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Short communication

The effects of substrate depth heterogeneity on plant species coexistence on an extensive green roof

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ABSTRACT

Green roofs are often planted with mixtures of plant species. Studies of green roof plant community composition over time show that species diversity often declines, in part due to competition between plant species. The incorporation of substrate depth heterogeneity into green roof designs is expected to increase habitat heterogeneity, and could reduce interspecific competition among plants, but this has not been tested empirically. Two species with contrasting responses to substrate depth and water availability, *Festuca rubra* and *Sedum acre*, were planted in a rooftop substrate depth heterogeneity experiment. There were a total of four treatments: three homogeneous treatments (substrate depth 5 cm, 10 cm, and 15 cm) and one heterogeneous treatment (patches with substrate depths of 5 cm and 15 cm), with the same substrate volume and average depth as the 10 cm homogeneous treatment. By the end of the study period there was little difference in the ratio of species' cover between the 10 cm and 5/15 cm treatment. However, there was significantly less spread of each species into areas planted with the other species in the 5/15 cm treatment compared to the 10 cm treatment, and the 5/15 cm (heterogeneous treatment) had significantly greater overall plant cover. The results suggest that, while the effects are subtle, soil depth heterogeneity could allow coexistence of species associated with different conditions for longer than homogeneous conditions, and could result in greater plant species diversity in green roof ecosystems.

1. Introduction

Recent research indicates that the choice of plant species used in green roof vegetation can affect the provisioning of ecosystem services such as storm water retention (Dunnett et al., 2008a; MacIvor and Lundholm, 2011; Nardini et al., 2012; Nagase and Dunnett, 2012), reduction of hot-season roof temperatures (Lundholm et al., 2010), and biomass production and carbon capture (Getter et al., 2009; Song et al., 2013). Such differences in plant performance stem from anatomical, morphological and physiological traits of plant species (Farrell et al., 2012, 2013a) and can be used to engineer green roof ecosystems for optimal performance.

Species mixtures have the potential to improve green roof functioning relative to monocultures (Ranalli and Lundholm, 2008; Cook-Patton and Bauerle, 2012). Combinations of functionally distinct species are predicted to enhance overall resource consumption and to increase plant biomass (Kinzig et al., 2001), which in turn may affect several green roof ecosystem services (Lundholm et al., 2010).

In natural plant communities, sustained coexistence is expected only when species competing for resources have key differences in their resource requirements or in their responses to the abiotic environment (Chesson, 2000). While there are many possible ways in which such niche differentiation can allow greater species diversity, some of the most common mechanisms involve spatial heterogeneity in the environment. Plant species that vary in their response to environmental conditions are thought to be able to coexist if the environment is heterogeneous and the species can disperse to those microsites with optimal characteristics for their growth and survival (Lundholm, 2009). In engineered ecosystems, we can incorporate heterogeneity at the appropriate scales and plant species associated with these different conditions.

Spatial heterogeneity has been incorporated into green roof designs with the purpose of increasing species diversity of arthropods and plants (Brenneisen, 2006). Green roof designers vary substrate depths and create habitat heterogeneity by adding surface features such as coarse woody debris, piles of stones or different kinds of substrate (Bates et al., 2013). These measures are thought to encourage greater species diversity in invertebrate and

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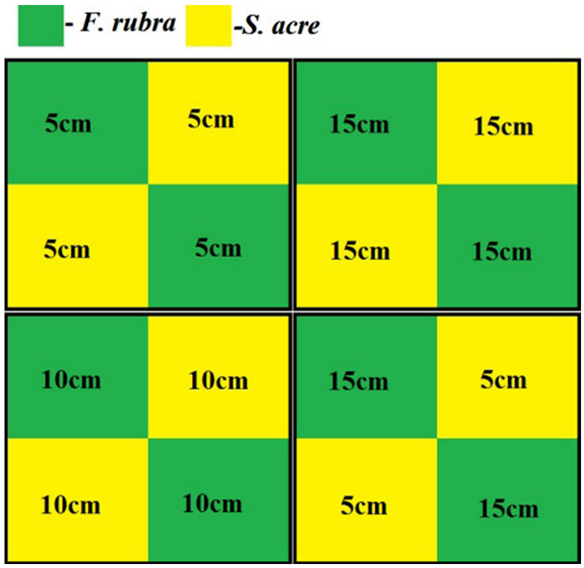

Fig. 1. Orientation of *F. rubra* and *S. acre* in the four different treatments.

plant communities by allowing more species to find appropriate microsites than on a more homogeneous roof. While there is little published on the effects of these designed features, one empirical study has shown a positive relationship between indices of habitat heterogeneity and species diversity of invertebrates (Gedge and Kadas, 2005). A recent study comparing three types of green roofs also showed that roofs with more structural complexity in the vegetation (i.e. spatial heterogeneity generated by the plant canopy) did support more species of arthropods (Madre et al., 2013). Bates et al. (2013) observed that the survival of certain plant species is facilitated by specific microsites on green roofs where habitat heterogeneity was purposefully incorporated into the system, warranting further exploration of the role of spatial heterogeneity on green roofs. Spatial heterogeneity in substrate depth should create corresponding variability in substrate moisture and thus support both species that require wetter conditions and drought-tolerant species, leading to greater overall diversity (Brenneisen, 2006; Köhler and Poll, 2010).

Here we hypothesized that two species with contrasting responses to substrate depth would display a greater ability to coexist under conditions of heterogeneous substrate depth, compared with homogeneous conditions. This study involved experimentally comparing green roof systems featuring heterogeneous substrate depths with homogeneous substrate depths, while controlling for mean substrate depth. We used a grass, expected to dominate in deeper substrates, and a *Sedum*, expected to dominate in shallower substrates. We expected plant sizes and coverage between the two species to be more even in the heterogeneous vs. homogeneous treatments, indicating a greater likelihood of coexistence.

2. Methods

The study site was located on the roof of the five-story Atrium building at Saint Mary's University in Halifax, Nova Scotia, Canada (44°39′ N, 63°35′ W) (Fig. 1). This experiment included four different substrate depth treatments: three homogeneous treatments, 15 cm, 10 cm, and 5 cm and one heterogeneous treatment, wherein half of the substrate had a depth of 5 cm, and the other half a depth of 15 cm (henceforth, the 5/15 cm treatment). We created the depth treatments by varying the depth below the substrate surface, in order to maintain an even substrate surface, so we could examine the effects of substrate depth alone without also changing the vertical profile of the substrate. According to previous research, we predicted that the *Sedum* should outperform the grass at 5 cm and the grass should outperform the *Sedum* at 15 cm in terms of growth (Dunnett and Kingsbury, 2004). Therefore, the mixed 5/15 cm substrate depth should decrease the competition between these two species. The volume of substrate used in the 10 cm treatment was equal to that used in the 5/15 cm treatment, and these two treatments had the same average substrate depth, allowing us to separate the potential effects of average substrate depth from those of spatial heterogeneity in substrate depