community on a green roof to observe any succession or changes through time that may affect the habitat and biotic community found on the roof.

One challenge facing green roof researchers is the ability to scale up these analyses from a roof scale to an entire jurisdiction and investigating what functions may be lost or gained in the process. A green roof scaling research initiative may be to test how habitat connectivity in urban areas can be increased as green roof installations are linked with regional greenspace plans and policies may be developed to encourage connected greenspace throughout the built landscape. One hypothesis may be that unless the practice occurred on a large proportion of the buildings within a designated green roof connectivity corridor, there would be little landscape-scale habitat benefit to individual green roof systems.

The data collected from these green roof sites demonstrates that a relatively novel urban land cover, a green roof, has the potential to provide ecological services in urban areas. This study also illustrated how the green roofs are specialized in their application and performance is highly dependent upon and constrained by design considerations and project planning goals. In considering green roofs as ecosystems, Oberndorfer et al. (2007) relate green roofs to other constructed ecosystems and extend future research directions to include water quality, air quality, ecosystem function, and cost-benefit analysis. These types of investigations can be performed as more green roofs are built and monitored over extended periods of time and greater spatial scales. As researchers continue to investigate ways to improve urban ecosystem function, the understanding and application of multi-functional land cover like green roofs will be expected to increase. While trade-offs and limitations are inherent in designed systems, the recognition that green roofs are a unique land cover will help drive realistic expectations for how best to incorporate them into urban ecosystems.

Table 2.1 Plant species on the green roof study sites

Family	Genus and species	Variety	Location
Apiaceae	*Eryngium yuccifolium*	--	Tufts
Asclepiadaceae	*Asclepias verticillata*	--	Tufts
Asteraceae	*Echinacea tennesseensis*	Rocky Top	Tufts
Asteraceae	*Aster ericoides*	--	Tufts
Asteraceae	*Antennaria plantaginifolia*	--	Tufts
Aizoaceae	*Delosperma cooperi*		UGA
Aizoaceae	*Delosperma nubigenum*		UGA
Caryophyllaceae	*Dianthus petraeus*	noeanus	Tufts
Crassulaceae	*Sedum album*	--	Tufts, UGA
Crassulaceae	*Sedum sexangulare*	--	Tufts, UGA
Crassulaceae	*Sedum rupestre*	--	Tufts
Crassulaceae	*Sedum spurium*	--	Tufts
Crassulaceae	*Sedum kamtschaticum*	--	UGA
Fabaceaee	*Baptisia australis*	Purple Smoke	Tufts
Lamiaceae	*Agastache rupestris*	--	Tufts
Lamiaceae	*Salvia nemorosa*	Marcus	Tufts
Onagraceae	*Oenothera tetragona*	Cold Crick	Tufts
Poaceae	*Festuca glauca*	Sea Urchin	Tufts
Poaceae	*Eragrostis spectabilis*	--	Tufts
Plantaginaceae	*Veronica oltensis*	--	Tufts
Plumbaginaceae	*Armeria maritima*	Compacta	Tufts
Rosaceae	*Fragaria vesca*	Lipstick	Tufts

Table 2.2 Energy load reductions using a modular green roof system using UGA modular green roof data compared with an uninsulated built up roof.

City	Building type	Cooling load reduction (%)	Heating load reduction (%)
Athens	commercial (1 story)	5.0	0.9
Athens	commercial (3 stories)	2.6	0.7
Athens	commercial (8 stories)	2.5	0.3
Atlanta	"big box"	12.1	31.7

Table 2.3 Precipitation and temperature in Boston over the study period (July – Oct 2007) compared to 30 year climate averages.

	Precipitation (cm)		Temperature (deg C)	
	30 year mean	2007	30 year mean	2007
July	7.77	13.41	23.28	22.72
August	8.56	1.65	22.39	22.61
September	8.81	4.6	18.17	19.83
October	9.63	5.28	12.28	15.11

Figure 2.1 University of Georgia integrated green roof system

Figure 2.2 University of Georgia modular green roof system

Figure 2.3 Experimental design of UGA modular green roof system

Figure 2.4 Experimental modular green roof on Tisch Library at Tufts University Medford, MA

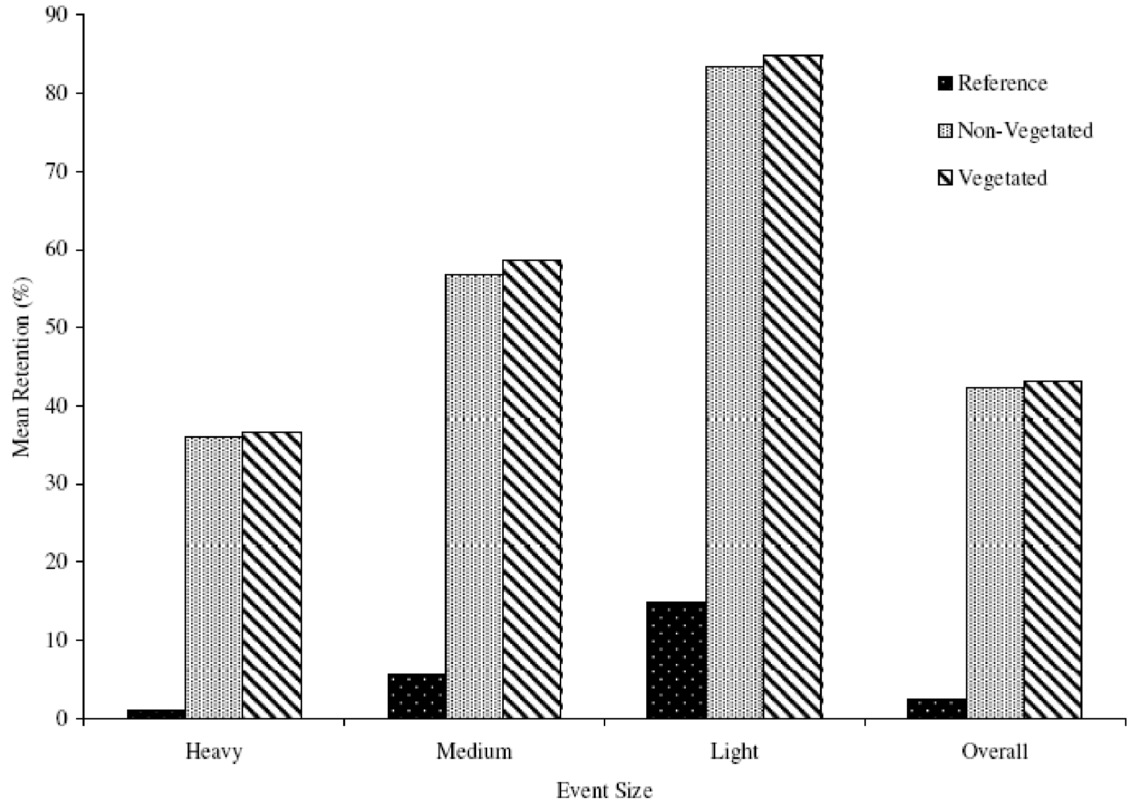


Figure 2.5 Percent retention for different sized storms and three treatments on the UGA modular system. Light storms were <6mm, medium storms were 6-25 mm, heavy storms were >25 mm

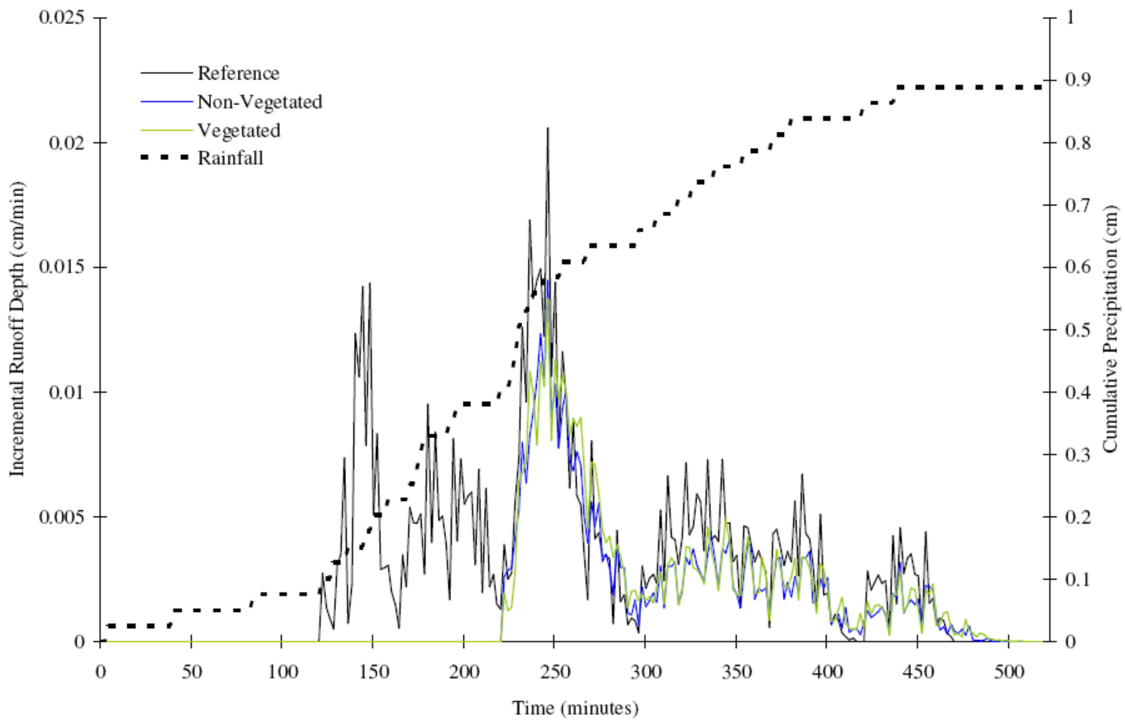


Figure 2.6 Runoff hydrograph of a representative storm in July 6, 2005 from the UGA modular system

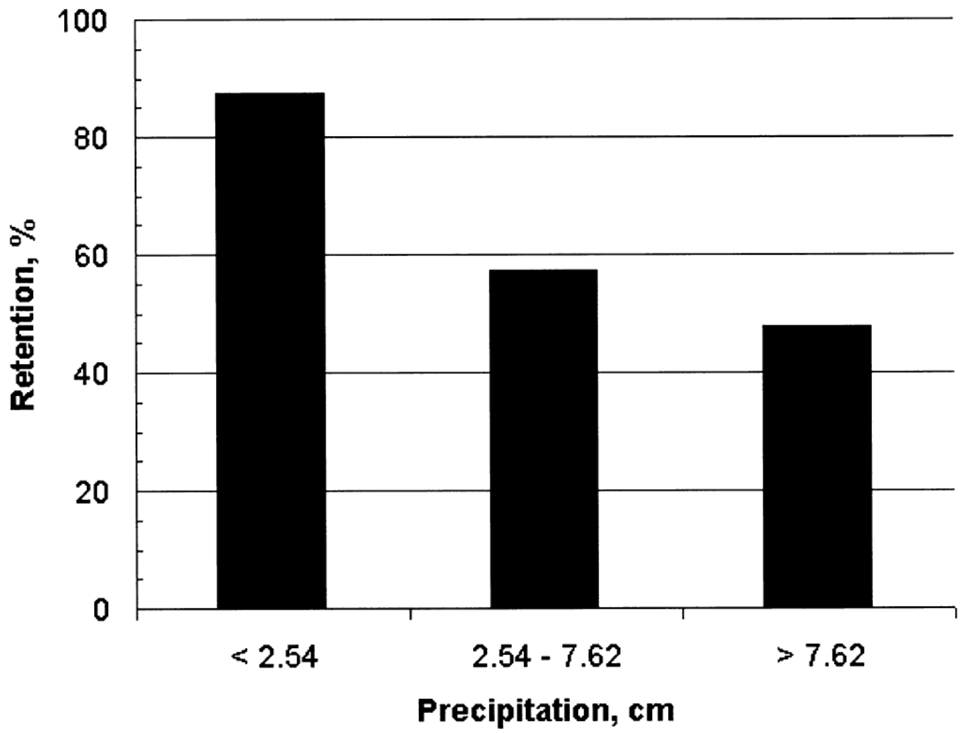
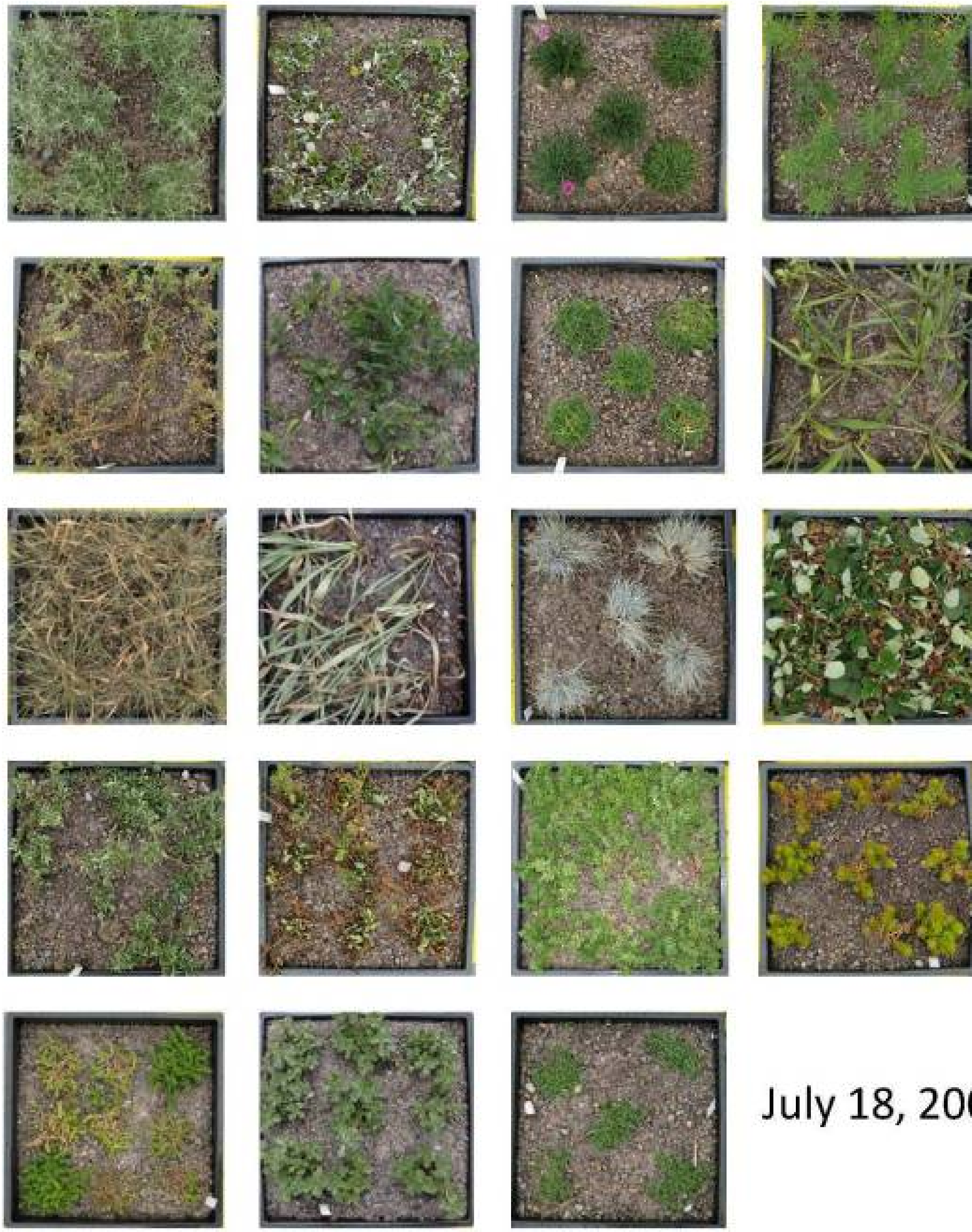
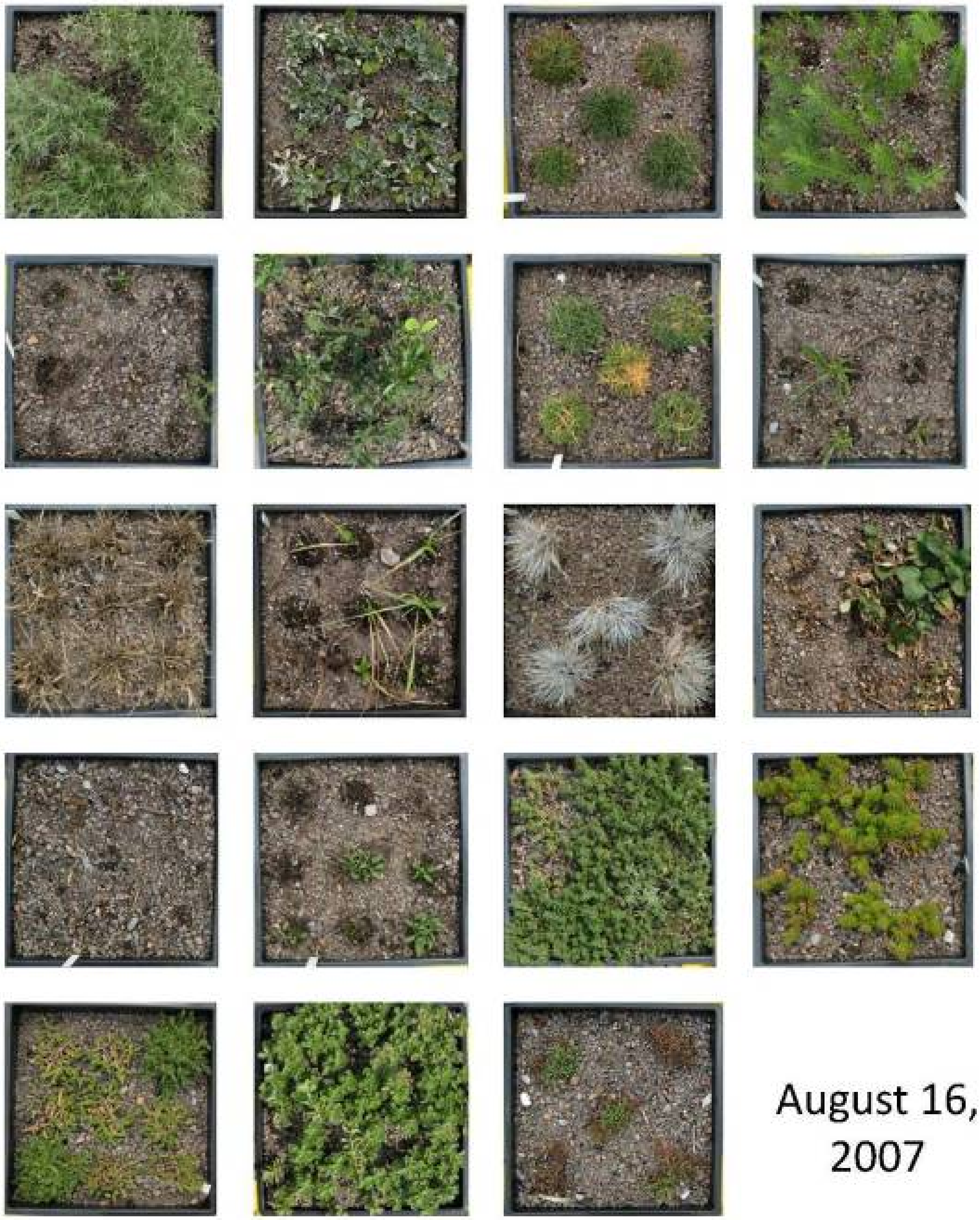


Figure 2.7 Retention percentage on the UGA integrated roof system for three precipitation depth categories from 2003 – 2004 (from Carter and Rasmussen, 2006)



July 18, 2007



August 16, 2007

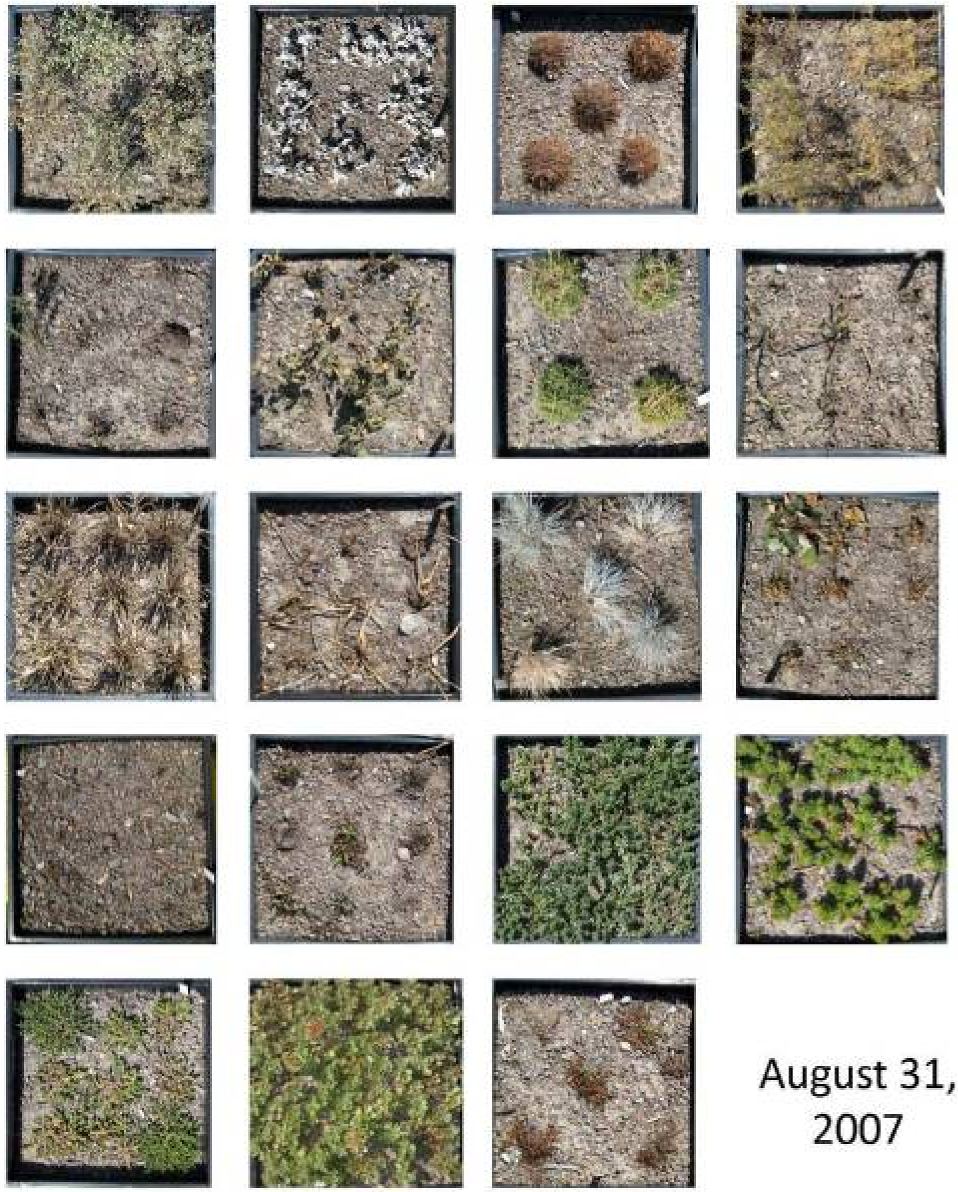


Figure 2.8 Representative overhead photos of each of the 19 species at 3 time points at the Massachusetts site: (a) July 18, 2007, (b) August 16, 2007, and (c) August 31, 2007. Each module pictured is the 3rd replicate of each species.

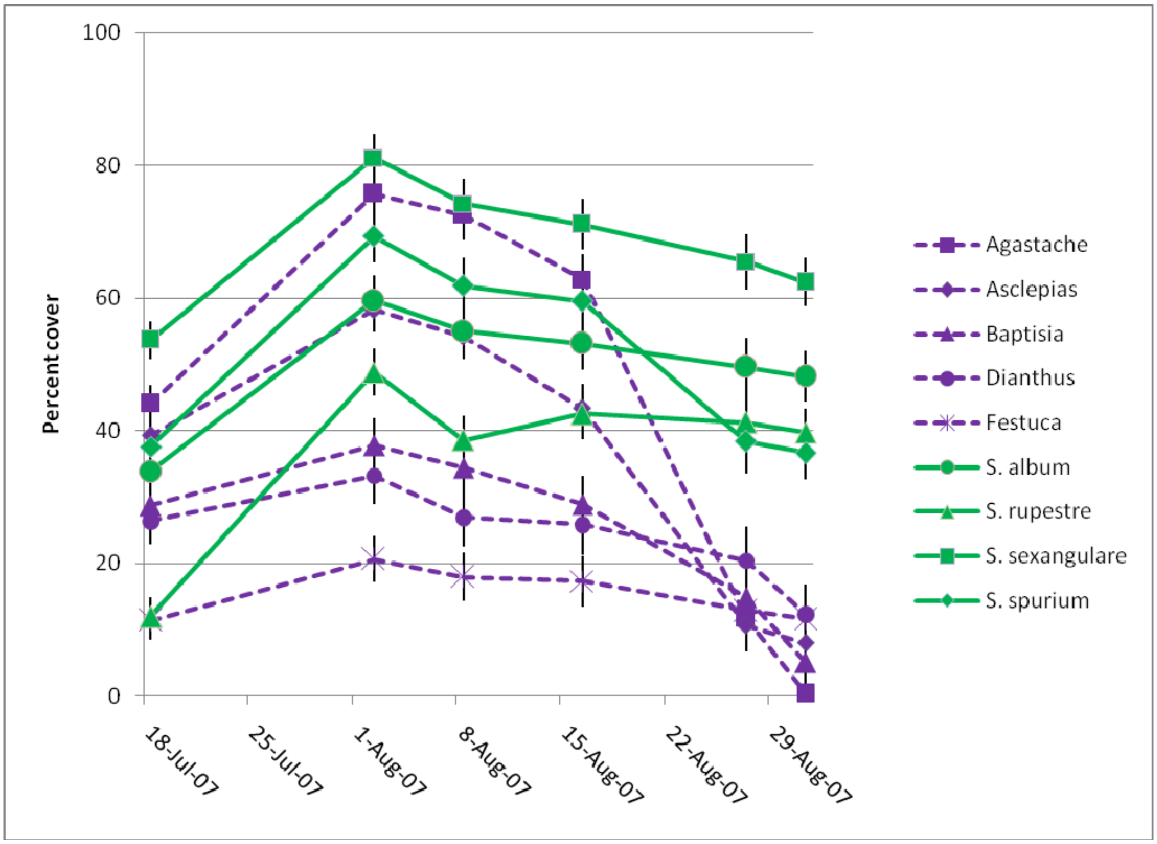


Figure 2.9 Change in percent plant cover during July and August 2007 on experimental green roof at Tufts University. *Sedum* species are shown in green and non-*Sedum* species are shown in purple. For clarity, only the 5 fastest growing non-*Sedum* species are shown in this figure. Percent plant cover was determined by analyzing overhead photos of plants using Image J. Data presented are means ± standard error (n=10).

CHAPTER 3
Native plant enthusiasm reaches new heights: Perceptions, evidence, and the future of green roofs

Abstract

The use of native plants on green roofs has attracted considerable attention in recent years. With this comes the implicit assumptions that native plants are better adapted, provide greater environmental benefit and are more aesthetically pleasing than non-native plants. We examined papers published in scholarly journals and papers presented at *Greening Rooftops for Sustainable Communities* conferences to identify who is promoting the use of native plants on green roofs, their rationale for doing so, and the scientific evidence to support the assertion that natives are better adapted. Architects, landscape architects and biologists were the most likely to promote native plants and engineers were the least likely. Many of the reasons for using native plants on green roofs originate from ground-level landscaping and have simply been transplanted to the roof, without regard for the fact that the rooftop is a fundamentally different environment than the ground. Nearly half of all pro-native papers used the term “native” without definition, frequently employing it as an expedient alternative to "beneficial," rather than as a quality arising from an organism's relationship to a specific environment in a specific geographical location. This review highlights the need for greater rigor and transparency when promoting the use of native plants and further demonstrates how misconceptions can result in sub-optimal green roof design and performance.

Introduction

Modern green roofs originated in Europe, where their primary function is to reduce stormwater runoff. Traditionally, these roofs were planted with low-growing, drought-tolerant succulent plant species, especially *Sedum*. Today, there is a great deal of interest in increasing the diversity of plant species used on green roofs with a particular focus on the use of native plants (e.g. Kephart, 2005; MacDonagh et al., 2006; Schroll et al., 2009). On the Greenroofs.com database, there are over 100 green roofs listed that self-report the use of native plants. Most were constructed after 2005 and the majority of them are located in the United States. Numerous organizations are actively promoting the use of native plants on green roofs, including non-profits like the Ladybird Johnson Wildflower Center and the Peggy Notabaert Nature Museum, governmental organizations such as New York City's Greenbelt Native Plant Center and the City of Toronto's Green Roof Pilot Program, and commercial organizations, such as Rana Creek and Conservation Design Forum.

In 2008, the California Academy of Sciences building opened to the public. The focal point of this building and a symbol of its commitment to sustainability is its undulating green roof planted with California native plants. In addition to earning a LEED Platinum rating, the green roof has won awards from the American Society of Landscape Architects and Green Roofs for Healthy Cities. The architect, Renzo Piano, described the inspiration for the green roof "like lifting up a piece of the park and putting a building under it" (California

Academy of Sciences, About the Building). Burke (2003) expressed a similar sentiment regarding the concept behind the green roof at the Gap headquarters in San Bruno, California. “Imagine a building design in which the native landscape on the site is merely lifted up into the sky, and the building program is placed underneath.” Both Piano’s and Burke’s statements show the current philosophy of green roofs as an extension or continuation of ground-level landscaping. In contrast to ground-level landscaping, however, the climate on a roof is generally colder in winter, hotter in summer, and prone to rapid soil drying (Luckett, 2009; Snodgrass and Snodgrass, 2006). Because the rooftop is a fundamentally different environment than the ground, using native plants on green roofs is not straightforward and if done improperly can result in extensive plant mortality. Here we explore the reasons why native plants are being promoted for use on green roofs, how they have been selected, and the evidence for their success.

Before we explore how and why native plants are being promoted for use on green roofs, we must first explore the definitions of “native.” Definitions of “native” vary substantially in their specificity. The Sustainable Sites Initiative defines a native plant as one which is “native to the EPA Level III Ecoregion of the site or known to naturally occur within 200 miles of the site” (p. 17). The United States Environmental Protection Agency’s Green Landscaping program provides a broader definition, defining a native plant as one that has “evolved over thousands of years in a particular region” (EPA Green Landscaping, Native Plants Brochure). In practice, working definitions of what constitutes a native plant differ wildly. These conceptions are complicated not only by distance (is

200 miles an appropriate radius?) but also by time (how long must a plant be established in a given region before it becomes a native?). Definitions are important because within a given geographical region, there are typically multiple ecosystems. For example, within the geographically small state of Massachusetts, there are salt marshes, wetlands, old-growth forests, coastal heathlands, rocky coastlines, and many more. Thus, a plant native to Massachusetts will likely not be able to grow equally well in all parts of the state.

Both aesthetic and scientific arguments are used to promote the use of native plants in ground-level landscaping. The aesthetic arguments are either culturally based –i.e. native plants are part of our cultural heritage (e.g. MacDonagh et al., 2006) or design driven—i.e. native plants blend into the surrounding landscape (e.g. Kiers, 2004). Scientific arguments are based on maintenance requirements, habitat creation, and the potential for plants to become invasive. The following quote from the EPA Green Landscaping website (EPA Green Landscaping, Benefits) illustrates many of the common reasons given for preferring native plants in ground-level landscaping:

> "Landscaping with native plants improves the environment. Native plants are hardy because they have adapted to the local conditions. Once established, native plants do not need pesticides, fertilizers, or watering…Landscaping with native wildflowers and grasses helps return the area to a healthy ecosystem. Diverse varieties of birds, butterflies and animals,

> are attracted to the native plants, thus enhancing the biodiversity of the area. The beauty of native wildflowers and grasses creates a sense of place, both at home and work. The native plants increase our connection to nature, help educate our neighbors, and provide a beautiful, peaceful place to relax."

In order to understand the rationale behind these aesthetic and scientific reasons, it is helpful to explore the origins of the native plant movement. These origins can be divided into three main categories: 1) cultural and aesthetic arguments put forth primarily by early landscape architects, 2) an alternative to turf grass promoted by environmentally conscious landscapers, and 3) environmental reasons explored by conservation biologists.

The first origin comes from landscape architecture. Common today in native plant literature is the legacy of Jens Jensen and other early landscape architects. Jensen's view of nature is an idyllic one, rife with images of harmony and interdependence. "A grove of these maples has within it the power of solemnity and beauty, and the oak and the maple are friends. They grow together, and they are tolerant of the smaller friends and associates that cling to their feet" (Jensen, 1939). Similar imagery and personification can be found today: "they are good plants, they do provide habitat, but they behave themselves, and they get along together like kindergartners" (Kephart, quoted in Cantor, 2008, p. 238).

The second origin comes from ecological landscaping. In reaction against front yard monocultures of turf grass in the suburban United States, several groups, such as the National Wildlife Federation, began to encourage the use of native plants in landscaping. Their argument was that turfgrass requires a great deal of water, fertilizer, pesticide, and mowing. These groups advocated using native plants that are adapted to local conditions and would consequently require fewer resources and less maintenance. In 1973, the National Wildlife Federation started the Certified Wildlife Habitat program, encouraging people to replace their existing lawn with a diverse native plant community (National Wildlife Federation, History of the Backyard Wildlife Program). In 1995, the National Environmental Policy Act made it a requirement for all federal projects to incorporate native plants (Federal Register, 1995). Moreover, native plants are considered to be important components of the natural food web and thus worth promoting (Tallamy, 2007). The Sustainable Sites Initiative, currently being developed by the American Society of Landscape Architects, the Lady Bird Johnson Wildflower Center and the United States Botanic Garden, is working toward establishing a set of standards for environmentally friendly landscaping [similar to the LEED (Leadership in Energy and Environmental Design) certification program created by the United States Green Building Council]. In the current version, projects earn points by using native plants (Credit 4.7, p. 109).

The third origin has its roots in restoration ecology and conservation biology. Horticulturists have been responsible for the release of many invasive plant species, including purple loosestrife (Blossey et al., 2001) and English ivy

(Reichard and White, 2001). In light of this, many conservation biologists encourage the use of native plants in landscaping (Tallamy, 2007) and eradication of non-native plants in the wild (Patten and Erickson, 2001). Although the majority of non-native species do not become invasive, the few that are invasive have caused widespread damage (e.g. kudzu). Williamson (1993, cited by Williamson and Fitter, 1996) describes this using a rule of 10, with 10% of non-natives surviving in their introduced range, 10% of those becoming established, and 10% of those becoming invasive. The difficulty of predicting which plants will become invasive (Bergelson, 1994; Perrins et al., 1992), and in which habitats (Alpert et al., 2000), is part of why invasiveness presents such a troubling conundrum. That the current discussion often equates "non-native" with "invasive" obscures the facts and points clearly to the need for additional scientific research on the subject. Invasive species are quickly becoming a popular topic for ecological research and may soon become a popular theme in landscape architecture and green roof design. Although this origin is based in science, discussions are often emotionally charged. In a letter published in *Conservation Biology*, Patten and Erickson (2001) argue that "Non-native species should be recognized for the scourges they generally are. Indeed, all should be treated as threats to the native ecosystem unless proven otherwise…" In the introduction to *Invasive Plants of the Upper Midwest* (2005), Czarapata paints an equally dramatic picture, "Many high-quality woodlands, often comprised of 120 or more native plant species, were being quietly and tragically transformed into haunting Eurasian jungles of buckthorn, honeysuckle, and garlic mustard."

It is clear that there is a strong preference for using native plants in ground-level landscaping. Green roofs, however, present a new ecosystem that is different enough from ground-level that the lessons of traditional landscape design must be carefully evaluated before they are applied. This paper seeks to evaluate the contemporary preference for native plants as it applies to green roofs. We quantify the extent of interest in using native plants on green roofs, and identify who is promoting their use. We also examine how they define the term "native," and their rationale for promoting native plants on green roofs. Next, we evaluate the scientific evidence regarding the assumed superior performance of native plants on green roofs. Our goal is to provide green roof designers with a better idea of the complexities of defining "native" and of the rationales behind the scientific reasons for using native plants on green roofs.

Methods

Determining the prevalence of the pro-native sentiment and the influence of career. In this review, we included papers from peer-reviewed scholarly journals and peer-reviewed papers presented at the annual *Greening Rooftops for Sustainable Communities* (*GRSC*) conference. Green roof research is just beginning to appear in scholarly journals, and the *GRSC* papers are currently the most prevalent sources of peer-reviewed writing in English on the topic of green roofs. We did not include books in this analysis because they are not peer-reviewed. We do discuss books in the Discussion.

We identified journals using searches for “green roof” OR “eco-roof” OR “living roof” on Web of Science and Scopus. We searched for the terms “native”, “indigenous”, in the full text of all papers. Papers containing these search terms were then read in their entirety. We only included papers in which authors were directly or indirectly promoting the use of native plants on green roofs. Papers in which authors discussed a general sentiment held by other people were not included.

The green roof industry has attracted researchers and practicioners from a wide variety of academic and professional backgrounds. We hypothesized that academic and professional background would affect the likelihood of promoting native plants. For example, a structural engineer is presumably less likely to promote native plants than a biologist. In addition, we hypothesized that among those who promoted natives, career could influence the reason for doing so. A landscape architect may be influenced by the work of Jens Jenson and aesthetics. A biologist may be more concerned with invasive species. For each paper, we identified the career of the first author, under the assumption that the first author was the lead of the study and did the majority of the writing. For *GRSC* papers, career of the first author was determined primarily by short autobiographical statements accompanying each paper. For journal articles, career was determined based on the academic department in which the author worked or the type of company for which the author worked. When necessary, these methods were supplemented with Google searches of the first author’s name. For our analysis, we focused on the four most common careers: Architect, Landscape Architect, Biologist, and Engineer. Within each career, we calculated the percent of papers that promoted native plants. To determine if the career of the first author influenced the likelihood of promoting native plants, a chi square test was performed.

Determining how authors defined the term 'native'. For papers (both journal and *GRSC*) that promoted the use of native plants on green roofs, we categorized how each defined the term "native." We focused on two components: a defined geographical region (e.g. Michigan, England, North America) and a defined biome (e.g. prairie, alpine, coastal). Ideally, a definition should include both of these components as there can be wide variation within a single geographic area and within a single biome. Examples of definitions that include both a geographical region and biome component are Nova Scotia coastal barren (Lundholm et al., 2009) and Georgia granite outcrops (Needle and Nicolow, 2006). To increase objectivity and reliability, each paper was read and scored independently by two reviewers after an initial training. When scores were different, the two reviewers re-read and discussed the paper to reach consensus. Data were analyzed using an exact contingency table.

Exploring the reasons for promoting natives. For papers (both journal and *GRSC*) that promoted the use of native plants on green roofs, we first categorized the reasons for using native plants as Aesthetic only, Scientific only, Aesthetic and Scientific, or no reason. Full descriptions of each reason and example quotes are found in Table 3.1. Aesthetic reasons generally focus on preserving a sense of local identity or blending with the surrounding landscape. Scientific reasons were further categorized as Adaptation, Habitat, Invasiveness, or Other scientific. The Adaptation argument posits that native plants are adapted to the local environment and consequently require less water, fertilizer and maintenance. The Habitat argument posits that native plants function as habitat for native fauna and serve to increase biodiversity. The Invasiveness argument posits that native plants are less likely than non-native plants to become invasive. All other scientific arguments were classified as 'Other scientific.' Categories were developed after an initial review of the literature and with guidance from Kendle and Rose (2000) and Gould (1997). For a paper that gave more than one reason, we included all reasons given and did not rank them. We hypothesized that career may affect the reasons for preferring natives. For example, one might assume that an architect or landscape architect is driven more by aesthetics than science while the opposite is true for a biologist. To test for this, we recorded the career of the first author for all papers. As described in Section 2.2, each paper was scored by two reviewers. Data were analyzed using an exact contingency table.

Evaluating the scientific evidence for the pro-native arguments. For all papers that discussed the use of native plants on green roofs, including those that expressed skepticism, we looked for quantitative results to support or refute each of the three primary scientific arguments: Adaptation, Habitat, and Invasiveness. We only included papers that provided sufficient information about the methods to understand the experiment conducted. We did not include papers or books in which only anecdotal evidence was provided. Despite thorough literature reviews, we only found papers addressing the Adaptation argument. For these papers, we recorded the conditions under which the experiment took place (sun exposure, irrigation, depth of growing media) and recorded the percent survival of the native and non-native plants tested.

Results

Determining the prevalence of the pro-native sentiment and the influence of career. We identified 360 papers written about green roofs (103 journal papers, 257 *GRSC* papers). Of these, 89 papers (25%) promoted the use of native plants on green roofs (20 journal papers, 69 *GRSC* papers, Table 3.2). Career had a significant effect on the likelihood of promoting natives ($\chi^2 = 18.7$, df = 4, p = 0.001). Architects were the most likely to promote natives (44% of papers) and engineers were the least likely (7% of papers). Landscape architects and biologists were intermediate.

Determining how authors defined the term 'native'. Only 55% of papers provided a definition of native (Fig. 3.1). Career did not have a significant effect on the choice of definition (Exact test, $p = 0.16$). Among architects, only 36% papers provided a definition. For landscape architects and biologists, geographically-based definitions were the most common and sometimes included a biome component (Fig. 3.1). Both across and within careers, there was a great deal of variability in definition, ranging from the building site (Burke, 2003) to a country (Grau et al., 2005).

Exploring the reasons for promoting natives. 73% of papers provided a scientific reason for promoting natives (Fig. 3.2). Career had a near-significant effect on the choice of reason (Exact test, $p = 0.059$). Architects and landscape architects frequently used both a scientific and an aesthetic reason, while most biologists used only scientific reasons. Of the three scientific reasons, Adaptation and Habitat were commonly used but Invasiveness was seldomly used (Fig. 3.3). Biologists were the most likely to provide an alternative scientific reason, such as increased transpiration (Mankiewicz and McDonnell, 2006; Ranalli et al., 2008). Only two papers used a reason that could not be categorized as either scientific or aesthetic. Both papers referenced regulations requiring the use of native plants in landscaping projects (Appl, 2007; Cabugos et al., 2007). 20% of papers did not provide a reason; this was similar across the three careers (Fig. 3.2).

Evaluating the scientific evidence for the pro-native arguments. Of the three main scientific reasons—Adaptation, Habitat, Invasiveness— we only found papers addressing the Adaptation argument (Table 3.3). We identified four journal papers and six *GRSC* papers that both explained their experimental methods and presented quantitative data regarding the survival and growth of native plants on green roofs (Table 3.4). Of the seven papers that directly compared the survival of both native and non-native plants on shallow soil, non-irrigated green roofs, all seven papers found higher survival of non-natives. Supplemental irrigation increased survival of natives (Schroll et al., 2009; Bousselot et al., 2009) as did shading (Licht and Lundholm, 2006). Lundholm et al. (2009) found high survival of 11 native plants on a green roof in Nova Scotia after two years of growth. From Table 3.4, it may appear that non-natives always outperform natives but it is important to look at the types of plants tested in these papers. For the most part, plants assigned to the non-native category were succulents, such as *Sedum*. Plants assigned to the native category tended to be grasses and herbaceous plants. A comprehensive review of plant performance on green roofs in North America is beyond the scope of this study, but such details can be found in Dvorak and Volder (2010).

While we did identify ten papers focusing on the habitat potential of green roofs (Bauman, 2006; Brenneisen, 2004; Brenneisen, 2006; Clark and MacArthur, 2007; Coffman and Davis, 2005; Coffman, 2007; Gedge and Kadas, 2004; Kadas, 2006; Lundholm et al., 2009, MacIvor and Lundholm, 2010), these experiments did not directly compare the habitat quality of native vs. non-native plants and thus will not be discussed in this paper. We found no papers that explored the potential for non-native green roof plants to become invasive.

Discussion

In this review, we identified the number of green roofs planted with native species, the prevalence of the pro-native sentiment, and the reasons for promoting the use of native plants on green roofs. Architects were the most likely to promote native plants and engineers were the least likely (Table 3.2). Part of the difficulty in evaluating the effectiveness of native plants on green roofs stems from ambiguity in usage of the term "native." Nearly half (45%) of papers used the term without definition (Fig. 3.1). This we view as problematic. Although not included in this review, an advertisement by Jelitto Perennial Seeds embodies this sentiment (Jelitto, 2009). This advertisement appears in nearly every issue of the *Living Architecture Monitor* (the primary green roof trade magazine in North America); it shows a world map superimposed over an expanse of *Sedum*. The slogan below reads “Sedum Seed. Beautiful. Useful. Native…To the Planet.” A further complication is that a green roof is by definition a human-created landscape, so a plant simply cannot be native to this environment. The lack of a common definition of “native” is a barrier to clear scientific dialogue in the study of green roofs.

Both aesthetic and scientific reasons were given, although scientific reasons were far more common, regardless of career (Fig. 3.2). These results echo the findings of a study by Hooper et al. (2008) on opinions of practicing landscape architects in Utah regarding native plants in landscaping. This study found that aesthetics were a powerful motivating factor but that scientific reasons were also expressed. In our study, landscape architects and architects were more likely to provide aesthetic reasons, most of which were about creating a building that blended into the surrounding landscape (e.g. Appl, 2007). Of the three scientific reasons, Adaptation and Habitat were commonly used and Invasiveness was rarely used (Fig. 3.3).

The Adaptation argument posits that native plants are well-adapted to the environment in which they evolved and, as a result, they require less maintenance (water, fertilizer, pesticides) than non-native plants. While this is often true at ground level, this argument rarely applies on a rooftop. Water efficiency was one of the most commonly cited reasons for preferring natives (e.g. Williams, 2009), even though most native plants chosen for green roofs actually require more water than the traditional non-native *Sedums* (Carter and Butler, 2008; Durhman et al., 2006; Monterusso et al., 2005; Rowe et al., 2006). Even the critically aclaimed green roof atop the California Academy of Sciences is irrigated with potable water (Kephart, 2009). Alan Good, the landscape exhibits supervisor for the California Academy of Sciences was quoted in a 2009 article in *Landscape Architecture* “If you let it go [without water] for two days, even in April, there will be a lot of dieback; the leaves will shrivel up.” (McIntyre, 2009). This occurs despite the fact that native plants were chosen to “thrive with little water” and “flourish in Golden Gate Park’s climate” (California Academy of Sciences, The Living Roof).

There are, of course, examples of green roofs that have successfully incorporated native plants into the design. Most famously are the four buildings at the Wollishofen water plant in Zurich, Switzerland. Built in 1914, these roofs were covered with 5 cm of gravel and 15 cm of local topsoil (Brenneisen, 2006). After 90 years, 175 plant species have colonized the roofs (Landolt, 2001 as cited by Brenneisen, 2006). While this is an impressive number, it does not mean that all native plants thrived on the roofs. Presumably, there were many other plant species that colonized the roof but were unable to establish. Another example is the Church of Jesus Christ of Latter Day Saints Conference Center in Salt Lake City, Utah, which is planted with 34 native plant species. Many of these plants survived and thrived (Dewey, 2004). In both of these examples, it’s important to consider the design characteristics of the green roof. The local topsoil used on the Wollishofen roofs likely has a greater water-holding capacity than the growing media used on most modern green roofs. Furthermore, impeded drainage on the roofs led to areas of moist soil, allowing more mesic plant species to establish (Brenneisen, 2006). The Church of Jesus Christ of Latter Day Saints Conference Center green roof’s growing media is 1 m deep and the roof is irrigated (Dewey, 2004). It is likely that the death of native plants on green roofs is far more common than can be gleaned from published papers, since ‘negative’ results are often suppressed in scientific literature (Dwan et al., 2008; Easterbrook et al., 1991).

While a blanket statement of "natives are better adapted," is overly simplistic, it does make sense to look within a given geographic region for an ecosystem with characteristics similar to a green roof. Lundholm (2005) uses this "habitat template" approach in Nova Scotia, looking to nearby coastal barrens which have rocky, low-fertility soils similar to those found on a green roof. Greater attention to this approach will result in a larger palette of plant species suited for use on green roofs and can allow green roof designers to create green roof plant communities which reflect the diversity of the surrounding environment.

The Habitat argument posits that native plants co-evolved with other native species (herbivores, pollinators, predators) and thus will provide higher quality habitat than non-native plants that did not co-evolve with these species. This argument was used with relatively equal frequency by architects, landscape architects, and biologists (Fig. 3.3). We found no papers that directly compared the habitat value of native plants as compared to non-native plants on green roofs. It is likely that native plants will be better hosts for herbivores and their avian predators (Tallamy, 2007) but this has not been examined. However, recent work on pollinator diversity in urban areas shows that native pollinators can use flower resources of non-native plants (Matteson et al., 2008). Future research should focus on quantifying abundance and diversity of both invertebrates and vertebrates on green roofs of different ages, sizes, designs, and plant species composition. Furthermore, special attention should be paid to how animals are using a green roof. Are certain plant species used more than others? Could the habitat value be improved by adding nesting boxes or including several distinct types of microhabitats within a single green roof?

The Invasiveness argument posits that native plants are less likely than non-natives to become invasive. Only six of the 89 pro-native papers referenced the risk of non-native plants becoming invasive. There was no effect of career on the likelihood of using this reason. We found no papers that compared the potential of native or non-native plants used on green roofs to become invasive in the surrounding area. Presumably, the traits that allow survival in the harsh conditions of a green roof (e.g. tolerance of drought and extreme temperatures) are likely very different from those that allow success as an invader (e.g. rapid growth in disturbed habitats).

Of the 89 papers promoting the use of native plants on green roofs, very few expressed any skepticism toward the idea and this varied by career. Only one of the 14 architects expressed skepticism (Russell and Schickedantz, 2003) compared to four of the 17 landscape architect papers (Dvorak and Volder, 2010; Kohler, 2009; McGlade, 2004; Pearce, 2003) and 11 of the 34 biologist papers (Bousselot et al., 2009; Bousselot et al., 2010; Durhman et al., 2004; Durhman et al., 2006; Getter and Rowe, 2006; Lundholm et al., 2009; Monterusso et al., 2005; Rowe et al., 2005; Schroll et al., 2009; White and Snodgrass, 2003; Williams et al., 2010). The group that was the most likely to promote the use of native plants on green roofs (architects) was also the least skeptical group. It is encouraging that most of the recent books about green roofs include a more thorough discussion of natives and acknowledge that not all natives are suitable for life on a roof (Cantor, 2008; Dunnett and Kingsbury, 2004; Luckett, 2009; Snodgrass and Snodgrass, 2006; Snodgrass and McIntyre, 2010; Weiler and Scholz-Barth, 2009; Werthmann, 2007). Snodgrass and McIntyre's (2010) *Green Roof Manual* devotes 17 pages to a carefully-constructed discussion on the use of native plants on green roofs (pp. 190-207). In contrast, Earth Pledge's (2005) *Green Roofs: Ecological Design and Construction* begins with an uncompromisingly rosy view of native plants, stating that "flowering and native plants help cool the urban landscape and combat the pollinator crisis in our region" (p. 9). Native plants are mentioned in 11 of the 40 building case studies presented in the book.

The results of this review underscore the ubiquity of the pro-native argument as well as a lack of consensus on how to define "native" and why native plants should be preferred over non-native plants. This is not merely an academically interesting trend. In the current draft of the Sustainable Sites Initiative, a developer can earn points by using native plants in the landscaping (Credit 4.7). In SSI, landscaping includes all non-building pieces of the site, such as gardens, permeable pavement, green roofs, green walls, rain gardens, stormwater wetlands. Points are earned based on function, not the structure. For example, a project can earn 5-10 points for Credit 3.5 "Manage stormwater on site." The guide does not specify how this must be done, so conceivably the points could be earned by installing a green roof. This could easily lead to a new standard of green roof construction that only allows native plants. The results of this literature review underscore the potential problems that could result from this decision.

Conclusions and recommendations

These findings make clear that the industry needs to take a critical look at the use of native plants on green roofs. The design professions, primarily architects and landscape architects, are largely responsible for bringing green roofs to North America. Their pioneering efforts were undertaken largely without benefit of supporting research, and we have seen truly remarkable developments in green roof design in the past decade. The research, however, has not yet caught up with design. An example of this can be found in the 2008 book *Green Roofs in Sustainable Landscape Design*. Cantor, a landscape architect, devotes 19 pages to a discussion of the value of integrated design teams (pp. 40-59), but less than half a page to the importance of evaluating performance of a green roof after it is constructed (p. 59). We certainly do not seek to diminish the great progress made by the design professionals. Rather, we seek to encourage more scientists to engage in green roof research. We suggest two styles of experiments that could be especially useful as we move forward. The first is what Felson and Pickett (2005) call a 'designed experiment' or a scientific experiment that is incorporated into an architectural design or other constructed environments. An example of this kind of experiment is the Jordan Cove watershed project in Waterford, CT (Felson and

Pickett, 2005). A single residential subdivision was divided into two plots. One functioned as the control treatment, with traditional stormwater management structures. The second functioned as the experimental treatment and included numerous innovative stormwater best management practices. By planning the experiment during the design process, the project had much more potential to generate useful data. The second type of experimental design is citizen science. An example of this is the Audubon Society's Christmas Bird Count, begun in 1900 (National Audubon Society, Christmas Bird Count). Each year, citizen scientists across North America survey bird populations in their area. The data are then compiled and made available to the public and to researchers. Data from these surveys has resulted in hundreds of peer-reviewed journal articles (National Audubon Society, Christmas Bird Count Bibliography of Scientific Articles). This technique could be applied to green roofs in that researchers could train building occupants or maintenance personnel to collect data on plant performance and insect diversity. Data from several green roofs could be pooled to better inform design.

Finally, there needs to be more attention to the dissemination of knowledge on plant performance. We need to know what plants thrive and die to avoid making the same mistake repeatedly. With the blossoming of social networking sites, it is very easy to connect with colleagues and share ideas online. Currently, there exist two online forums for sharing information with a broad audience. Greenroofs.com hosts a green roof project database and there are currently over 1000 projects listed. Many include descriptions, photos, contact information for the designers, and links to external websites. In addition, Capitol Greenroofs created a social networking website for green roof professionals. Since its creation in February 2008, over 1500 people have joined and a number of lively discussions have taken place. These types of forums are especially important for green roof practitioners who do not publish in academic journals. By encouraging more scientific research on green roof plant communities and the open sharing of ideas and findings, the North American green roof industry can make great progress and gain a better understanding of how to create beautiful, functional green roofs.

Table 3.1. Summary of reasons used for promoting the use of native plants on green roofs.

Reason		Description	Example of this idea applied to green roofs	Potential problems
Aesthetic		Native plants provide a sense of place and blend into the natural landscape.	"Bedrock bluff plants native to Minnesota…are shown conceptually emerging out of the European green roof technology foundation… Limestone rocks, simulating bedrock bluff prairie outcroppings, add to the metaphor of the bedrock bluff prairie green roof." (MacDonagh et al., 2006)	Evaluation by this criteria is driven largely by personal preference and opinion.
Scientific	Adaptation	Native plants are adapted to the local environment and consequently require less water, fertilizer, maintenance.	"Planting indigenous plant materials adapted to similar environmental conditions use minimal amounts of water..." (Kephart, 2005)	A roof is not a native environment. Plants did not evolve in a rooftop environment. Thus, they may not be suited to life on a roof.
	Habitat	Native plants function as habitat for native fauna and serve to increase biodiversity.	"Incorporating regionally native plants into a green roof can help to replace habitat removed by urban development, encourage biodiversity and help provide ecological niches for arthropod and avian species that depend on these native plant taxa." (Bousselot et al., 2009)	This depends largely on the type of plant. For example, a native grass will not provide pollen and nectar resources to a native bee.
	Invasiveness	Native plants are less likely to become invasive than non-native plants.	"The focus on native plants in this application exploits the existing characteristics of climatic adaptation, which may help to reduce total water and nutrient demand, and avoid problems associated with the introduction of potentially invasive species." (Simmons and Gardiner, 2007)	Only a very small number of non-native plants become invasive.

Table 3.2. Papers (journal and *GRSC* conference) written about green roofs and the proportion of those that promote the use of native plants on green roofs. Papers are categorized by the career of the first author; only the four most common careers are listed individually.

Career	Total papers	Pro-native papers	Percent pro-native
Architect	32	14	44%
Landscape arch.	50	17	34%
Biologist	110	34	31%
Engineer	75	5	7%
Other / unknown	93	19	20%
Total	*360*	*89*	*25%*

Table 3.3. The number of papers that used each of the three most common scientific reasons (Adaptation, Habitat, Invasiveness) to promote the use of native plants on green roofs. The number of papers that conducted an experiment to test the validity of each reason. The subset of those papers that had results that supported that reason.

	Number of papers		
	Used	Tested	Supported
Adaptation	40	10	1
Habitat	35	0	0
Invasiveness	6	0	0

Table 3.4. Overview of survivorship of native and non-native plants on green roofs in sun and shade, with and without irrigation. Only papers with a clear methods section and quantitative data were included.

Source	Full sun: No irrigation, Native	Full sun: No irrigation, Non-native	Full sun: Irrigation, Native	Full sun: Irrigation, Non-native	Shade: No irrigation, Native	Shade: No irrigation, Non-native
Bousselot et al. 2009			100 %	100 %		
Carter and Butler 2008	0 %	31 %				
Durhman et al. 2006	0 %	100 %				
Licht and Lundholm 2006	13 %	100 %			78 %	100 %
Lundholm et al. 2009	100 %	n/a				
Martin and Hinckley 2007			14 %	n/a		
Monterusso et al. 2005	22 %	100 %				
Rowe et al. 2006	17 %	100 %				
Schroll et al. 2009	20 %	100 %	100 %	100 %		
Wolf and Lundholm 2008	10 %	75 %	100 %	100 %		

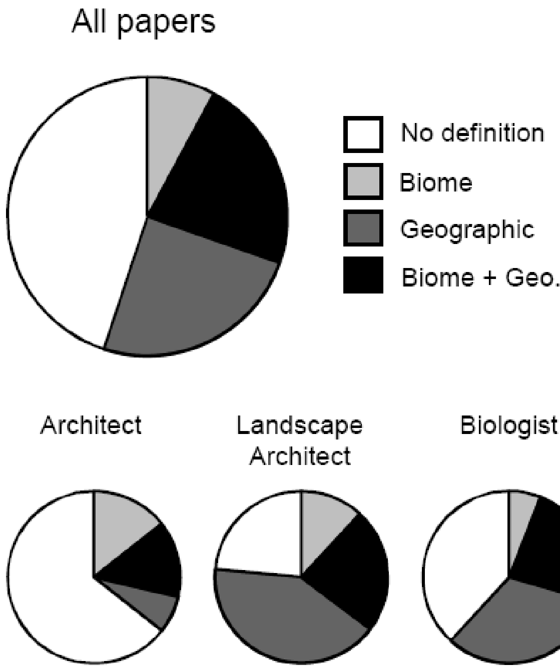


Figure 3.1. Definition of native provided by papers promoting the use of native plants on green roofs. The large panel shows the total number of papers promoting natives (n=89). The smaller panels show the breakdown for the three most common careers. Each paper was classified as No definition, Geographic, Biome, or Geographic + Biome.

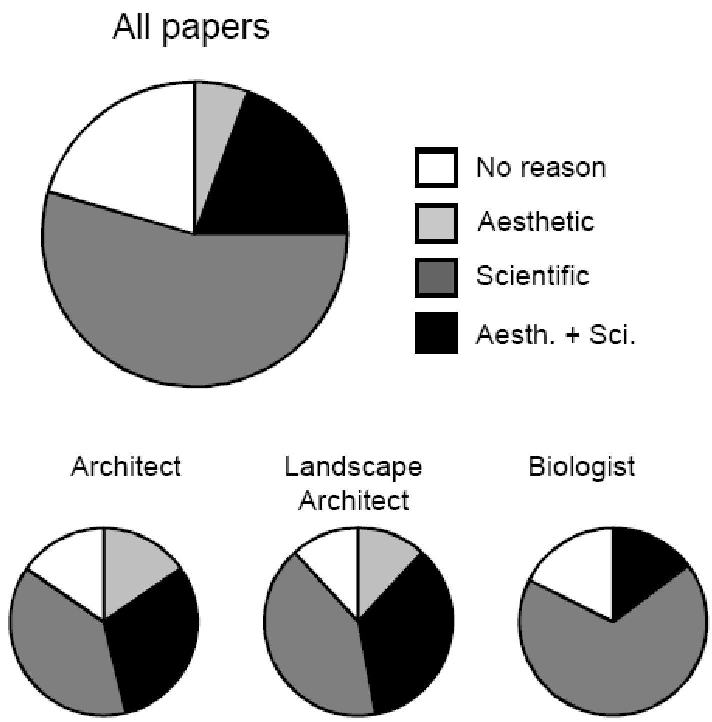


Figure 3.2. Aesthetic and scientific reasons for using native plants on green roofs. The large panel shows the total number of papers promoting natives (n=89). The smaller panels show the breakdown for the three most common careers (architects n=14, landscape architects n=17, biologists n=34). Papers were classified as providing a scientific reason, an aesthetic reason, both scientific and aesthetic reasons, or no reason.

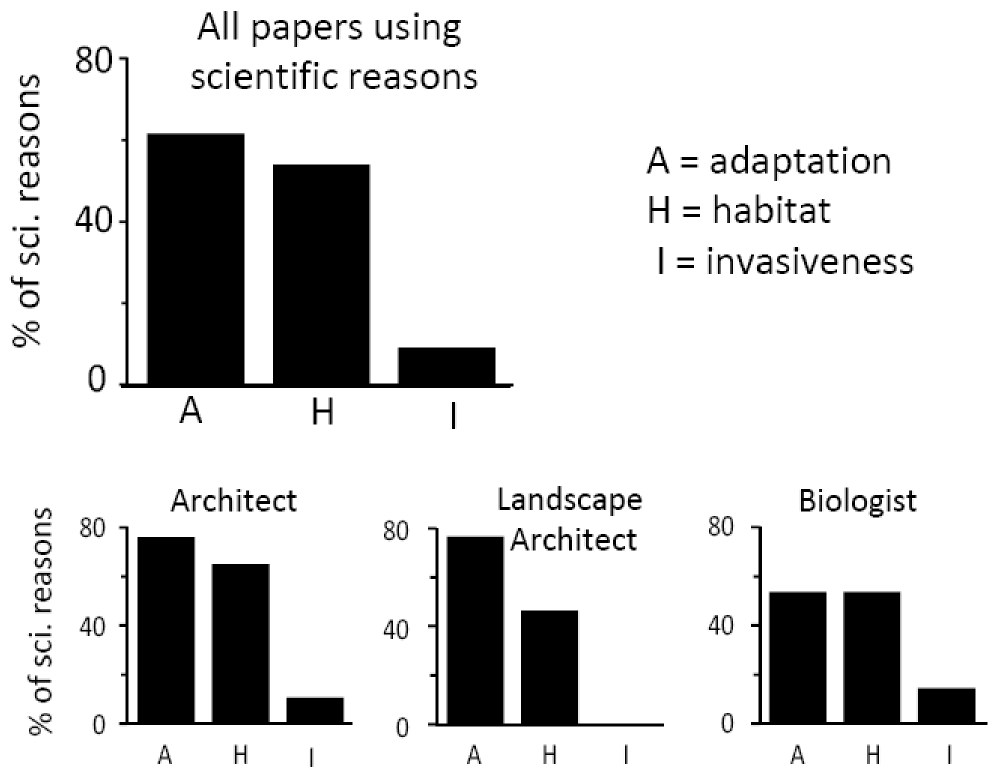


Figure 3.3. Scientific reasons for using native plants on green roofs. The large panel shows the total number of papers that used scientific reasons to promote natives (n=65). The smaller panels show the breakdown for the three most common careers. Each bar graph depicts the commenness of the three main scientific arguments as a percent of all scientific reasons. Some papers provided more than one reason, so percents within a career do not sum to 100.

CHAPTER 4
Sedum facilitates the growth of neighboring plants on a green roof under water-limited conditions

Abstract

Sedum species are important green roof plants because of their tolerance of high temperatures and drought conditions. There is, however, increasing interest in using a broader palette of plants to maximize the habitat value of green roofs. In some systems, such as deserts, stress tolerant plants can act as nurse plants by facilitating the growth and survival of neighboring plants. Similarly, we hypothesized that *Sedum* can increase the performance of less stress-tolerant plants, thus increasing plant diversity. Using a green roof at Tufts University, we tested the effect of *Sedum album* on the growth and survival of *Agastache rupestris* (Lamiaceae) and *Asclepias verticillata* (Asclepiadaceae) during natural wet and dry periods. We found that the effect of *S. album* on the performance of neighboring plants was species specific and depended on water availability. When water was limiting, *S. album* acted as a facilitator; in contrast, when water was abundant, *S. album* acted as a competitor. In conclusion *Sedum* can facilitate the growth of neighboring plants during water stress and may allow less tolerant plants to thrive.

Introduction

Sedum species (Crassulaceae), because of their tolerance of stress, are the most extensively planted species on green roofs. Recent interest in habitat conservation and biodiversity has led to a rejection of the traditional monoculture of *Sedum* in favor of green roofs with greater plant diversity (Oberndorfer et al., 2007). Unfortunately, few plant species are well suited to life on a green roof (Dunnett and Kingsbury, 2004; Monterusso et al., 2005; Durhman et al., 2006; Rowe et al., 2006; Martin and Hinckley, 2007; Carter and Butler, 2008). For example, Monterusso et al. (2005) monitored the growth and survival of drought-tolerant Michigan native prairie species on an extensive green roof in Michigan. Of the 18 species surveyed, only two had high survival during the three year experiment. Similarly, we surveyed growth and survival of a wide range of drought-tolerant plants (19 species total, representing 12 plant families) on a green roof in Massachusetts and found high mortality for all but one of the non-*Sedum* species (Carter and Butler, 2008).

Clearly, few plants are able to survive and grow on green roofs. While using deeper substrate or supplemental water can increase the diversity of plants, these strategies are generally not effective or practical for retrofitted or inaccessible green roofs. Are there other ways to increase the palette of green roof species? In desert systems, some drought tolerant shrubs, called nurse plants, actually facilitate the growth of neighboring plants, such as Saguaro cactus seedlings, by cooling the soil and creating a favorable microclimate (Turner et al., 1966; Franco and Nobel, 1989). The effect of the nurse plant on soil moisture is more complicated—by cooling the soil, there will be less evaporation from the soil surface but depending on the root structure and water demand of each species, root competition for water may occur (Turner et al., 1966; Franco and Nobel, 1989). It has repeatedly been shown that water deficit is a major cause of mortality of non-*Sedum* green roofs plants (Monterusso et al., 2005; Martin and Hinckley, 2007; Carter and Butler, 2008). Perhaps *Sedum* could act as a nurse plant and increase survival and growth of neighboring plants during periods of water deficit.

The concept of interspecies facilitation in plant communities has been studied in many habitats, including deserts (Franco and Nobel, 1989; Holzapfel and Marshall, 1999), salt marshes (Bertness and Shumway, 1993; Bertness and Hacker, 1994), alpine meadows (Chu et al., 2008), and cobble beaches (Bruno, 2000; Goldenheim et al., 2008). To the best of our knowledge, this is the first study on the role of facilitation in green roof plant communities. With high substrate and air temperatures, high irradiance, and rapid substrate drying, a green roof in summer qualifies as a harsh environment.

In this study we conducted three experiments to test the hypothesis that *Sedum* can facilitate the growth and survival of non-*Sedum* plants that might not otherwise be able to persist on a green roof. First, we grew two species of potential green roof plants with and without *Sedum album* to measure the effect of *S. album* on growth and survival of these plants. Second, we directly measured substrate temperature in modules with and without *Sedum* to determine if *Sedum* species reduce peak substrate temperature. Finally, we grew *S. album* by itself and with green graminoid plastic plants to see if shading by a competitor would decrease its growth.

Methods

Study Site and Green Roof Design. These experiments were conducted on the Tisch Library Green Roof at Tufts University in Medford, Massachusetts between June and October 2008. This experimental green roof was created in June 2007 using a modular green roof system. Modules were made of black plastic with dimensions 38 cm x 38 cm. They were arranged on the green roof in rows of four (Fig. 4.1). Because the modules were black, those along the edge of the plots absorbed heat such that the substrate along the edge reached high temperatures (up to 50 °C). To minimize heat absorbance, the sides of the outside modules were covered with light blue duct tape. In addition, the outside rows of modules were planted with *Sedum* and treated as an unsampled border row (Fig. 4.1). Experimental modules were positioned randomly within a single plot. Modules and contained a 13 cm deep layer of substrate composed of a blend of 55:30:15 expanded shale aggregate, USGA sand, leaf compost, with a field capacity of 0.35 cm^3 water / 1 cm^3 substrate (purchased from Read Custom Substrates; Canton, MA). *Sedum* species were planted on the green roof in July 2007. The other experimental plant species (described below) were planted on the green roof during the first two weeks of June 2008. Within a week of planting, controlled release fertilizer (Scott's Osmocote Plus 15-9-12) was mixed into the top 2 cm of the substrate at a concentration of 3.6 g fertilizer per liter substrate. Before the experiment began, we created a watering schedule in which plants would be watered every 2 days for the first week after planting and then watering frequency would be decreased over the course of the first month. After this point, plants would only receive supplemental water after two weeks without rain, at which point they would be watered once every five days until the next rain event. This watering schedule was modified slightly in that watering was terminated early (June 22, 2008) due to frequent rain. All plants were watered on August 29, 2008 after 13 days without rain and again on September 4, 2008 after an additional 5 days without rain. Weather data were acquired (courtesy of Weather Underground) from a Davis Vantage Pro 2 weather station in Medford, Massachusetts (Lat: N 42 ° 24 ' 55 ", Lon: W 71 ° 6 ' 41 "), approximately 1 km from the Tisch Library Green Roof.

Experiment 1. Sedum's effect on the growth and survival of neighboring plants

To test the hypothesis that *Sedum* can increase the survival of neighboring plants, we studied the growth of two focal species with and without *Sedum album. S. album* was chosen because it has high growth and survival in green roof habitats (Dunnett and Kingsbury, 2004; Monterusso et al., 2005; Durhman et al., 2006; Rowe et al., 2006; Carter and Butler, 2008). In addition, we observed during the summer of 2007 that this species has a relatively shallow, ephemeral root system as compared to congeners commonly grown on green roofs (Butler, personal observation 2007). We expected that these traits would minimize belowground competition.

Our two focal plants were *Agastache rupestris*, or licorice mint, (Lamiaceae) and *Asclepias verticillata*, or whorled milkweed, (Asclepiadaceae) (purchased from North Creek Nurseries; Landenberg, PA). Both species are herbaceous perennials, commonly used landscape plants and not considered invasive (USDA; Kemper Center). *A. rupestris* is native to mountain slopes in the southwestern United States (Kemper Center) and *A. verticillata* is native to prairies and open meadows throughout most of the United States (Missouri Plants). These plants were chosen for the following three reasons: 1) they are long-flowering and commonly visited by insect pollinators (Kemper Center; Missouri Plants), 2) they showed fast growth and relatively high drought tolerance during the previous summer (Carter and Butler, 2008), and 3) they both have an upright growth form, which could minimize aboveground competition for light.

Treatments. For each species, there were three cover treatments, each of which had 10 replicate modules. Each module contained five individuals (landscape plugs) of a focal species, either *A. rupestris* or *A. verticillata*. The control treatment was a focal species grown alone (Control). The experimental treatment was *Sedum album*, in which the focal species were planted into modules that already contained *S. album*. We hypothesized that *S. album* would decrease peak substrate temperatures. If this is true, one potential mechanism could be increased reflectance of green leaves as compared to dark-brown substrate. To test the effect of surface color on substrate temperature, we used a second control treatment in which the substrate around the focal species was covered with a layer of green shredded cellophane enclosed in plastic mesh bags (hereafter referred to as Green Cellophane). Green Cellophane was added to modules within two weeks of planting.

Measurements. Mortality was estimated four times during the summer (July 2, July 16, August 14, September 16, 2008) based on the presence or absence of living aboveground tissue. If a plant was previously assumed dead and began to grow, we counted it as alive for all prior measurements. Growth was measured in two ways: percent plant cover and biomass. By using both of these measurements, we were able to look at both short-term and long-term effects of cover treatment and weather on growth. Between June 19 and November 14, 2008, we took weekly overhead photos of each module. Data presented in this paper are from June 19 to September 24, 2008 since no further growth was detected after that time. Using these photos, percent plant cover was measured using one of two methods: ImageJ image analysis software (NIH) or visual estimation. When possible, we calculated plant cover with ImageJ. When this was not possible, due to the presence of flowers or neighboring plants or the quality of the photograph, we estimated percent cover visually to the nearest 5% using the overhead photographs. All visual estimates were performed in random order by the same observer on two separate occasions. To increase accuracy and reliability, we used both methods to measure percent plant cover of a subset of images. Results from both methods were generally within 5% of each other. Percent cover data measured after harvest was adjusted to account for the cover lost by experimental manipulation. We harvested one plant (shoots and roots) of *A. rupestris* and *A. verticillata* from a subset of modules (n = 8) on September 4, 2008. To avoid confounding position effects within a module, we harvested the individual in the southeastern corner of each module. After harvest, plants were immediately moved to moistened sealed plastic bags. Within one hour of harvest, plants were moved to a refrigerator at 4-5°C. Before weighing, plants were washed to remove insects and substrate and then blotted dry. Fresh mass was measured separately for shoots and roots. Plants were then dried at 50°C to constant weight. Dry mass was then measured separately for shoots and roots. We hypothesized that plants grown with *S. album* would allocate more biomass to roots because of increased root competition.

Data processing and calculations. To look at the effect of *S. album* on growth of focal species under different environmental conditions, we divided the summer into four time periods based on precipitation. Because a green roof has only a thin layer of substrate with a low water-holding capacity, the number of days between rain is a better predictor of growth than total volume of rain. We identified an early season wet period (June 19 – July 2), an early season dry period (July 2 – 21), a late season wet period (July 21 – August 19), and a late season dry period (August 19 – September 8). During the early season wet period (June 19 – July 2, 2008), plants received water at least every other day from rain and supplemental water. During the early season dry period (July 2 – 21, 2008), there was a 9-day period with less than 0.5 cm rain (Fig. 4.3a). While this is not unusual for the region, we expected that this length of time could cause drought stress for *A. rupestris* and *A. verticillata*, based on growth data collected for these species at the same site during the previous summer (Carter and Butler, 2008). During the late season wet period (July 21 – August 19, 2008), 50% of the days had rain greater than 0.2 cm. The longest time between rain events was three days. During the late season dry period (August 19 – September 8, 2008), there was an almost rain-free (0.13 cm total rain) period of 21 days (beginning August 16, 2008). As described in the methods, all plants were watered on August 29 after 13 days without rain and on September 4, 2008 after an additional 5 days without rain. Daily high temperature was highest during the early season dry period (29.6 ± 3.4 ^{o}C) and similar for the other three time periods (early season wet: 27.3 ± 2.7 ^{o}C, late season wet: 26.3 ± 3.0 ^{o}C, late season dry: 26.3 ± 2.1 ^{o}C). Each time period begins and ends on a day when overhead photographs were taken. For each time period, we calculated a modified version of relative growth rate using percent plant cover data as shown below (Equation 1):

$$\text{Relative Growth Rate} = \left(\frac{\text{Final} - \text{Initial Percent Plant Cover}}{\text{Initial Percent Plant Cover}}\right) \div \text{Number of Days} \qquad (1)$$

Experiment 2. Sedum's effect on substrate temperature

To determine the effects of *S. album* and green cellophane on substrate temperature, we measured substrate temperature of a subset of modules from Experiment 1 (two randomly chosen modules per species per treatment). In addition, we measured substrate temperature in modules with substrate only and in modules planted with one of four *Sedum* species: *S. album*, *S. rupestre*, *S. sexangulare*, and *S. spurium* (purchased from Emory Knoll Farms; Street, MD). Substrate temperature data were collected every 30 minutes from July 29 to August 19, 2008 and again from September 3 to October 6, 2008 using ibutton temperature data loggers (Maxim ibutton high capacity temperature logger DS 1922L) enclosed in watertight petri dishes. Each module contained one data logger, which was buried in the center of the module 5 cm below the surface. Data shown in this paper are from August 1, 2008. This date was chosen because it had the highest substrate temperatures.

Experiment 3. Effect of shading by neighbor plants on Sedum's growth

In addition to testing the effect of *S. album* on the performance of neighboring plant species, we also investigated the potentially negative effect of shading by neighboring plants on *S. album*. We expected that shade would decrease growth of *S. album* because this species is considered to be intolerant of shade (Dave's Garden; Emory Knoll Farms; Kemper Center; Plants for a Future). To look at the effect of shading independent of root competition, we grew *S. album* in modules with and without green graminoid plastic plants. Shaded modules contained two tufts of plastic plants, which were similarly sized to fully-grown *A. rupestris* or *A. verticillata*. Percent plant cover was measured on June 19 and again on October 31, 2008 using overhead photographs.

Statistical Analyses. A two-way ANOVA was conducted to assess the effect of cover treatment and focal species on survival. The same test was used to assess the effect of cover treatment and focal species on total dry mass and relative root mass (percent of total dry mass). A repeated measures ANOVA, with Greenhouse-Geisser correction, was conducted to assess the effect of cover treatment and focal species on percent cover throughout the summer. For each species at each of the seven sampling dates, a one-way ANOVA was conducted to assess the effect of cover treatment on percent plant cover. A repeated measures ANOVA, with Greenhouse-Geisser correction, was conducted to assess the effect of cover treatment and focal species on relative growth rate. For each species within each time period, a one-way ANOVA, followed by a Tukey HSD post-hoc, was conducted to assess the effect of cover treatment on relative growth rate within a single time period. A two-way ANOVA was conducted to assess the effect of cover treatment and focal species on maximum substrate temperature on August 1, 2008, followed by a Tukey HSD post-hoc to test for differences across cover treatments. The effect of shading on *S. album* percent cover was determined using a two-tailed t-test.

Results

Experiment 1. Sedum's effect on the growth and survival of neighboring plants

We expected that in periods of water deficit, *S. album* would increase growth and survival of the focal species. In periods of abundant rain, we expected that *S. album* would act as a competitor, decreasing growth of the focal species. Because of root competition during these wet periods, we expected that plants grown with *S. album* would allocate more mass to roots than plants in the control and Green Cellophane treatments. *S. album*'s effect on growth of neighboring plants was species-specific and weather dependent. Both focal species had high survival and there was no effect of cover treatment on survival (Table 4.1a). Both species achieved higher coverage and greater biomass when grown alone compared to plants grown with *S. album* (Table 4.1a, Table 4.2, Fig. 4.2). Plants grown with *S. album* did not allocate more mass to roots, but *A. verticillata* allocated a higher percentage of mass to roots than *A. rupestris* in all treatments (Table 4.1a). Percent plant cover data suggest that *S. album* facilitates growth of *A. rupestris* and *A. verticillata* during dry periods (Fig. 4.2). *S. album* decreased growth of *A. rupestris* when water was abundant, but increased growth when water was limiting. *S. album* generally slowed growth of *A. verticillata*. Green Cellophane resulted in growth similar to control plants across most time periods, except in Late Season Wet, in which it slowed growth of both species (Fig. 4.2c).

Experiment 2. Sedum's effect on substrate temperature

As predicted, all *Sedum* species reduced peak substrate temperature (Fig. 4.3a). On August 1, 2008, *Sedum* species reduced peak substrate temperature by 5-8^{o}C as compared to modules with only substrate (Fig. 4.3a). Soil temperatures were similar for the four *Sedum* species tested. Surprisingly, Green Cellophane decreased peak substrate temperatures more than *S. album* (Table 4.1b, Fig. 4.3b).

Experiment 3. Effect of shading by neighbor plants on Sedum's growth

In contrast to our expected results, shading did not decrease the growth of *S. album* (Table 4.1c). On October 31, 2008, 19 weeks after the experiment began, both treatments had close to full coverage and there was no difference in plant cover between shading treatments.

Discussion

In this experiment, we investigated the potential for *Sedum* to facilitate the growth and survival of neighboring plant species on a green roof. We found that both facilitation and competition occur between *S. album* and the focal species. *S. album* had a net negative effect on maximum percent cover and total biomass accumulation for both focal species (Fig. 4.2, Table 4.1a, Table 4.2), presumably due to growth inhibition early in the summer when water was plentiful. In contrast, facilitation was important during dry periods. For both species, percent coverage dropped during dry periods, except when grown with *S. album*. Facilitation appeared to be especially important for *A. rupestris* later in the growing season (Fig. 4.2). Previous research has shown that plants respond differently to water deficit depending on season and developmental stage (Heschel and Riginos, 2005). In the annual, *Impatiens capensis*, early season drought caused the plant to adopt a drought-avoidance strategy, characterized by low water use efficiency and early flowering (Heschel and Riginos, 2005). In contrast, late season drought caused the plant to adopt a drought-tolerance strategy with high water use efficiency. In this experiment, both focal species were perennials, which may or may not cause a different response to drought. Because a perennial plant can reproduce multiple times in its lifetime, it may be advantageous to always have a drought-tolerance strategy. Such a strategy may decrease fitness in a single dry year, but it could maximize lifetime fitness because the plant is able to survive the drought and reproduce in the following years.

We hypothesized that *S. album* would facilitate the growth and survival of the focal species by decreasing peak substrate temperatures, similar to the effect of desert shrubs on seedlings of saguaro cacti (Turner et al., 1966; Franco and Nobel, 1989). While *S. album* did decrease peak substrate temperatures, it is unlikely that this mechanism alone accounted for the facilitation that occurred. Green Cellophane decreased peak substrate temperatures by up to 8°C (Fig. 4.3b) but, surprisingly, it did not have a positive effect on the growth of focal species during drought (Fig. 4.2). One possibility for this is that the shredded cellophane impeded upward growth of new stems. This was especially noticeable for *A. verticillata*, which had multiple stolons that grew outward from the main plant before producing new stems (personal observation). In nearly all of the modules with *A. verticillata* and green cellophane, we found shoots that had grown through the cellophane. It is unlikely that the cellophane impeded water infiltration into the substrate, although we did not measure this directly. It is also unlikely that the Green Cellophane treatment had any toxic effects on the plants because both materials used to construct these covers—mesh bath sponges (polyethylene) and shredded cellophane (primarily regenerated cellulose)—are products designed for human use and are classified as inert and non-toxic (Sweetman, 2009; BP Solvay, 2009). A potential mechanism for the positive effect of *S. album* is that *S. album* reduces water loss from the substrate. Due to transpiration, plants accelerate water loss from soil, but recent research has shown that pots planted with *Sedum acre*, a commonly used green roof species, actually retained more water than pots with substrate alone (Wolf and Lundholm, 2008). This surprising result is likely explained by the high degree of photosynthetic plasticity in *S. acre* and many of its congeners. These species can switch from C3 to CAM photosynthesis in response to water deficit (Earnshaw et al., 1985; Gravatt and Martin, 1992; Castillo, 1996). In CAM photosynthesis, stomata open at night to reduce water loss through transpiration. It has been hypothesized that *Sedum's* ability to switch between C3 and CAM photosynthesis is the reason for its success as a green roof plant (VanWoert et al., 2005; Durhman et al., 2006), allowing it to grow quickly when water is abundant (typical of C3) and survive drought (typical of CAM). This plasticity may also affect interspecies interactions. It is possible that facilitation will be most pronounced in a *Sedum* species that is primarily CAM, because it will use less water than a C3 congener, leaving more water available to its neighbor. Future studies should further investigate photosynthetic plasticity in green roof *Sedum* and the role that this may have on interspecies interactions.

Data collected in Europe and the United States suggest that green roofs can provide habitat for birds (Baumann, 2006), bees (Prelim data), spiders (Brenneisen, 2006), mites, beetles, grasshoppers, and butterflies (Coffman and Davis, 2005). Green roofs may be especially effective as refuges for both domestic honey bees as well as wild hymenopteran pollinators, many of which are able to thrive in fragmented habitats typical of urban areas (Fetridge et al., 2008). Wild bee populations are declining in North America (Colla and Packer, 2008) and Europe (Biesmeijer et al., 2006) – a phenomenon with massive economic costs, as the role of insect pollinators in agriculture has been valued at $217 billion worldwide (Gallai et al., 2009). Interspecies facilitation may provide an easy and low-cost method to reduce the abiotic stress of a green roof, which could expand the range of plants able to live in this habitat and consequently, increase the habitat value of this space for insects and other invertebrates. Thus, *Sedum* may have an important role in bio-diverse green roofs. Future studies should test for interspecies facilitation using additional focal species and additional *Sedum* species. In addition, long-term experiments over several growing seasons will help to elucidate interspecies dynamics within the green roof plant community.

Recent discussion of the habitat potential of green roofs has deteriorated into an oversimplified, highly polarized debate of *Sedum* versus natives. While the goal of this paper is not to contemplate the nuances of this debate, we would like to briefly discuss one of the most common reasons given for using native plants on green roofs, which is based on what Gould (1997) refers to as "the functional argument based on adaptation." The assumption is that in a given habitat, natives will better adapted than non-natives because they evolved in this habitat. This argument makes a great deal of sense in the context of a lush, green lawn in a desert. Plants that have evolved in this region, such as cacti and other succulents, are better adapted to this habitat than turf grass and will consequently require less maintenance. This logic, however, simply does not translate to a green roof. Because a green roof is, by definition, a human-created habitat, a plant cannot be native to or adapted to this habitat. We recommend that green roof designers continue to be cautious with plant choice to prevent the introduction, establishment, and spread of invasive species. Some of the most notorious invasive plants are ornamentals, such as purple loosestrife (Swearingen, 2009b), water hyacinth (WSDoE, 2009), and english ivy (Swearingen, 2009a). However, we believe that by moving away from a reflex response of "natives good, non-natives bad" we will achieve greater success in creating bio-diverse, ecologically valuable green roofs. We hope that the interspecies facilitation described in this paper encourages a similar approach among green roof enthusiasts on both sides of the *Sedum*-native debate.

Table 4.1 Significance of experimental factors on plant performance and substrate temperature.

a) *Sedum*'s effect on neighboring plants: Survival (n = 10), total dry mass (n = 8), and relative root mass (n = 8) data were analyzed using a two-way ANOVA with cover treatment and focal species as the main effects. Percent cover and relative growth rate (n = 10, except n = 4 for *A. rupestris* Green Cellophane, n = 7 for *A. verticillata* Green Cellophane) were analyzed using a two-way repeated measures ANOVA with a Greenhouse-Geisser correction. The main effects were cover treatment and focal species and the repeated measurements were sampling date (Date) and growth period (Period) respectively.

b) *Sedum*'s effect on substrate temperature: High substrate temperature on August 1, 2008 (n = 2) was analyzed using a two-way ANOVA with cover treatment and focal species as the main effects.

c) Effect of shading on *Sedum*: Percent plant cover on June 19 and October 31 (n = 10) was analyzed using a two-tailed t-test with shading as the independent variable.

a)

Survival (Aug 14)	**df**	**F**	**p**
Cover	2	2.35	ns
Species	1	3.13	+
Cover * Species	2	0.78	ns

Total dry mass (Sept 4)			
Cover	2	11.49	***
Species	1	3.52	+
Cover * Species	2	0.31	ns

Relative root mass (% of total dry mass)			
Cover	2	0.05	ns
Species	1	19.21	***
Cover * Species	2	0.44	ns

Percent cover (7 dates)			
Date	2.15	84.01	***
Date * Cover	4.31	11.40	***
Date * Species	2.15	13.72	***

Relative growth rate (4 growth periods)			
Period	2.42	50.27	***
Period * Cover	4.84	5.32	***
Period * Species	2.42	5.62	**

b)

High substrate temp.	**df**	**F**	**p**
Cover	2	12.54	**
Species	1	0.69	ns
Cover * Species	1	1.44	ns

c)

Percent cover	**df**	**F**	**p**
Initial (June 19)	18	0.63	ns
Final (Oct 31)	18	0.45	ns

Table 4.2 Total dry mass and relative root mass (percent of total dry mass) of plants harvested on September 4, 2008. Data presented are means + standard error (n = 8). For total dry mass, values within a row marked by different letters were statistically different (ANOVA, Tukey HSD post-hoc, p<0.05).

	Control	Green Cellophane	*Sedum album*
Total dry mass (g)			
A. rupestris	8.58 ± 1.04 b	9.61 ± 1.17 b	4.60 ± 0.44 a
A. verticillata	7.41 ± 1.03 b	7.21 ± 1.25 ab	3.65 ± 0.74 a
Relative root mass (%)			
A. rupestris	34.0 ± 3.0	33.5 ± 2.2	30.8 ± 2.1
A. verticillata	45.0 ± 6.7	48.3 ± 4.5	49.7 ± 4.5

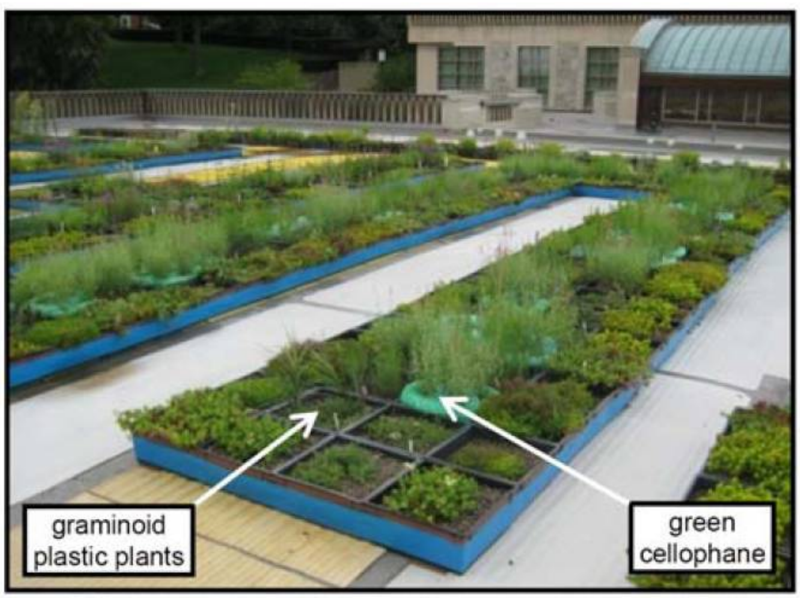


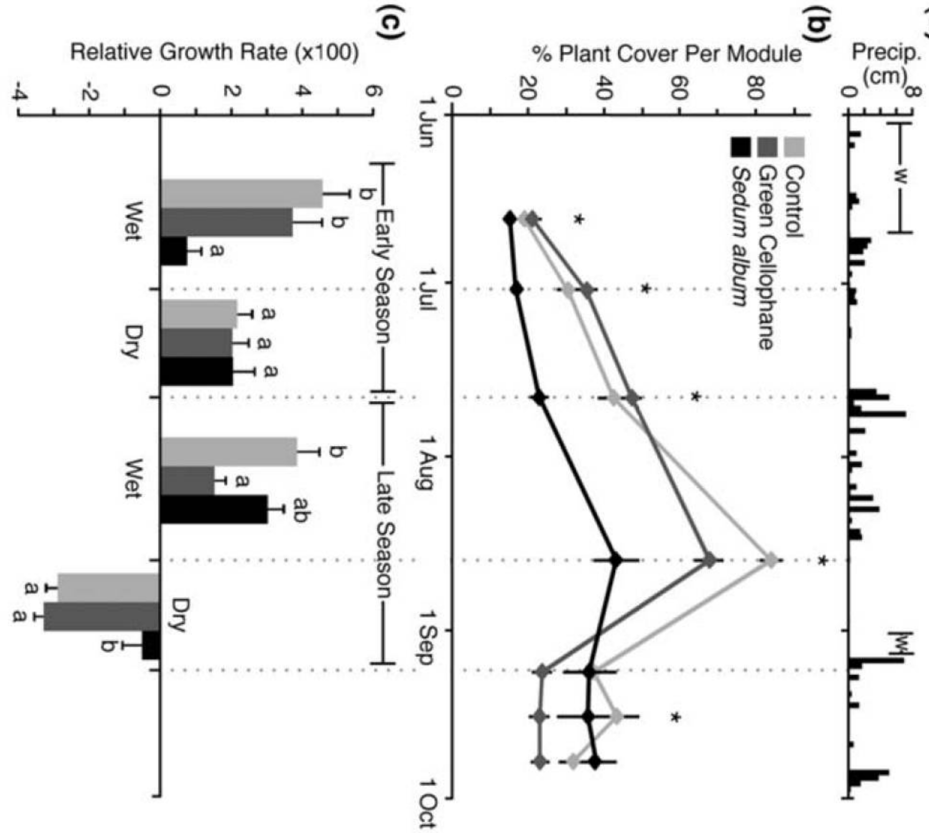
Figure 4.1 Experimental setup of the facilitation experiment. Note the graminoid plastic plant, green cellophane, and the unsampled border row. Photo taken by C. Butler on August 11, 2008.

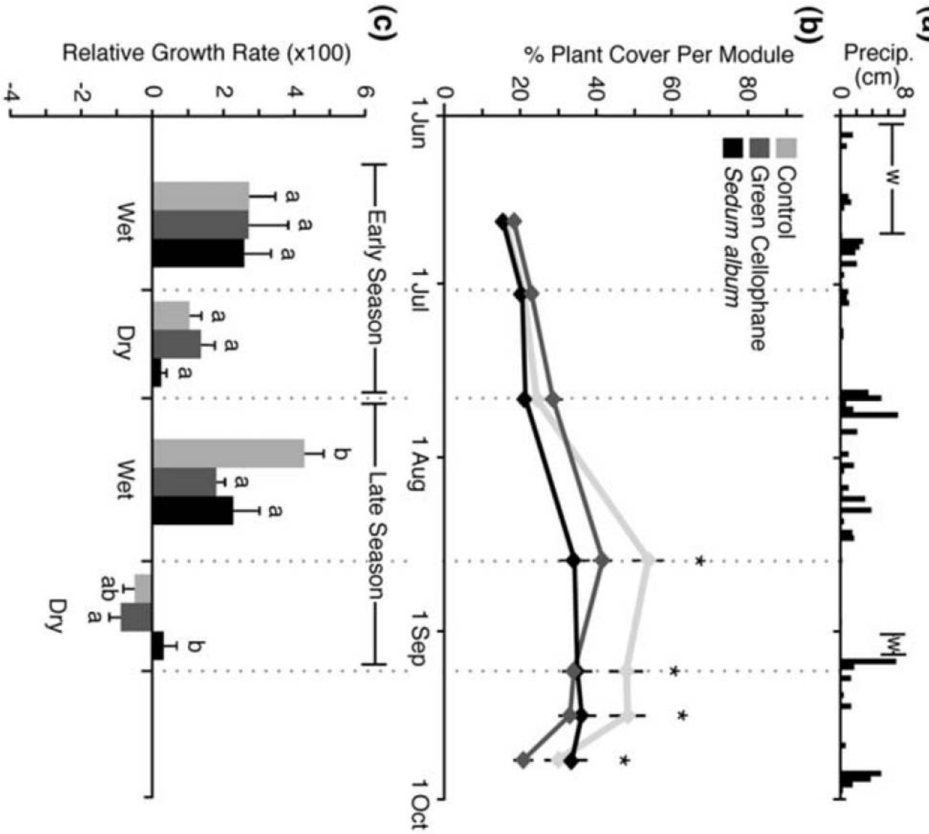
Figure 4.2 Growth of *Agastache rupestris* (left panel) and *Asclepias verticillata* (right panel) between June 19 and September 24, 2008.

a) Precipitation and supplemental water (left and right panels display the same data). Total daily precipitation is represented by black bars. Supplemental water is represented by |-w-|.

b) Percent plant cover per module. Each point represents mean + standard error (n = 10 replicate modules per species per treatment, except *A. rupestris* Green Cellophane (n = 4 on June 19, n = 9 for remaining dates) and *A. verticillata* Green Cellophane (n = 7 on June 19). Dates marked with an asterisk had significant differences among treatments (ANOVA, $p < 0.05$).

c) Relative growth rate ((Final – Initial percent cover) / (Initial percent cover) / number of days) for four periods of time. Vertical dotted lines connecting panels b and c denote which sample dates were used for the initial and final time points for each of the graphs in panel c. Data presented are means + standard error. Bars within each of the four time periods marked by different letters are statistically different (ANOVA, Tukey HSD post-hoc, $p < 0.05$).


(a)
Precip. (cm)
w
(b)
% Plant Cover Per Module
Control
Green Cellophane
Sedum album
1 Jun
1 Jul
1 Aug
1 Sep
1 Oct
(c)
Relative Growth Rate (x100)
Early Season
Late Season
Wet
Dry
Wet
Dry


(a)
Precip. (cm)
w
(b)
% Plant Cover Per Module
Control
Green Cellophane
Sedum album
1 Jun
1 Jul
1 Aug
1 Sep
1 Oct
(c)
Relative Growth Rate (x100)
Early Season
Late Season
Wet
Dry
Wet
Dry

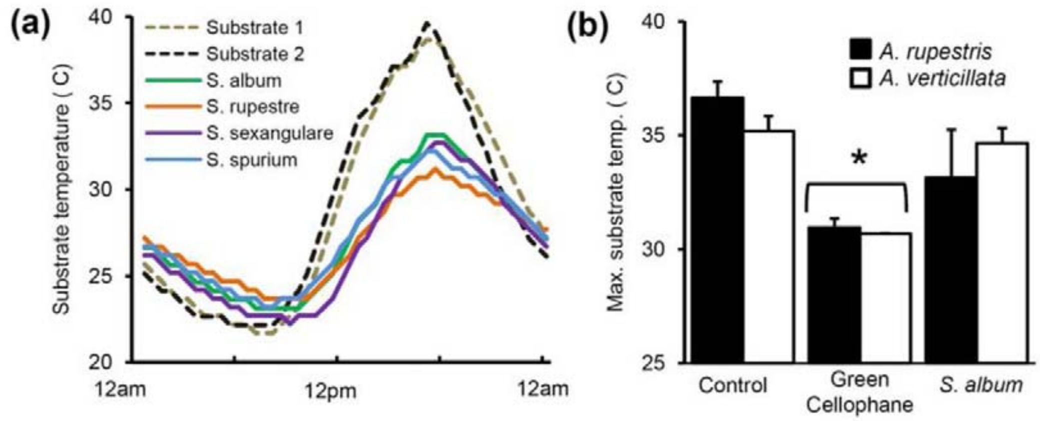


Figure 4.3 Substrate temperature on August 1, 2008 on the Tisch Library Green Roof (Medford, MA). Substrate temperature was measured every 30 minutes using one data logger in the center of each module at a depth of 5 cm. High air temperature for August 1, 2008 was 28.9 C. Rain occurred one day prior.

a) Substrate temperature profile over 24 hours. Each line represents temperature data from one module.

b) Maximum substrate temperature for *Agastache rupestris* and *Asclepias verticillata* growing in three treatments: Control (no cover), Green Cellophane, and *S. album*. Data presented are means + standard deviation of two replicate modules per treatment. Green Cellophane is significantly different from the other cover treatments (ANOVA, Tukey HSD post-hoc, $p < 0.05$).

CHAPTER 5
Sedum cools soil and can improve neighboring plant performance during water deficit on a green roof

Abstract

Green roofs have the potential to function as islands of biodiversity within urban and suburban environments. However, plant diversity is constrained by the harsh environment of a green roof, especially summertime water deficit and heat stress. We hypothesized that *Sedum* species, which are highly tolerant of the roof-top environment, would reduce peak soil temperature and increase performance of neighboring plants during summer water deficit. To test these hypotheses, we grew focal plant species with and without *Sedum* on a green roof. We then monitored growth during wet periods and drought tolerance during dry periods. During a three year experiment, *S. album* reduced maximum growth of neighbor plants, *Agastache rupestris* and *Asclepias verticillata*, during favorable growth conditions, but increased performance of neighbors during summer water deficit. In a second experiment, four species of *Sedum* were each found to decrease peak soil temperature by 5 - 7 °C. All species decreased total growth of neighboring *Agastache* ‘Black Adder’ during favorable growth conditions, but again increased performance during summer water deficit. These results suggest that the palette of green roof plants can be expanded by using *Sedum* species as nurse plants.

Introduction

A green roof is a roof that is partially or completely covered with vegetation. Green roofs reduce stormwater runoff (Berndtsson et al., 2009; Carter and Jackson, 2007; Getter et al., 2007), insulate the building (Kumar and Kaushik, 2005), act as an amenity (Getter and Rowe, 2006; Loder, 2010), and create habitat for local fauna (Kadas, 2006; MacIvor and Lundholm, 2011). In contrast to ground-level landscaping or ornamental roof gardens, most green roofs (also called extensive green roofs) typically have a very thin layer of coarse growing media. An ideal green roof is self-sustaining and requires minimal maintenance, including irrigation (Snodgrass and McIntyre, 2010; Weiler and Scholz-Barth, 2009). As a consequence, green roof plants must be able to survive frequent harsh conditions. Often the largest stressor is summer water deficit (Carter and Butler, 2008), which is exacerbated by extreme heat (Martin and Hinckley, 2007) and high wind (Retzlaff and Celik, 2010). One taxon that seems especially well-suited to life in this environment is *Sedum* (Crassulaceae). *Sedum* species are low-growing succulent plants that can grow rapidly when water is available yet also survive long periods without water (Carter and Butler, 2008; Durhman et al., 2006; Monterusso et al., 2005).

Recent attempts to grow non-*Sedum* plant species on roof tops have tended to focus on native plants (Bousselot et al., 2009; Butler et al., 2010; Licht and Lundholm, 2006; Martin and Hinckley, 2007; Schroll et al., 2009). Lundholm (2005) suggested a 'habitat template' approach, looking to natural ecosystems with physical characteristics similar to those on a roof to identify potential species. While this method is promising (Lundholm et al., 2009; Lundholm et al., 2010), it has yet to be widely adopted (Butler et al., 2010). As a consequence many studies have observed high mortality of non-*Sedum* species (Carter and Butler, 2008; Martin and Hinckley, 2007; Monterusso et al., 2005) unless irrigated (McIntyre, 2009; Schroll et al., 2009). The use of irrigation, however, is generally not encouraged because it goes against the goal of creating a self-sustaining community, wastes water, and requires a more complicated system. Even species that might otherwise survive might be unsuitable for green roofs, either for practical or aesthetic reasons. From a practical perspective, a deep root system can alleviate drought stress in a terrestrial environment, but this will not increase survival in 10 cm of growing media on a green roof. From an aesthetic perspective, leaf abscission in response to drought may improve fitness in the wild, but this adaptation is not aesthetically pleasing in a garden setting.

Perhaps the solution lies in using stress-tolerant plants to facilitate the performance of other plant species. In many stressful habitats, such as deserts, alpine tundras, and salt marshes, stress-tolerant 'nurse plants' reduce abiotic stress and increase performance and survival of neighboring plants (Bertness and Callaway, 1994; Callaway and Walker, 1997; Holmgren et al., 1997). The concept of nurse plants and interspecies facilitation can be traced back to an elegant field experiment by Turner and colleagues (1966). They found that in the Sonoran desert, shading by shrubs reduced peak soil temperature by 4-9 °C, dramatically increasing survival of seedlings of the saguaro cactus, *Carnegiea gigantea,* growing under these shrubs. Similar results have been found for the columnar cactus *Neobuxbumia tetetzo* growing in the Tehuacan Valley in central-southern Mexico (Valiente-Banuet and Ezcurra, 1991). Green roof *Sedum* species have been shown to cool soil temperature by 5-8 °C (Butler and Orians, 2009). Furthermore, some species of *Sedum* can actually reduce water loss from soil (Durhman et al., 2006; Wolf and Lundholm, 2008), possibly because they are performing CAM photosynthesis. This led us to hypothesize that *Sedum* could facilitate the performance of other species.

Facilitation, however, can be transient (Callaway and Walker, 1997). For example, a desert shrub may cool the soil, allowing cactus seedlings to establish but later compete with the cactus seedlings for water. Facilitation and competition may also occur simultaneously and the relative importance of the two forces might depend upon weather conditions. We expected facilitation to be pronounced during during dry periods when termperatures are maximal.

Specifically, we hypothesized that *Sedum* species would cool the soil, act as competitors in wet conditions and facilitators in dry conditions. To test these hypotheses, we conducted two experiments. The first experiment examined the effect of *Sedum album* on the performance of two neighboring plant species—*Agastache rupestris* and *Asclepias verticillata*—during three years on a green roof in Massachusetts. The second experiment examined the effect of four species of *Sedum* on the performance of a single species *Agastache* ‘Black Adder’ on a green roof in Massachusetts.

Methods

Study site and green roof design. The experiments were conducted on the Tisch Library Green Roof at Tufts University in Medford, Massachusetts. This experimental green roof was constructed in June 2007 using a modular green roof system. Modules were made of plastic with dimensions 38 cm x 38 cm. Modules contained a 13 cm deep layer of growing media composed of a blend of 55:30:15 expanded shale aggregate, sand, leaf compost, with a field capacity of 0.35 cm^3 water / 1 cm^3 substrate (purchased from Read Custom Soils; Canton, MA). At the beginning of each growing season, controlled release fertilizer (Scott's Osmocote Plus 15-9-12) was mixed into the top 2 cm of the growing media at a concentration of 3.6 g fertilizer per liter media. Modules were arranged in rows of four. To avoid edge effects, experimental modules were surrounded by a border row of modules planted with *Sedum* species.

Experiment 1. Effect of *S. album* on *Ag. rupestris* and *As. verticillata*

Study species. Our three focal species were *Sedum album* (stonecrop, Crassulaceae, purchased from Emory Knoll Farms; Street, MD), *Agastache rupestris* (licorice mint, Lamiaceae) and *Asclepias verticillata* (whorled milkweed, Asclepiadaceae, purchased from North Creek Nurseries; Landenberg, PA). These species are herbaceous perennials, commonly used landscape plants and not considered invasive (Kemper Center for Gardening; USDA Plants Database). *S. album* is native to Europe where it grows on rocky, thin soil. Its history as a rooftop plant is evident by its common name in Portugal where it selfestablishes on terra cotta roofs: ‘arroz-dos-telhados’ or ‘roof rice’ (Smith and Figueiredo, 2009). *S. album* was chosen because it has high growth and survival in green roof habitats (Carter and Butler, 2008; Durhman et al., 2006; Monterusso et al., 2005; Rowe et al., 2006). In addition, we observed during the summer of 2007 that this species has a relatively shallow, ephemeral root system as compared to congeners commonly grown on green roofs (personal observation). We expected that these traits would minimize belowground competition. *Ag. rupestris* is native to mountain slopes in the southwestern United States (Kemper Center for Gardening) and *As. verticillata* is native to prairies and open meadows throughout most of the United States (Missouri Plants). *Ag. rupestris* and *As. verticillata* were chosen for the following three reasons: 1) they are long-flowering and commonly visited by insect pollinators (Kemper Center for Gardening; Missouri Plants), 2) they showed fast growth and relatively high drought tolerance in a green roof habitat (Carter and Butler, 2008), and 3) they both have an upright growth form, which could minimize aboveground competition for light.

Planting and experimental treatments. A population of *S. album* was planted in July 2007. *Ag. rupestris* and *As. verticillata* were planted in June 2008. Plants were grown from landscape plugs at a density of five plants per module. Each focal species was grown by itself and with *S. album*. Number of replicates varied based on plant availability (*Ag. rupestris* alone n = 11, *Ag. rupestris* + *S. album* n = 14, *As. verticillata* alone n = 17, *As. verticillata* + *S. album* n = 16). Focal species were planted, then four large clumps (15 cm diameter) of *S. album* from the existing rooftop population were transplanted into each of the experimental modules within a week. *S. album* initially covered about 40-50% of the soil surface. By August 11, 2008, it had reached full coverage.

Watering regime. Plants were watered to saturation every 2 days for the first week after planting and then watering frequency was gradually decreased over the course of the first month. A watering regime was created *a priori* based on normal precipitation patterns for eastern Massachusetts and based on known drought tolerance of a variety of green roof plants tested in 2007 (Carter and Butler, 2008). After the initial establishment period, plants would only receive supplemental water after two weeks without rain, at which point they would be watered once every five days until the next rain event. This watering schedule was modified slightly in that watering was terminated early (June 22, 2008) due to frequent rain. All plants were watered on August 29, 2008 after 13 days without rain and again on September 4, 2008 after an additional 5 days without rain. Plants received no supplemental water during the remainder of 2008 and all of 2009. Plants received water on July 2, 2010 after seven days without rain. In the two weeks prior, the study site had received less than 1 cm of rain (National Climatic Data Center).

Data collection. Both experimental and historical weather data were acquired from a weather station at Boston Logan International Airport (National Climatic

Data Center). We focused on July and August weather because these are the warmest months in eastern Massachusetts (National Climatic Data Center).

Overhead photos of each module were taken weekly during the growing season (approximately April – October) of 2008, 2009, and 2010. These photos were used to quantify growth during wet periods, leaf loss during water deficit, and survival. In general, leaf loss during wet periods was negligible and growth was negligible during water deficit. To quantify growth during the wet period of each of the three years, we measured maximum percent plant cover for each module, estimated visually to the nearest 5%. All visual estimates were performed in random order by the same observer. To quantify leaf retention following water deficit, we chose two dates bracketing the most severe dry period during each year. The first date was just before water stress and the second date was after leaf abscission (August 19 and September 8, 2008; August 13 and August 24, 2009; June 21 and July 13, 2010). As a result, the decrease in percent cover represents leaf loss, not temporary wilting. Using these photos, percent plant cover at both time points was estimated visually to the nearest 5%. Again, all visual estimates were performed in random order by the same observer. Example overhead photos of *Ag. rupestris* and *As. verticillata* before and after water deficit are shown in Figure 1. Finally, survival was quantified at the end of each growing season using overhead photos. Modules were considered alive if there was at least one remaining plant from the original five that were planted in 2008.

Data analysis. For maximum percent plant cover, we calculated the mean and standard error per focal species (*Ag. rupestris, As. verticillata)* per treatment (alone, with *S. album*) per year (2008, 2009, 2010). Because modules were measured repeatedly, we performed a repeated-measures ANOVA with focal species (*Ag. rupestris, As. verticillata)* and treatment (alone, with *S. album)* as fixed factors and year (2008, 2009, 2010) as the repeated measure. We then performed t-tests to compare between treatments for each focal species in each year. When data did not meet Levene's Test for Equality of Variances, df were adjusted (SPSS v. 17).

For leaf retention and survival, data were analyzed using exact tests to compare between treatments for each focal species in each year. For leaf retention following water deficit, we determined the proportion of modules per focal species per treatment per year which retained at least half of their leaf area following water deficit. For survival, we determined the proportion of modules per focal species per treatment per year with any surviving plants.

Experiment 2. Effect of various *Sedum* species on *Agastache* 'Black Adder'

Study species. For the second experiment, there were five study species: *S. album*, *S. rupestre*, *S. sexangulare*, *S. spurium,* and *Agastache* 'Black Adder'. *S. album* was used in Experiment 1. The other three species of *Sedum* are commonly used on green roofs, but differ in growth rate, drought tolerance, leaf shape, and root depth (Snodgrass and Snodgrass, 2006). We hypothesized that the species would differ in their interaction with the focal plant *Ag.* 'Black Adder' based on their morphology and physiology. In theory, a deep rooted, fast-growing species would act primarily as a competitor, while a shallow-rooted, slow-growing, drought-tolerant species would act more as a facilitator. *Ag.* 'Black Adder' is a horticultural hybrid of *Ag. rugosum* and *Ag. foeniculum*. This hybrid was chosen over its congener *Ag. rupestris* for three reasons: 1) it is less drought-tolerant, allowing treatment differences to become apparent with mild periods of water deficit, 2) it has an upright growth habit with less branching, which would likely minimize shading of *Sedum* species, and 3) its leaf morphology allows for rapid, reliable visual measures of wilt.

Planting and experimental treatments. All *Sedum* species were planted on the Tisch Library Green Roof in 2007 and allowed to grow naturally. *Ag.* 'Black Adder' was initially planted on the Tisch Library Green Roof in June 2009 at a density of five plants per module. In May 2010, *Ag.* 'Black Adder' was transplanted into modules containing one of the four species of *Sedum* (initial cover 60-80%) at a density of one *Ag.* 'Black Adder' per module.

Watering regime. Plants were watered twice during the first week after transplanting. After this, plants only received water from rain. The exception to this was that all plants were watered on July 2, 2010 after seven days without rain. In the two weeks prior, the study site had received less than 1 cm of rain (National Climatic Data Center).

Data collection. Soil temperature at 5 cm depth was measured at 30 minute intervals between July 11 and August 25, 2010. One data logger (Maxim ibutton high capacity temperature logger DS1922L) was placed midway between the focal plant and the edge of the module in each of four modules per treatment. We looked at the maximum daily soil temperature for days with high air temperatures over 30° C. Due to the upright growth habit of *Ag.* 'Black Adder', overhead photos and percent plant cover were not suitable for quantifying growth and drought tolerance. Instead, weekly side photos were taken. Maximum growth was estimated by counting the number of stems (alive and recently dead) taller than 20 cm per plant on July 13, 2010. Drought tolerance was measured on July 13, 2010 after 11 days without rain. We used a health score of 0-2: a score of 2 represents green leaves and green stems. A score of 1 represents dead leaves and green stems. A score of 0 represents dead leaves and brown stems. Example photos of the three health classes are shown in Figure 2. Survival was measured on July 13, 2010 after the first major water deficit and again on October 3, 2010 after repeated water deficits.

Data analysis. For maximum soil temperature, we performed a repeated measures one-way ANOVA (with sphericity assumed) with *Sedum* species as the independent factor and day as the repeated measure. This was followed by a post-hoc Tukey's HSD test with *Sedum* species as the independent factor. For number of stems, we performed a one-way ANOVA with *Sedum* species as the independent factor. For health score, we performed a one-way ANCOVA with

Sedum species as the independent factor and number of stems as a covariate. For survival on July 13, 2010 and October 3, 2010, we used an exact test.

Results

Weather. Summer weather patterns varied from year to year (Table 5.1). The 30-year mean summer (July and August) temperature for Boston, Massachusetts was 22.8 °C; the 30-year mean summer rainfall was 16.7 cm (approximately 8 cm per month). 2008, 2009, and 2010 were typical in terms of temperature. Over the 30 years, every year had at least one 5-day period without rain, and on average there were at least three 5-day periods of no rain each summer. Ten day gaps without rain were less frequent; approximately 37 % of years experienced a gap this long. The 30-year mean maximum number of days without rain was 9.9 days. The shortest time without rain was six days in 1985 and 1989. The longest time without rain was 20 days in 1995. Although 2008 and 2009 had higher than average rain, the maximum number of days between rain for the three years was typical (12 days in 2008, 9 days in 2009, 9 days in 2010).

Experiment 1. Effect of *S. album* on *Ag. rupestris* and *As. verticillata*

In general, *S. album* reduced neighbor growth (percent plant cover) under favorable conditions but increased neighbor performance (leaf retention) during periods of water deficit. In 2008 and 2009, *Ag. rupestris* and *As. verticillata* achieved a higher maximum percent plant cover when grown alone (Fig. 5.3a, 5.3b; Table 5.2a). This trend, however, was not seen in 2010. Instead, all plants grew less and there was no difference between treatments. In 2008, *Ag. rupestris* retained more leaves following water deficit when grown with *S. album* (Fig. 5.3c, Table 5.2b). In 2009, a similar trend was seen, but the difference was not statistically significant. In the third year, 2010, *Ag. rupestris* showed similar leaf retention in both treatments. In 2008, *As. verticillata* had high leaf retention following water deficit irrespective of treatment (Fig. 5.3d), but in the second year, 2009, *As. verticillata* had greater leaf retention when grown with *S. album*. In the third year, 2010, *As. verticillata* had low leaf retention in both treatments.

There was no significant effect of treatment on survival of either focal species (Table 5.2c). For *Ag. rupestris*, there was a non-significant trend toward plants having higher survival when grown with *S. album* (Fig. 5.3e). For *As. verticillata,* only one module of the 33 total modules died throughout the three-year experiment (Fig. 5.3f).

Experiment 2. Effect of various *Sedum* species on *Agastache* 'Black Adder'

During warm weather (daily high air temperature 30 °C or greater), soil in the modules with only *Ag.* 'Black Adder' was significantly hotter than soil in modules with both *Ag.* 'Black Adder' and one of the four species of *Sedum*. (Fig. 5.4, one-way ANOVA, $F = 38.82$, $df = 4$, $p < 0.001$; Tukey's HSD post-hoc $p < 0.05$). Differences among *Sedum* species were minimal with one exception. Soil in modules with *Ag.* ‘Black Adder’ and *S. album* was hotter than soil in modules with *Ag.* ‘Black Adder’ and *S. sexangulare* (Tukey’s HSD post-hoc, $p = 0.03$).

During wet periods, *Ag.* ‘Black Adder’ grew more stems when grown alone than when grown with any of the four species of *Sedum* (Fig. 5.5a, one-way ANOVA, $F = 10.94$, $df = 4$, $p < 0.001$). There was no difference among the four species of *Sedum*. During water deficit, however, *Ag.* ‘Black Adder’ retained more leaves when grown with any of the four species of *Sedum* as compared to plants grown alone (Fig. 5.5b, one-way ANCOVA, treatment $F = 3.31$, $df = 4$, $p = 0.019$). This difference was not due to differences in plant size as measured by the number of stems per plant (one-way ANCOVA, number of stems as covariate: $F = 2.724$, $df = 1$, $p = 0.106$). There was no difference among *Sedum* spp.

Despite a trend toward lower survival of plants grown alone after the first water deficit, this difference was not significant (Fig. 5.6a, exact test, $p = 0.59$). There was also no difference after repeated periods of water deficit (Fig. 5.6b, exact test, $p = 0.60$).

Discussion

In these experiments, we investigated the potential for *Sedum* species to cool the soil and to increase performance of neighboring plants during summer water deficit. Indeed, all four of the *Sedum* species tested cooled the soil, and this effect varied only slightly by species. Although *Sedum* decreased the total growth of focal species in both experiments during wet periods, *Sedum* generally increased leaf retention of neighboring plants following water deficit. That *Sedum* species act as competitors during productive conditions and facilitators in hot, dry conditions, is consistent with general predictions made by Bertness and Callaway (1994).

Several mechanisms could contribute to facilitation. First, competition could reduce plant size and make the plants less susceptible to subsequent drought. Our analysis, however, did not reveal an effect of plant size on performance. Future studies should evaluate other measures of plant size (e.g., leaf biomass). Second, cooling the soil could decrease the abiotic stress experienced by non-*Sedum* species. In a previous experiment, however, soil cooling alone (by means of adding a layer of green shredded cellophane) did not lead to increased performance during water deficit (Butler and Orians, 2009). Third, *Sedum* species might reduce water loss from the substrate. While most plants accelerate water loss from soil, via transpiration, recent research has shown that pots planted with *Sedum acre*, commonly used on green roofs, actually retained more water than pots with soil alone (Wolf and Lundholm, 2008). This surprising result may be due to the high degree of photosynthetic plasticity in *S. acre* and many of its congeners. These species can switch from C_3 to CAM to CAM-idling in response to water deficit (Castillo, 1996; Earnshaw et al., 1985; Gravatt and Martin, 1992). In traditional CAM photosynthesis, stomata open at night to reduce water loss through transpiration. During CAM-idling plants use recycled respiratory carbon dioxide for photosynthesis (Sipes and Ting, 1985; Luttge, 2004) and this would further limit water loss. Overall, it has been hypothesized that *Sedum's* ability to switch between C_3 and CAM photosynthesis is the reason for its success as a green roof plant (Durhman et al., 2006; Monterusso et al., 2005), allowing it to grow quickly when water is abundant (typical of C_3) and survive drought (typical of CAM).

Overall, we suggest that the positive effect of *Sedum* will be strongest for focal species that grow upright and thus do not compete for light. In hot, dry periods, these plants are the most likely to experience stress from hot soil. For most of the non-*Sedum* species surveyed on this roof, a period of 5 days without rain in the summer results in severe wilting and partial leaf loss (personal observation). This is not surprising given the low water-holding capacity of green roof growing media. We therefore suggest that days between rain may be a more meaningful metric of drought stress than total monthly rainfall. In the past 30 years, every year has had at least one five day period without rain. On average, each year had three of these events. Furthermore, 9.9 days without rain is typical. This length of time without rain is sufficient to cause severe stress or even mortality to many non-*Sedum* green roof species (Carter and Butler, 2008).

Timing of water deficit is also very important. For the study region, the longest period without rain typically occurs in late summer (August). In the first two years of the experiment, this dry period started in August (August 20, 2008 and August 1, 2009). In the third year, however, the longest dry period began earlier, on June 28, 2010. We hypothesize that this difference in timing was why *Ag. rupestris* and *As. verticillata* reached a lower maximum size in the third year than in the previous two years. Furthermore, it is likely that smaller plants would fare better during water deficit because they have less leaf mass to maintain. In contrast, a late season water deficit would be more damaging than a mid-season water deficit because plants have more leaf area to maintain and may also be allocating energy to reproduction. Previous research has shown that plants respond differently to water deficit depending on season and developmental stage (Heschel and Riginos, 2005). In the annual, *Impatiens capensis*, early season drought caused the plant to adopt a drought-avoidance strategy, characterized by low water use efficiency and early flowering (Heschel and Riginos, 2005). In contrast, late season drought caused the plant to adopt a drought-tolerance strategy with high water use efficiency. The susceptibility of plants to water stress is likely to increase as they grow older and larger.

Might we expect *Sedum* to facilitate the growth of other plant species in other regions? To answer this question, it is helpful to compare weather patterns between regions. In Massachusetts, the site of this experiment, mean summer rainfall is approximately 8 cm / month and mean summer temperature is 23 °C (Table 5.1). These conditions are wetter and/or cooler than many other areas of the United States where green roofs are being constructed, such as San Francisco, California (mean summer rainfall 0.2 cm/month) or Austin, Texas (mean summer temperature 29 °C). Although conditions in Massachusetts are more mild, few plant species other than *Sedum* can survive growing alone during summer water deficits (Carter and Butler, 2008). Numerous other studies have also identified summer water deficit as a major cause of plant mortality on green roofs (Bousselot et al. 2009; Durhman et al., 2006; Martin and Hinckley, 2007;

Monterusso et al., 2005; Schroll et al., 2009). Interspecies facilitation may provide an easy and low-cost method to reduce the abiotic stress of a green roof, which could expand the range of plants able to live in this habitat and consequently, increase the habitat value of this space for insects and other invertebrates. Thus, *Sedum* may have an important role in bio-diverse green roofs.

Table 5.1. Historical and experiment-specific summer (July and August) weather patterns (temperature, total rainfall, number of ≥ 5 day periods without rain, maximum number of days without rain, onset of period without rain) in Boston, Massachusetts. All data are from the NCDC weather station at Boston Logan Airport. Data for 1980 – 2009 are means ± standard deviation. Data for individual years (2008, 2009, 2010) are means of daily temperature and total summer precipitation.

Year(s)	Mean summer temp. (C)	Total summer rain (cm)	Number of ≥ 5 day periods without rain	Max number of days without rain
1980-2009	**22.8 ± 0.9**	**16.7 ± 6.1**	**3.3 ± 1.2**	**9.9 ± 3.2**
2008	22.5	26.6	1	12
2009	22.3	25.8	3	9
2010	24.4	19.6	3	9

Table 5.2. Summary of statistical tests from Experiment 1. a) Maximum percent plant cover for *Ag. rupestris* and *As. verticillata* (species) grown with and without *S. album* (treatment) in 2008, 2009, 2010 (year). Data were analyzed with a two-way repeated measures ANOVA with species and treatment as fixed factors and year as the repeated measure. Effect of treatment on the maximum percent plant cover of *Ag. rupestris* and *As. verticillata* in 2008, 2009, 2010. Data for each species from each year were analyzed using a t-test. Degrees of freedom were adjusted if the data had unequal variances. b) Leaf retention after water deficit for *Ag. rupestris* and *As. verticillata.* Data were analyzed using an exact test to determine the effect of treatment on leaf retention of each focal species in each year. c) Survival after water deficit for *Ag. rupestris* and *As. verticillata.* Data were analyzed using an exact test to determine the effect of treatment on survival of each focal species in each year.

a) Maximum percent plant cover

Overall effects	**F**	**df**	**p**
year	86.39	2	< 0.001
year * treatment	9.45	2	< 0.001
year * species	11.86	2	< 0.001
year * treatment * species	5.01	2	< 0.001

Ag. rupestris	**t**	**df**	**p**
2008	7.02	19.79	< 0.001
2009	5.48	13.74	< 0.001
2010	0.69	14.06	0.499

As. verticillata	**t**	**df**	**p**
2008	4.91	25.90	< 0.001
2009	4.94	31	< 0.001
2010	1.28	31	0.209

b) Leaf retention following water deficit

Ag. rupestris	**df**	**p**
2008	1	0.005
2009	1	0.111
2010	1	0.697

As. verticillata	**df**	**p**
2008	--	--
2009	1	0.044
2010	1	0.491

c) Survival

Ag. rupestris	df	p
2008	--	--
2009	1	0.183
2010	1	0.435

As. verticillata	df	p
2008	--	--
2009	--	--
2010	1	0.485

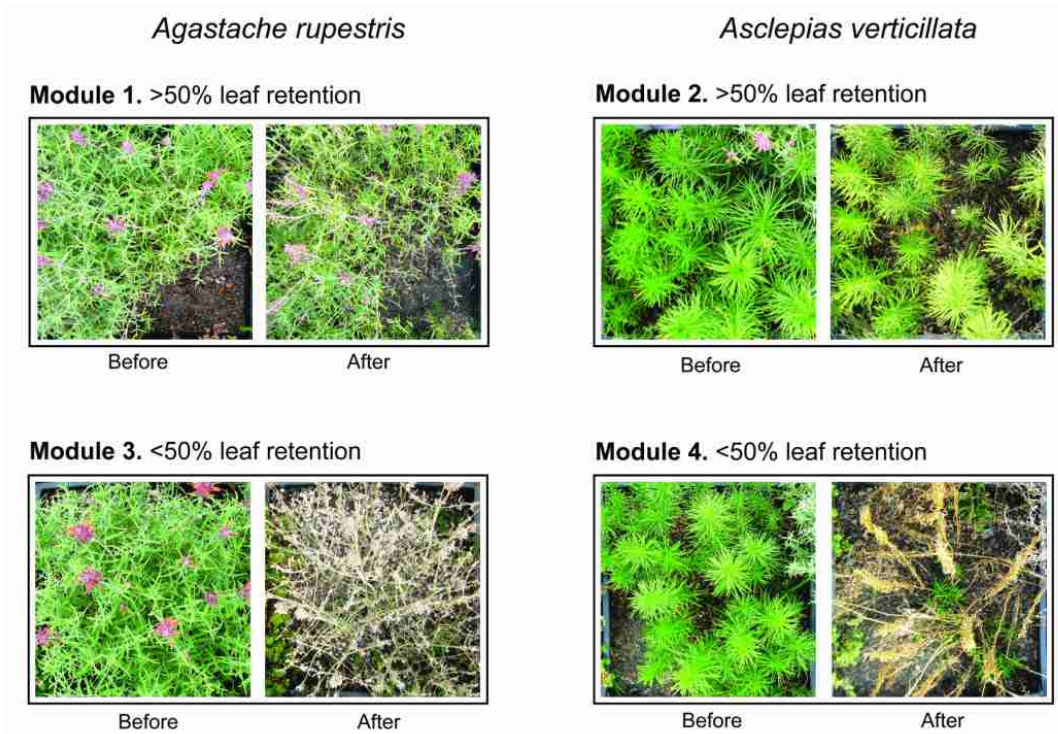


Figure 5.1. Photographs of specific modules of *Ag. rupestris* and *As. verticillata* before and after water deficit. The left photo of each pair was taken before water deficit (July 29, 2009) and the right photo of each pair was taken after water deficit (Sept 8, 2009). The top row of photos (Modules 1 and 2) are representative of modules in which plants retained at least half of their leaf area following water deficit. The bottom row of photos (Modules 3 and 4) are representative of modules in which plants lost at least half of their leaf area following water deficit. For clarity, all plants shown are those grown alone and not with *S. album*.

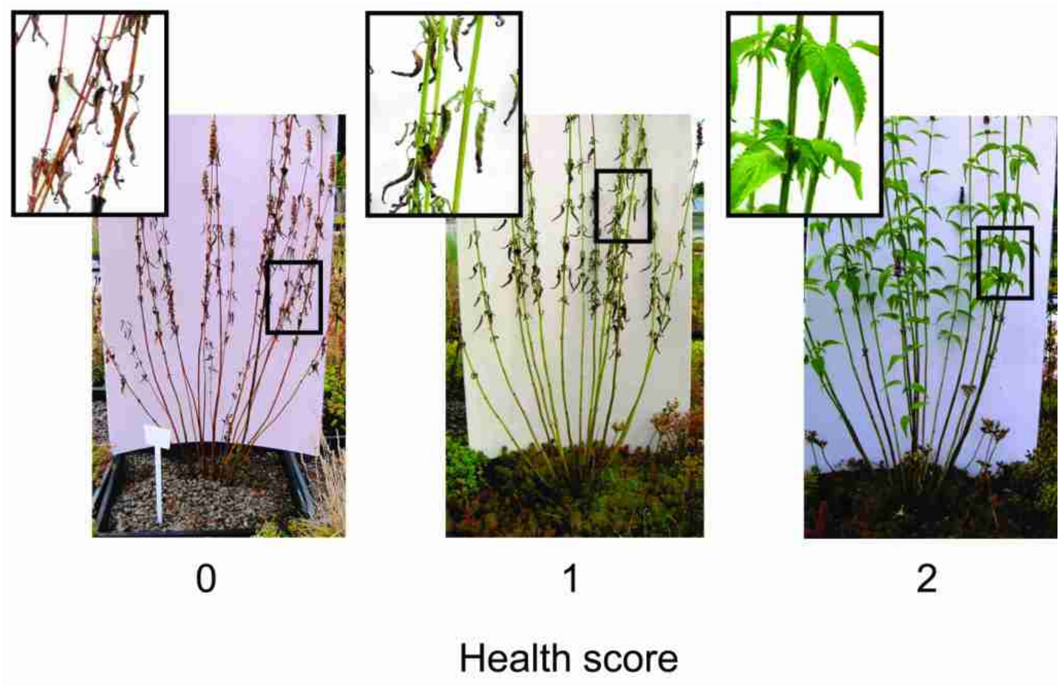


Figure 5.2. Photographs of *Ag.* ‘Black Adder’ illustrating the three health classes: 0 (dead leaves, brown stems), 1 (mostly dead leaves, green stem), and 2 (green leaves, green stem). All photos were taken on July 13, 2010.

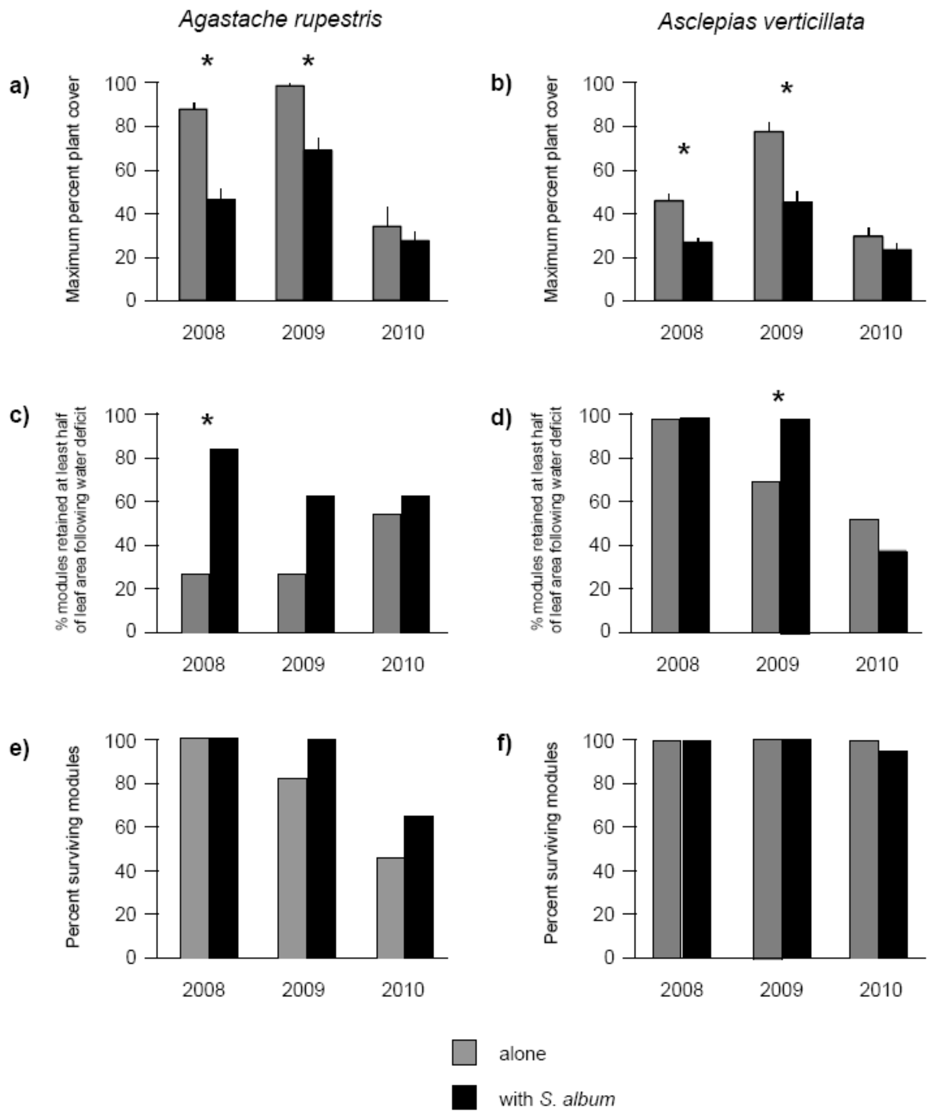


Figure 5.3. Performance of *Ag. rupestris* and *As. verticillata* grown alone and with *S. album* for three years (2008, 2009, 2010) on a green roof. For all panels, gray bars represent plants grown alone and black bars represent plants grown with *S. album.* Pairs of bars marked with asterisks are significantly different from each other (a and b. ANOVA, post-hoc Tukey's HSD; c and d, Fisher's exact test p <0.05). Maximum percent plant cover achieved each year by *Ag. rupestris* (a) and *As. verticillata* (b) alone and with *S. album*. Data shown are means ± standard error (*Ag. rupestris* alone n = 11, *Ag. rupestris* + *S. album* n = 14, *As. verticillata* alone n = 17, *As. verticillata* + *S. album* n = 16. Percent of modules of *Ag. rupestris* (c) and *As. verticillata* (d) alone and with *S. album* that retained at least half of their leaf area following water deficit. Percent surviving modules of *Ag. rupestris* (e) and *As. verticillata* (f) alone and with *S. album* at the end of each growing season.

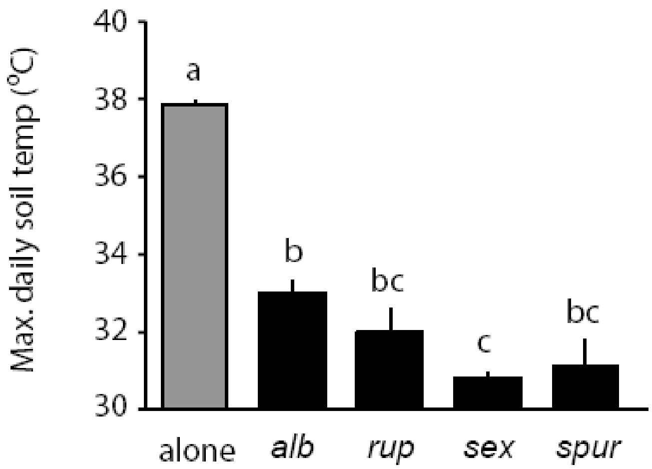


Figure 5.4. Maximum daily soil temperature in modules of *Ag.* ‘Black Adder’ grown alone (gray bar) and with one of four *Sedum* species (black bars; *alb = S. album, rup = S. rupestre, sex = S. sexangulare, spur = S. spurium)*. Data shown are only from days with a high air temperature greater than 30 °C (21 days between July 11, 2010 and August 25, 2010). Data shown are means ± standard error (n=4 per treatment). Bars with the same letter are not significantly different from each other (1-way ANOVA, post-hoc Tukey’s HSD $p < 0.05$).

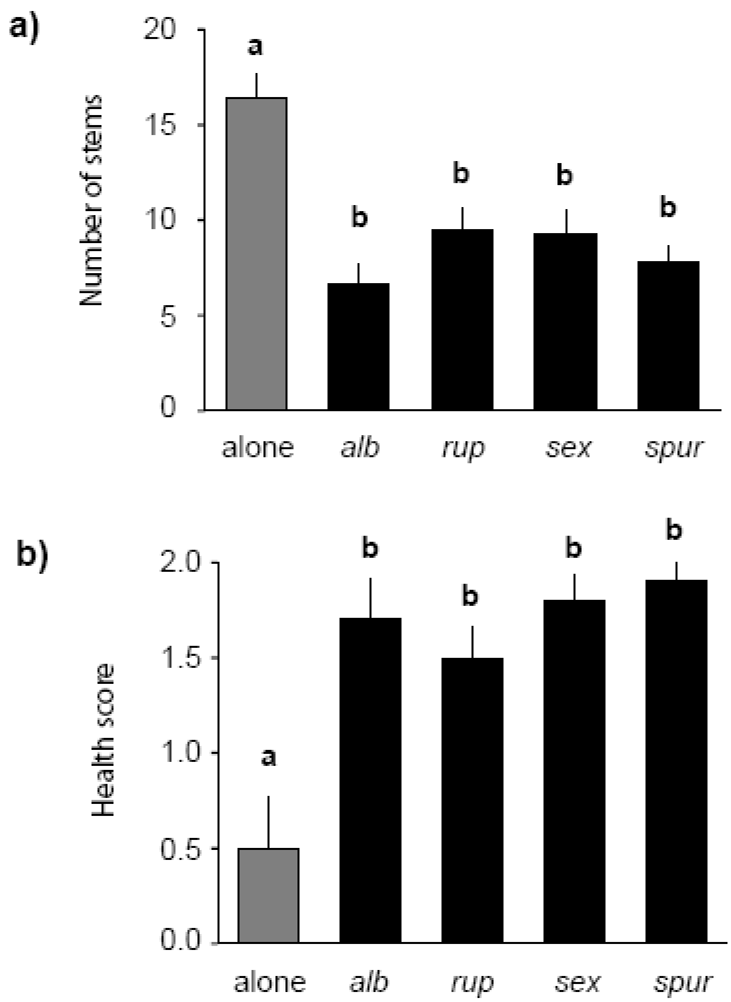


Figure 5.5. Growth of *Ag.* 'Black Adder' during favorable conditions and performance under water deficit. (a) Number of stems per plant of *Ag.* 'Black Adder' grown alone (gray bar) and with four *Sedum* species (black bars; *alb = S. album, rup = S. rupestre, sex = S. sexangulare, spur = S. spurium)*. Stems were counted on July 13, 2010. Data shown are means ± standard error (n=10). Bars with the same letter are not significantly different from each other (1-way ANOVA, post-hoc Tukey's HSD $p < 0.05$. (b) Health score of *Ag.* 'Black Adder' after water deficit grown alone (gray bar) and with four *Sedum* species (black bars; *alb = S. album, rup = S. rupestre, sex = S. sexangulare, spur = S. spurium)*. Data shown are means ± standard error (n=10). Bars with the same letter are not significantly different from each other (ANCOVA, post-hoc Tukey's HSD $p < 0.05$).

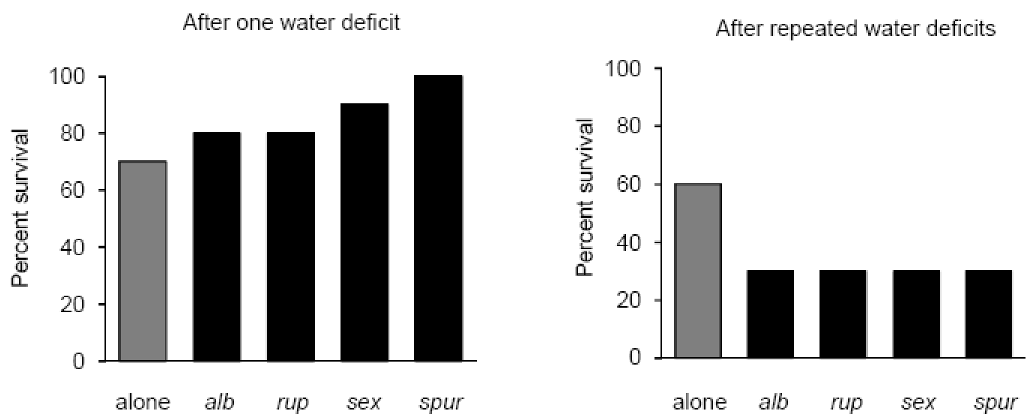


Figure 5.6. Percent of modules (n=10) of *Ag.* 'Black Adder' that survived (a) after one water deficit and (b) after repeated water deficits. Gray bars represent plants grown alone. Black bars represent plants grown with one of four *Sedum* species (black bars; *alb = S. album, rup = S. rupestre, sex = S. sexangulare, spur = S. spurium).*

CHAPTER 6
Plasticity in CAM-C_3 photosynthesis expressed in eight species of green roof *Sedum* (Crassulaceae)

Abstract

The capacity for plants to survive in arid environments depends, in part, on photosynthetic mode (e.g., C_3, C_4, CAM) and photosynthetic plasticity. In this experiment, we sought to determine if contrasting *Sedum* species could switch between C_3 and CAM in response to both short and long term changes in water availability. We grew eight contrasting species of *Sedum* in a greenhouse under varying water conditions. We chose these plants because they are becoming increasingly popular for use on green roofs, novel environments with rapidly changing water availability. To determine photosynthetic mode and the degree of photosynthetic plasticity, we measured day and night carbon dioxide uptake and dawn and dusk leaf acidity. There was variation not only in photosynthetic mode but also in the magnitude of plasticity. There were examples of C_3, CAM-cycling, and CAM-idling, but none of the species exhibited nocturnal uptake of carbon dioxide, typical of archetypal CAM. *S. album* and *S. rupestre* responded to an increase in water availability within a single day, decreasing nocturnal acid accumulation by half. The results of this study provide a better understanding of the diversity of facultative CAM plants and provide insight into the role of photosynthetic mode and plasticity in *Sedum*'s success on green roofs.

Introduction

Plants have evolved many different strategies to cope with life in water-limited environments. One such strategy is Crassulacean Acid Metabolism (CAM) photosynthesis. CAM photosynthesis was named from the family in which it was discovered (Crassulaceae), but it is found in 16000 species, 328 genera, and 33 families (Winter and Smith 1996). The primary advantage of CAM photosynthesis over C_3 is increased water use efficiency. In C_3 photosynthesis, carbon fixation occurs during the day. For every gram of carbon dioxide absorbed from the atmosphere, the plant uses 400-500 g of water (Taiz and Zeiger 2006). In archetypal CAM (also called obligate CAM, full CAM), the majority of carbon fixation occurs at night, when the water gradient between the interior of the leaf and the atmosphere is at its minimum. As a consequence, an archetypal CAM plant loses only 50-100 g of water for every gram of carbon dioxide gained (Taiz and Zeiger 2006). Instead of using ribulose-1,5-biphosphate carboxylase oxygenase (RuBisCO) as the first acceptor of atmospheric carbon dioxide, as is done in C_3 plants, archetypal CAM plants use phosphoenolpyruvate carboxylase (PEPC). Because plants cannot perform the Calvin Cycle at night, CAM plants convert carbon dioxide into malic acid and store it in vacuoles overnight. The following day, CAM plants use malic acid as a carbon source for the Calvin Cycle. This results in diel acid fluctuations in CAM plants (high concentration of acid at dawn, low concentration of acid at dusk), setting them apart from C_3 plants, which fix carbon during the day without diel changes in leaf acidity.

In addition to archetypal CAM described above, there is a variety of plants that are considered facultative CAM (also called C_3-CAM intermediates), able to perform both C_3 and CAM photosynthesis (Cushman 2001). In CAM-cycling, plants exhibit C_3-type gas exchange but CAM-like nocturnal acid accumulation, due to the refixation of respiratory CO_2 (Table 6.1). In CAM-idling, plants refix respiratory CO_2 behind closed stomata during the day. Some facultative CAM species switch in a very predictable, permanent manner. For example, in the annual ice plant, *Mesembryanthemum crystallinum* (Aizoaceae), seedlings and young plants perform C_3 photosynthesis. After three months, there is a developmentally-determined shift to CAM photosynthesis (Winter et al. 1978, Edwards et al. 1996), initiated by *de novo* synthesis of PEPC (Winter and Smith 1996). Other facultative CAM species, such as *Sedum telephium* (Crassulaceae), are able to switch between C_3 and CAM in a rapid and reversible manner, sometimes as fast as within a single day (Conti and Smirnoff 1994). It has been hypothesized that species such as these that exhibit photosynthetic plasticity can grow quickly when water is available and also survive when water becomes limiting (Gravatt and Martin 1992, Durhman et al. 2006).

CAM photosynthesis is not as well-studied as C_3 and C_4 photosynthesis, arguably because these plants are not as common in nature or in agriculture (Dodd et al. 2002). Recently, however, interest in facultative CAM plants, especially *Sedum,* has blossomed due to their newfound importance as green roof plants (VanWoert et al. 2005, Durhman et al. 2006, Getter and Rowe 2006). Green roofs, or vegetated roofs, are becoming increasingly common in North America and worldwide. Their primary function is to reduce stormwater runoff from buildings (Mentens et al. 2006, Berndtsson et al. 2009, Carter and Jackson 2007, Getter and Rowe 2006). *Sedum* is the most commonly used genus grown on green roofs (Snodgrass and Snodgrass 2006), because these plants grow in shallow soil, spread rapidly and can survive prolonged droughts (VanWoert et al. 2005, Durhman et al. 2006, Carter and Butler 2008).

Within the genus *Sedum*, C_3, archetypal CAM, CAM-cycling, and CAM-idling have all been documented (Gravatt and Martin 1992, Cushman and Borland 2002, Schuber and Kluge 1981). However, we do not know if most green roof *Sedum* species can switch rapidly between photosynthetic modes. In order for facultative CAM to be adaptive in a green roof environment, the shift between photosynthetic modes should be rapid and reversible, allowing a plant to respond to pulses of wet and dry conditions.

In this experiment, we determined the photosynthetic mode and examined both short-term and long-term photosynthetic plasticity in eight species of *Sedum* spanning a range of growth rates and drought tolerance. We hypothesized that the most common, successful green roof species would be able to switch rapidly between CAM and C_3. The goals of this experiment were to: 1) classify the photosynthetic mode of each of the experimental species under well-watered and drought conditions, 2) determine if species can switch rapidly between CAM and C_3 in response to changes in soil water status, and 3) determine if there is a correlation between photosynthetic plasticity and performance (namely growth and drought tolerance) on a green roof.

Methods

Study species

Sedum is a large genus (500 species) within the Crassulaceae. We studied eight *Sedum* species that differ in native range and habitat: *S. album*, *S. cauticola* 'Lidakense', *S. kamtschaticum*, *S. rupestre* 'Angelina', *S. sexangulare*, *S. spectabile, S. spurium,* and *S. ternatum* 'Larinem Park' (Table 6.2). With the exception of *S. ternatum*, they are native to sunny, dry, rocky soils in Europe and Asia (Missouri Botanical Garden). *S. ternatum* is native to shaded, moist forest understory in eastern United States and has relatively low drought tolerance (Missouri Botanical Garden). The eight study species also differ in numerous morphological traits, including growth habit and leaf morphology (Table 6.1). We also found that they differ in stomatal density (1-way ANOVA, $F = 6.52$, $df = 6$, $p = 0.002$), and leaf absolute water content (1-way ANOVA, $F = 13.68$, $df = 7$, $p < 0.001$).

While photosynthetic plasticity has been measured in several *Sedum* species, only four of the eight species used in this experiment have been previously evaluated. *S. album* exhibits CAM-cycling (Earnshaw et al. 1985, Bachereau et al. 1998). *S. kamtschaticum* exhibits C_3 photosynthesis in both well-watered and drought conditions (Kim and Choo 2007). *S. ternatum* and *S. spectabile* exhibit C_3 photosynthesis in well-watered conditions and CAM cycling during drought (Gravatt and Martin 1992, Lin et al. 2003). We note that *S. spectabile* is also called *Hylotelephium spectabile* (Missouri Botanical Garden) and due to inconsistent nomenclature, it may even be the same species as *Sedum* *telephium*, which has been used in numerous experiments on photosynthetic plasticity (Groenhof et al. 1990, Borland and Griffiths 1990, Borland 1996, Conti and Smirnoff 1994).

S. cauticola, S. spectabile, and *S. ternatum* were purchased as plugs (North Creek Nurseries, Landenberg, Pennsylvania) in 2009 (the year of this study) and were planted at a density of three plugs per pot. The remaining five species (*S. album, S. kamtschaticum, S. rupestre, S. sexangulare,* and *S. spurium*) were purchased as plugs (Emory Knoll Farms, Street, Maryland) in 2007, grown on an experimental green roof on the Tufts University Medford campus for two years before being used in this experiment. Roof-harvested species were planted at an equivalent density to nursery-grown plants. To minimize the effects of previous growth environment, all plants were grown in the greenhouse for seven weeks before the start of the experiment. During this time, all plants were watered to saturation twice weekly (Fig. 6.1).

Experimental Setup and Watering Regime

All plants were grown in round plastic pots (20 cm diameter) filled with approximately 15 cm of an industry-standard green roof medium consisting of 55% lightweight expanded shale, 30% sand, and 15% leaf compost (gravimetric water content one hour after watering = 13.6 ± 1.8 %), purchased from Read Custom Soils, Canton, Massachusetts). Plants were grown in a greenhouse and not fertilized. During the experiment (6 July – 18 Aug 2009), plants were grown without supplemental lighting. We measured air temperature every 30 minutes

(Maxim ibutton high capacity temperature logger DS1922L). The average daily high temperature was 37.9 ± 5.3 °C and average daily low temperature was 20.2 ± 2.8 °C.

To examine differences in photosynthetic pathway as a function of environmental conditions, plants were assigned randomly to one of two watering treatments, representative of a moderately wet and moderately dry summer in eastern Massachusetts. Wet plants were watered to saturation three times per week. Dry plants were watered to saturation once per week. Each watering treatment had four replicates of each species. To examine physiological responses to long-term drought, all plants were drought stressed during Weeks 4-6, and received no water (Fig. 6.1). Days were numbered as follows: July 13, 2009 (1st day of experiment) was designated as Day 1.1 (= Week 1, Day 1).

To determine if the watering treatments resulted in different soil moisture, pots were weighed before and after watering several times during the experiment. Plant mass accounted for less than 2% of the total mass of the pots so it was ignored in calculations. Based on pot mass one hour after watering and pot mass at the time of measurement, gravimetric water content was calculated for each pot on Day 3.2 and Day 6.2. We expected that the watering treatments would result in different soil moisture on Day 3.2, but not on 6.2. On Day 3.2, Wet plants had been watered 3 days prior and Dry plants had been watered 7 days prior. On Day 6.2, Wet plants had been watered 17 days prior and Dry plants had been watered 20 days prior. For each day, data were analyzed using a 2-way ANOVA with species and treatment as fixed factors.

Photosynthetic Mode and Plasticity

Two forms of plasticity were investigated: long-term and short-term. Long-term plasticity was inferred by comparing the mode of photosynthesis used by a single species during wet and dry watering regimes. Short-term plasticity was inferred by comparing the mode of photosynthesis within a single plant under rapidly changing water availability (days). By measuring both nocturnal acid accumulation in leaves and whole-plant carbon dioxide exchange, we were able to differentiate among C_3, archetypal CAM, CAM-cycling, and CAM-idling. Each type produces a unique profile of CO_2 flux and leaf acidity (Table 6.1). After two weeks of treatment, nocturnal acid accumulation and daytime and nighttime whole-plant carbon dioxide exchange were measured for a period of 64 hours. Nocturnal acid accumulation was measured on Night 6.2.

Nocturnal acid accumulation. The primary driver for diel changes in acidity is malic acid (Borland and Griffiths 1990, Martin et al. 1988). Thus, nocturnal malic acid production can be estimated by measuring titratable acidity in leaves at dawn and dusk. We used four replicate plants of each species in each watering treatment. We collected leaves at dusk (8:00pm) and dawn (5:30am) for 64 hours (Day 3.1 dusk through Day 3.4 dawn) and again at dusk on Day 6.2 and dawn on Day 6.3. For each plant, we collected between 0.5 – 1.0 gram of leaf material. For species with very small leaves (*S. album*, *S. rupestre*, *S. sexangulare*), we minimized the amount of stem included in the sample. Within 30 minutes of collection, the fresh mass of each leaf sample was measured. Leaves were then frozen in liquid nitrogen and stored at -20 °C. To measure titratable acidity, liquid nitrogen was added to leaves in a mortar and this mixture was grinded into a fine powder using a pestle. Leaf powder was added to a beaker containing 10 ml of 50% ethanol in deionized water. Titrations were performed at room temperature. The solution was stirred and the initial pH was measured (Orion 410A pH meter). Sodium hydroxide (0.01 N) was added in 0.25 ml intervals until the pH of the solution reached 7. Titratable acidity is presented as the µmols H^+ per gram fresh mass. To determine the total nocturnal acid production, dusk acidity was subtracted from dawn acidity. Means and standard errors were calculated for each species per treatment per night. Data were analyzed using a 2-way repeated measures ANOVA (fixed factors: treatment, species, repeated measure: day).

Whole-plant carbon dioxide flux. Whole-plant carbon dioxide (CO_2) flux was measured using an infrared gas analyzer (CIRAS-2 Portable Photosynthesis System, PP Systems, Amesbury, Massachusetts) attached to a clear plastic chamber (CPY-2 Canopy Assimilation Chamber, PP Systems, Amesbury, MA, chamber dimensions = 17 cm height x 15 cm diameter) placed on top of an individual pot. Measurements took place at ambient light and temperature. Whole-plant CO_2 flux was measured for each plant (n = 2 per species per treatment) once at each of the time points. Both nighttime (10pm-2am) and daytime (9am-1pm) CO_2 flux were measured for a period of approximately 60 hours (night on 3.1 to morning of 3.4). CO_2 concentration was fixed at 350 ppm. Net flux of CO_2 over a 30 second period was measured for each plant. Data were recorded as the change in concentration of CO_2 in the chamber during a 30 second sample period. These values were converted into µmols CO_2 absorbed or released per m^2 per second. Data were analyzed using a 3-way repeated measures ANOVA (Fixed factors: species, treatment, time of day, repeated measure: day).

Linking photosynthetic plasticity to performance on a green roof. Four of the eight species from this experiment were also used in a green roof survey experiment in 2007 that measured growth and drought tolerance of 19 plant species on an unirrigated green roof in Massachusetts: *S. album, S. rupestre, S. sexangulare,* and *S. spurium* (Carter and Butler 2008). We hypothesized that species with high constitutive levels of nocturnal acid accumulation would have low growth but high drought tolerance. However, species with high levels of plasticity would have fast growth and high drought tolerance. We defined growth as the maximum percent plant cover achieved during the growing season. We defined drought tolerance as the percent leaf retention following a severe summer water deficit. We compared *Sedum* green roof performance with two aspects of photosynthesis measured in this experiment: 1) maximum nocturnal acid accumulation and 2) plasticity in acid accumulation (difference between acid accumulation on Night 3.1 and 3.2).

Results

After an extended drought (17 days without water for Wet plants, 20 days without water for Dry plants), there was no effect of species or treatment on soil moisture (2-way ANOVA; species F = 0.14, df = 7, p = 0.99; treatment F = 1.49, df = 1, p = 0.23; species*treatment F = 0.34, df = 7, p = 0.93). Nocturnal acid accumulation varied across species (1-way ANOVA, F = 6.75, df = 7, p < 0.001). *S. album*, *S. rupestre*, and *S. spectabile* showed high levels of nocturnal acid accumulation (Fig. 6.2). *S. spurium*, *S. kamtschaticum*, and *S. cauticola* showed intermediate acid accumulation. *S. sexangulare* and *S. ternatum* had very low nocturnal acid accumulation.

On Day 3.2, the first full day of photosynthesis measurements, Dry pots were significantly drier than Wet pots (2-way ANOVA; treatment F = 331.09, df = 1, p < 0.001; species F = 2.66, df = 7, p = 0.021; treatment*species F = 2.29, df = 7, p = 0.043). In spite of this, there was no treatment effect on Night 3.1 nocturnal acid accumulation for any of the eight species (Fig. 6.3, Table 6.3b). There was, however, variation across species (Fig. 6.3), similar to that seen after the long drought (Fig. 6.2). On Night 3.1, *S. album*, *S. rupestre*, *S. spectabile*, and *S. spurium* had high levels of nocturnal acid accumulation while the other four species – *S. kamtschaticum*, *S. cauticola*, *S. sexangulare*, and *S. ternatum* – had consistently low levels of nocturnal acid accumulation on all three nights (Fig. 6.3). After soil moisture was measured on Day 3.2, all plants were watered. Interestingly, Day 3.2 was cloudy and the temperature was much lower (high temperature 23.7 °C), and nocturnal acid accumulation on Night 3.2 was lower for several species. Wet plants did not change but nocturnal acid accumulation of Dry plants was negligible. Four of the eight species showed consistently low (10-20 μmol H^+ / g fresh mass) levels of nocturnal acid accumulation on Nights 3.1, 3.2 and 3.3: *S. kamtschaticum*, *S. cauticola*, *S. sexangulare*, and *S. ternatum* (Fig. 6.3). On Night 3.3, nocturnal acid accumulation increased for *S. album*, *S. rupestre*, *S. spectabile*, and *S. spurium* and there was a treatment effect (Table 6.3d). Dry plants produced more acid than Wet plants for *S. album*, *S. spectabile*, and *S. spurium*.

Six of the eight species (all but *S. album* and *S. rupestre*) exhibited C_3-type gas exchange with daytime uptake of carbon dioxide and nighttime release of carbon dioxide (Fig. 6.4, Table 6.3e). *S. album* and *S. rupestre* showed no diel pattern in gas exchange. Nearly all measurements taken on these two species showed either a net release of carbon dioxide or no net movement of carbon dioxide, both during the day and at night. There was no nocturnal uptake of carbon dioxide by any of the species under any of the watering treatments (Fig. 6.4).

Maximum acid accumulation in response to drought and plasticity in acid accumulation appear to be negatively correlated with growth in favorable conditions for these four species (Fig. 6.5a, 6.5b). *S. rupestre* had high acid accumulation and high plasticity but low growth. In contrast, *S. sexangulare* had low acid accumulation and low plasticity but high growth. The trends regarding drought tolerance are less clear—all but *S. spurium* had high drought tolerance, regardless of maximum acid accumulation or plasticity (Fig. 6.5c, 6.5d).

Discussion

These *Sedum* species differed in both photosynthetic mode and plasticity. In general, *S. album*, *S. rupestre*, *S. spectabile*, and *S. spurium* had high levels of nocturnal acid accumulation, indicative of nocturnal synthesis of malic acid during CAM photosynthesis. *S. album* and *S. rupestre* exhibited carbon dioxide exchange typical of CAM-idling, in which plants recycle respiratory CO_2 behind closed stomata. In contrast, the other four species—*S. kamtschaticum, S. sexangulare, S. cauticola,* and *S. ternatum*—exhibited low levels of nocturnal acid accumulation, indicative of C_3 photosynthesis. *S. ternatum* exhibited consistent C_3 carbon dioxide exchange, with uptake during the day and release at night. Yet these photosynthetic systems were not necessarily fixed. *S. album* and *S. rupestre* were able, for example, to respond to cooler, wetter conditions within a single day, by reducing nocturnal acid accumulation by half.

Maximum nocturnal acid accumulation and plasticity appeared to be negatively correlated with growth potential, but did not show a relationship with drought tolerance. The results of this experiment further demonstrate the diversity of forms among facultative CAM plants. Within a single genus, we identified C_3, CAM-cycling, and CAM-idling. Furthermore, these results underscore the value of performing multiple measures of photosynthesis. Measuring CO_2 flux or leaf acidity alone would yield an incomplete picture of the type of photosynthesis occuring.

Photosynthetic plasticity has previously been studied in *Sedum*. Most of the experiments have looked at long-term plasticity, determining if plants can switch to CAM after an extended drought (Borland and Griffiths 1990, Gravatt and Martin 1992). The experiment presented here is novel in that it examines the role of photosynthetic plasticity in coping with rapid, short-term changes in water availability.

Many of the mechanisms for these shifts have been elucidated, but the adaptive significance largely remains a mystery (Herrera 2009). It is commonly assumed that CAM induction results in a higher water use efficiency. However, Gravatt and Martin (1992) found no correlation between the magnitude of malic acid accumulation and water use efficiency in five species of *Sedum*. Similar results were found in two species of *Peperomia*; both the obligate C_3 species and the facultative CAM species had similar water use efficiency (Helliker and Martin 1997).

One of the goals of this experiment was to see if *Sedum's* photosynthetic mode and plasticity help to explain its success as a green roof plant. This has been hypothesized previously (VanWoert et al. 2005, Durhman et al. 2006), but never tested experimentally. *Sedum* is able to grow rapidly during wet periods and survive during dry periods (Carter and Butler 2008). In one green roof experiment, a mix of *Sedum* species was able to survive for 88 days without irrigation (VanWoert et al. 2005). On green roofs, even if there is regular rain, the shallow soil dries out rapidly (VanWoert et al. 2005). Under these conditions, we hypothesized that photosynthetic plasticity would need to be rapid.

We predicted that the most common green roof plants would perform CAM during drought but would switch rapidly to C_3 when water became available. Such a trend was seen for *S. album* and *S. rupestre*, but not for *S. kamtschaticum* and *S. sexangulare*, equally common green roof plants. It is interesting to note that one of the common names for *S. sexangulare* is ‘tasteless stonecrop,’ presumably because of its lack of nocturnal acid accumulation. The results of this study provide a better understanding of the diversity of facultative CAM plants and provide insight into the role of photosynthetic mode and plasticity in *Sedum*’s success on green roofs.

Table 6.1. Four modes of photosynthesis found in *Sedum* species with descriptions of nocturnal acid accumulation and movement of carbon dioxide of each type. Adapted from Cushman 2001.

Type	Description	Nocturnal acid accumulation	Uptake of CO_2	
			Day	Night
C_3	daytime uptake of CO_2	No	Yes	No
Archetypal CAM	nocturnal uptake of CO_2 and recycling of respiratory CO_2	Yes	No	Yes
CAM-cycling	daytime uptake of CO_2 and recycling of respiratory CO_2	Yes	Yes	No
CAM-idling	recycling of respiratory CO_2 behind closed stomata	Yes	No	No

Table 6.2. Descriptive traits of the eight experimental species of *Sedum* (Crassulaceae). Leaf size was categorized as either small (leaf length less than 1cm), medium (leaf length between 1cm and 3cm), or large (leaf length greater than 3cm). For stomatal density and leaf absolute water content (AWC), data shown are means ± standard error (stomatal density n=4, AWC n=8). Within each column, values with the same letters are not significantly different (1-way ANOVA, Tukey's HSD post-hoc $p < 0.05$).

Species	**Native range**[1]	**Native habitat**[1]	**Growth habit**[2]	**Leaf size**[2]	**Leaf shape**[2]	**Use on green roofs**[2]	**Stomatal density**[3] ***(# / mm²)***	**Leaf AWC**[3] ***(%)***
S. album	Europe	Sunny, dry	Prostrate	Small	Needle	Common	9.4 ± 2.8 abc	94.3 ± 0.4 e
S. cauticola	Japan	Sunny, dry	Branching	Small	Flat	Rarely	11.4 ± 1.2 bc	92.8 ± 0.3 cde
S. kamtsch-aticum	Europe	Sunny, dry	Clumping	Medium	Flat	Common	7.9 ± 1.9 ab	91.7 ± 1.1 bcd
S. rupestre	Europe	Sunny, dry	Prostrate	Small	Needle	Common	7.5 ± 0.7 a	91.4 ± 0.5 abc
S. sexangulare	Europe	Sunny, dry	Prostrate	Small	Needle	Common	n/a	90.2 ± 0.1 ab
S. spectabile	East Asia	Sunny, dry	Upright	Large	Flat	Rarely	14.2 ± 1.1 c	94.0 ± 0.5 de
S. spurium	Europe	Sunny, dry	Prostrate	Small	Flat	Common	10.9 ± 1.4 abc	94.4 ± 0.2 e
S. ternatum	United States	Shade, moist	Prostrate	Small	Flat	Rarely	9.0 ± 0.5 ab	89.3 ± 0.3 a

[1] Missouri Botanical Garden website
[2] Personal observation
[3] Data collected in this study

Table 6.3. Summary of statistical tests. a) Nocturnal acid accumulation on Nights 3.1 through 3.3. Data were analyzed using a 2-way repeated measures ANOVA with species and treatment as fixed factors and day as the repeated factor. b) Nocturnal acid accumulation on Night 3.1. Data were analyzed using a 2-way ANOVA with species and treatment as fixed factors. c) Nocturnal acid accumulation on Night 3.2. Data were analyzed using a 2-way ANOVA with species and treatment as fixed factors. d) Nocturnal acid accumulation on Night 3.3. Data were analyzed using a 2-way ANOVA with species and treatment as fixed factors. e) Carbon dioxide exchange in daytime and nighttime from Day 3.1 to Day 3.4. Data were analyzed using a 3-way repeated measures ANOVA with species, treatment, and time of day (day, night) as fixed factors and day as the repeated measure. Significant effects are shown in bold

a) Nocturnal acid accumulation, Nights 3.1 through 3.3

	F	df	p
day	40.93	2	**<0.001**
day * sp.	4.02	14	**<0.001**
day * trt.	8.65	2	**0.001**
day * sp. * trt.	2.30	14	**0.009**

b) Nocturnal acid accumulation, Night 3.1

	F	df	p
species	11.16	7	**<0.001**
treatment	0.36	1	0.55
sp * trt	0.27	7	0.96

c) Nocturnal acid accumulation, Night 3.2

	F	df	p
species	1.41	7	0.23
treatment	1.14	1	0.29
sp * trt	2.12	7	0.060

d) Nocturnal acid accumulation, Night 3.3

	F	df	p
species	38.53	7	**<0.001**
treatment	32.27	1	**<0.001**
sp * trt	4.25	7	**0.001**

e) Carbon dioxide exchange, Days and Nights 3.1 through 3.4

	F	df	p
day	5.65	2	**0.008**
day * sp.	1.47	14	0.15
day * trt.	2.20	2	0.13
day *time	0.64	2	0.53
day * sp. * trt.	1.93	14	**0.040**
day * sp. * time	1.29	14	0.24
day * trt. * time	3.34	2	**0.049**
day * sp. * trt. * time	1.16	14	0.33

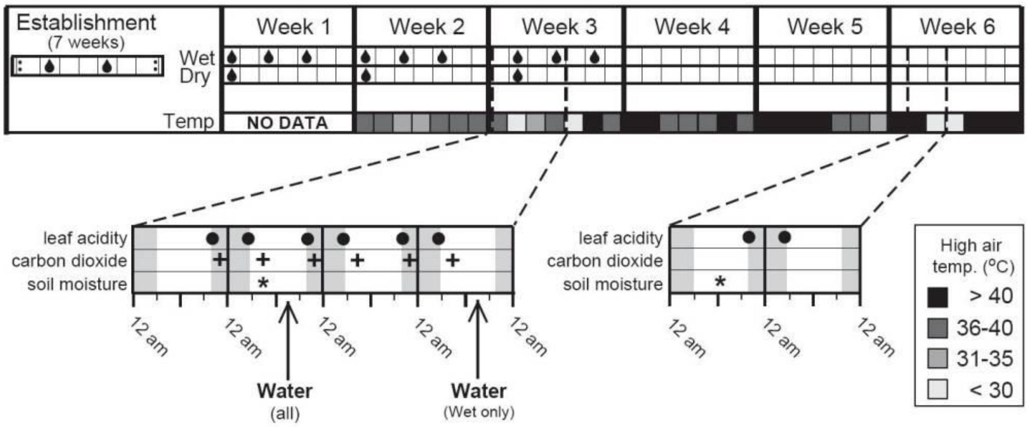


Figure 6.1. Timeline of experiment. The top panel shows an overview of the entire experiment, including a 7-week establishment period and the 6-week experiment. During the establishment period, all plants were watered twice per week (watering indicated by water drop). For the first three weeks of the experiment, Wet plants were watered three times per week and Dry plants were watered once per week. The bottom row of the top panel displays the high air temperature for each day of the experiment. The two lower panels depict two portions of time in which repeated measures of photosynthesis were conducted. Gray shading indicates nighttime. The time of each measurement (leaf acidity, carbon dioxide exchange, and soil moisture) is marked on the timeline.

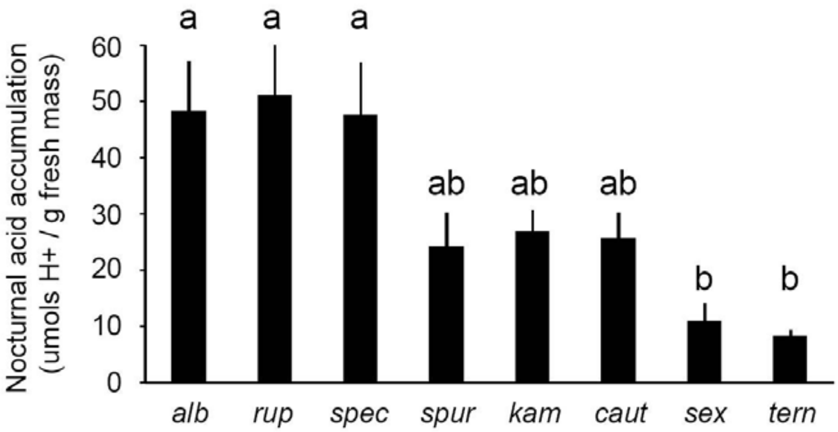


Figure 6.2. Nocturnal acid accumulation on Night 6.2 after an extended drought. Species are ordered from experiment-long high to low acid accumulation. Species names are abbreviated as follows: (*alb = S. album, rup = S. rupestre, spec = S. spectabile, spur = S. spurium, kam = S. kamtschaticum, caut = S. cauticola, sex = S. sexangulare, tern = S. ternatum*). Wet plants received water 17 days earlier and Dry plants received water 20 days earlier. Wet and dry treatments are combined. Data shown are means ± standard error (n=6). Bars with the same letter are not significantly different from each other (1-way ANOVA, post-hoc Tukey's HSD $p<0.05$).

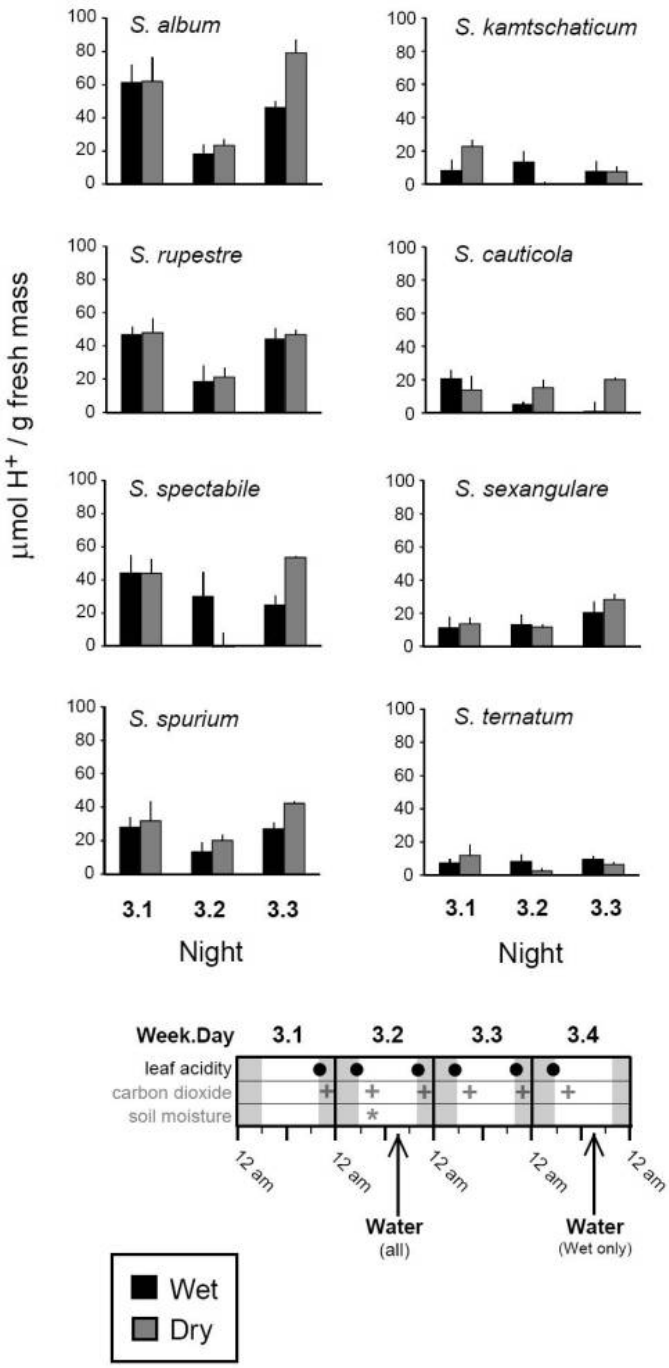


Figure 6.3. Nocturnal acid accumulation on Nights 3.1, 3.2, and 3.3. On Day 3.1, wet plants (black bars) had been watered 3 days prior and dry plants (gray bars) had been watered 7 days prior. Data shown are means ± standard error (n=4). Nocturnal acid accumulation was calculated by subtracting dusk leaf acidity from dawn leaf acidity for each individual. Below the graphs is the four-day detailed timeline of watering and measurements.

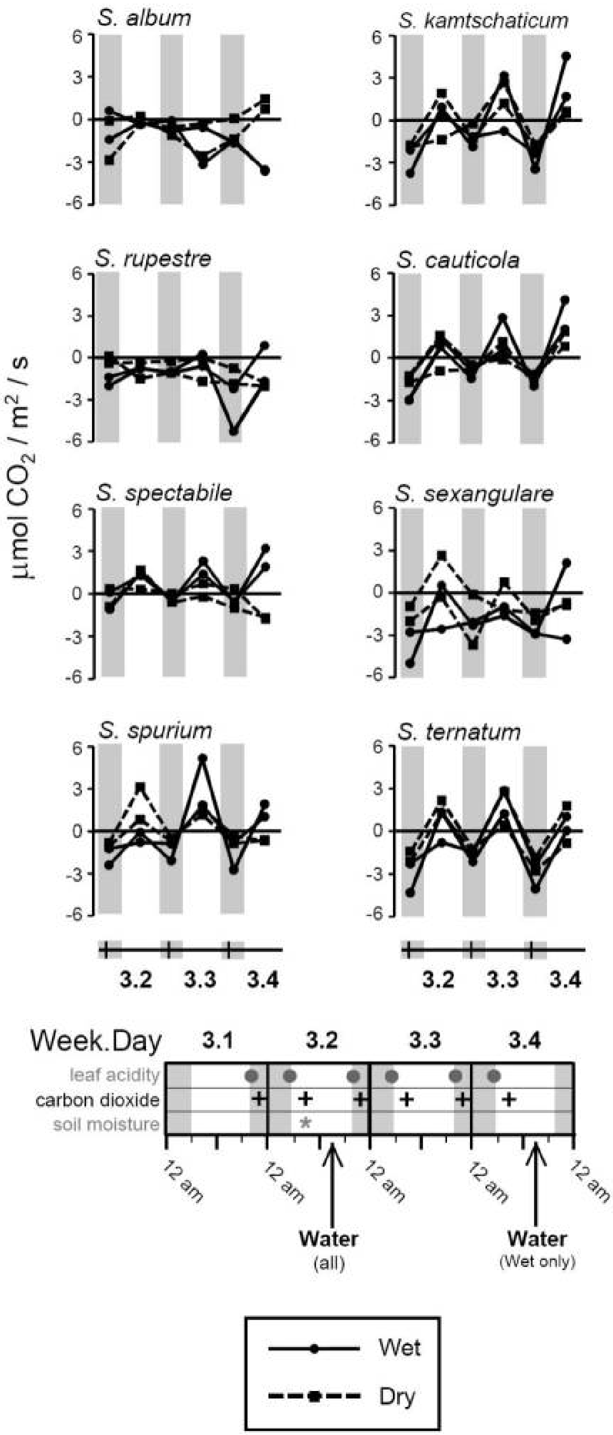


Figure 6.4. Daytime and nighttime whole-plant carbon dioxide exchange on Days 3.1 through 3.4. On Day 3.1, wet plants (solid line) had been watered 3 days prior and dry plants (dashed line) had been watered 7 days prior. Each line represents a single plant. Gray shading indicates nighttime. Below the graphs is the four-day detailed timeline of watering and measurements.

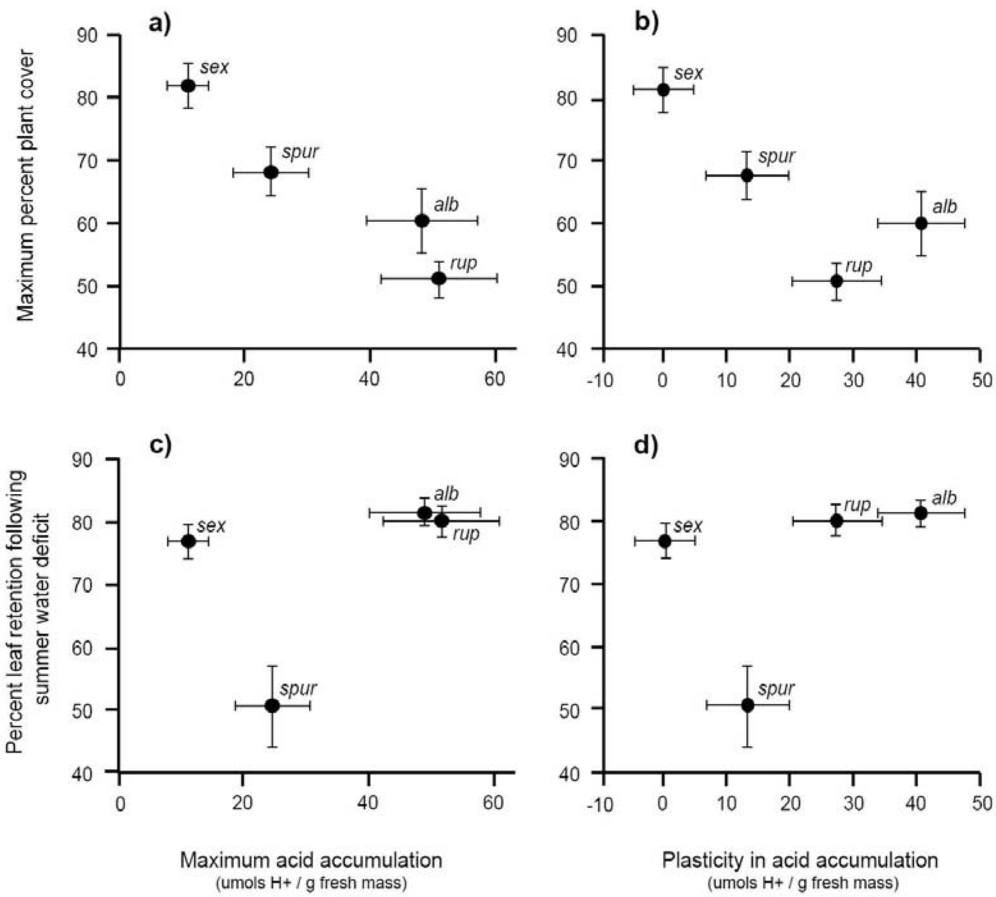


Figure 6.5. Relationship between maximum nocturnal acid accumulation with a) growth potential and c) drought tolerance. Relationship between plasticity in acid accumulation with b) growth potential and d) drought tolerance. Maximum nocturnal acid accumulation data are from Night 6.2, when plants were under severe drought stress. Plasticity in acid accumulation is the difference between nocturnal acid accumulation on Nights 3.2 and 3.3, before and after plants were watered. Growth potential and drought tolerance are from Carter and Butler (2008). Growth potential is defined as the maximum percent plant cover achieved during a single growing period. Drought tolerance is defined as the percent of leaf area retained after summer water deficit.

CHAPTER 7
Conclusions

Urban land cover is dominated by impervious surface that degrades both terrestrial and aquatic ecosystems relative to predevelopment conditions. Green roofs mitigate many negative environmental effects of urbanization, especially stormwater runoff and the urban heat island effect. There is also potential for green roofs to function as islands of biodiversity within urban and suburban environments. In this dissertation, I examined the ecology and physiology of green roof plant communities.

Key Findings

In Chapter 2, I conducted a rooftop experiment to assess suitability of 19 native and non-native plant species. Summer water deficit resulted in high mortality of all but the most popular green roof species: *Sedum*. These results underscore the importance of conservative plant choice and further illustrate the ability of *Sedum* species to grow rapidly during wet periods and survive severe drought.

In Chapter 3, I examined the preference for using native plants on green roofs. I identified 113 green roofs planted with native plants and 89 scholarly papers that promoted this practice. Both aesthetic and scientific reasons were given, although scientific reasons were far more common. The results of this review underscore the ubiquity of the pro-native argument as well as a lack of consensus on how to define "native" and why native plants should be preferred over non-native plants.

In Chapters 4 and 5, I tested the hypothesis that *Sedum* species would reduce peak soil temperature and increase performance of neighboring plants during summer water deficit. *Sedum* species decreased peak soil temperature by 5 - 7 °C. Overall, *Sedum* reduced neighbor growth during wet periods, but increased neighbor performance during summer water deficit. Thus, *Sedum* may have an important role in bio-diverse green roofs by reducing abiotic stress and expanding the range of plants able to live in this environment.

In Chapter 6, I investigated photosynthetic plasticity in *Sedum*. There was variation in photosynthetic pathway among the eight species tested, including examples of C3, CAM cycling, and CAM idling. Furthermore, several species exhibited rapid switching in photosynthetic pathway in response to short-term changes in water availability. Photosynthetic plasticity may play a role in *Sedum*'s success as a green roof plant.

Management implications--Green infrastructure in Somerville, MA

The research described in this dissertation took place on the border of Somerville and Medford, Massachusetts (literally, the city border runs through Tisch Library). While there is nothing wrong with Medford, I am a loyal Somervillen. As such, I will take this opportunity to explain how and why green roofs could be the cornerstone of a green infrastructure policy.

Somerville, Massachusetts is located two miles north of Boston. It was originally settled in 1630 as part of Charlestown and was established as a town in 1842. Housing a population of 77,478 in just over 4 square miles, Somerville is the most densely populated city in New England (US Census Bureau, 2000). The city is located in the Mystic River Watershed, a densely populated and environmentally hazardous area. The Mystic River is polluted with chemicals from waste disposal sites, contaminated sediments, nutrients, sewage, fuel hydrocarbons, road salt, and metals (Deshpande and Roden, 2005).

Two-thirds of Somerville has a combined sewer system and the other third has a separate system (Deshpande and Roden, 2005). In the separate system, only sewage is treated and stormwater is released untreated. This is a problem because the stormwater contains pollutants from roads. In the combined system, stormwater and sewage is combined into one system of pipes and all of this water is transported to the Deer Island Sewage Treatment Plant in Boston Harbor. The city of Somerville pays $11.5 million annually to the Massachusetts Water Resource Authority to treat stormwater and sewage at Deer Island. In wet weather, the system cannot accommodate the large volume of water and sewage can back up in people's houses. To solve this problem, there are wet weather outfalls called CSOs (combined sewer overflows). If the system is overburdened, untreated water leaves the system through these outfalls instead of into people's basements. This is good for people's basements but horrible for water quality in the rivers receiving this raw sewage.

In March 2010, large storms overwhelmed water treatment facilities in and around Boston. To prevent backups into houses, the Massachusetts Water Resources Authority released 15 million gallons of untreated sewage into Quincy Bay (Abel, 2010). This storm was record-breaking, but even typical levels of precipitation can produce large runoff volumes.

Currently, building owners pay for the potable water they take in and the waste water they produce. Building owners do not directly pay for the stormwater runoff created on their property. Water from rain gutters is generally released onto the ground and then flows into storm drains. Thus, the city (and consequently the taxpayers) pays a great deal of money on treating stormwater. But there is currently no incentive for a building owner to improve how they manage stormwater on their property.

If 3.5 ft precipitation per year, then each square foot of impervious surface produces 3.5 cubic feet of stormwater, which costs $0.31 per year. A residential lot (3,000 sq ft) produces 10,500 cubic feet stormwater, $930 per year. A small commercial lot(10,000 sq ft) produces 3500 cubic feet stormwater, $3,100 per year. A large commercial lot (50,000 sq ft) produces 175,000 cubic feet stormwater, $15,500 per year.

In Europe, 121 experimental extensive green roofs retained, on average, 50% of total annual precipitation (Mentens et al., 2006). A green roof at the Ford Motor Plant in Michigan retained on average 45% of rain, ranging from 19-98% for individual storm events (DeNardo et al., 2005). If a green roof in Somerville absorbs 50% of total precipitation, this would save $0.15 per sq ft per year. Over

10 years, a green roof would save $1.50 per sq ft per year. If one small commercial building (15,000 sq ft) installed a green roof, the City of Somerville would save $2250 per year in stormwater treatment. If the green roof was in place for 10 years, this would save the City $22,500. If one large commercial building (50,000 sq ft) installed a green roof, the City of Somerville would save $7500 per year in stormwater treatment. After 10 years, the City would save $75,000.

In 2010, I interned with Somerville Alderman Rebekah Gewirtz to investigate ways to promote the use of green roofs and other types of green infrastructure in Somerville. I presented my findings to the Somerville Board of Aldermen at their April 23, 2010 meeting. I recommend the creation of an incentive-based stormwater management program. In this program, Somerville residents would be rewarded financially and socially for instituting responsible stormwater practices on their property. In addition to green roofs, I also recommend five other stormwater best management practices (BMPs) that could be instituted in Somerville—pervious pavement, infiltration trenches, dry wells, rain barrels, and landscaping.

Future research

There are two avenues of research that would be especially valuable for the North American green roof industry: compiling a continent-wide database of plant performance on green roofs and surveying invertebrate diversity and abundance on green roofs.

As shown in Chapter 3, there is a disconnect between beliefs regarding what types of plants should be used on green roofs and what plants have proven to be suitable. There are several reasons for this. First, most green roof praciticioners rarely publish in scientific journals, so their knowledge travels primarily by word of mouth. Second, among green roof researchers who do publish in scientific journals, there is likely publication bias against so-called “negative results.” A solution to both of these dilemmas is the creation of a large-scale database of green roof plant growth and survival. Many of these databases already exist for gardeners. Such a database would be useful for green roof designers and researchers.

Data collected in Europe and the United States suggest that green roofs can provide habitat for birds, bees, spiders, mites, beetles, grasshoppers, and butterflies (Baumann, 2006; Brenneisen, 2006; Coffman and Davis, 2005; Colla et al., 2009; MacIvor and Lundholm, 2010). Green roofs may be especially effective as refuges for both domestic honey bees as well as wild hymenopteran pollinators, many of which are able to thrive in fragmented habitats typical of urban areas (Fetridge et al., 2008). Wild bee populations are declining in North America (Colla and Packer, 2008) and Europe (Biesmeijer et al., 2006) – a phenomenon with massive economic costs, as the role of insect pollinators in agriculture has been valued at $217 billion worldwide (Gallai et al., 2009). There have been two recent studies that have examined insect diversity and abundance on green roofs in Canada. Colla et al. (2009) found more than 50 bee species on two green roofs in Toronto. MacIvor and Lundholm (2010) found 253 morphospecies of insects on green roofs in Nova Scotia. These experiments begin to give us a sense of the insect diversity that green roofs can support. What would be great now is to build on these experiments by training citizen scientists to collect data from green roofs across the continent. An example of citizen science is the Audubon Society's Christmas Bird Count, begun in 1900 (National Audubon Society, Christmas Bird Count). Each year, citizen scientists across North America survey bird populations in their area. The data are then compiled and made available to the public and to researchers. Data from these surveys has resulted in hundreds of peer-reviewed journal articles (National Audubon Society, Christmas Bird Count Bibliography of Scientific Articles). In the case of the proposed study, citizen scientists could be building occupants, maintenance personnel, local students, or local community members. Such an endeavor would not only increase our knowledge of these emerging ecosystems but also engage citizens in scientific research.

By encouraging more scientific research on green roof plant communities and the open sharing of ideas and findings, the North American green roof industry can make great progress and gain a better understanding of how to create beautiful, functional green roofs.

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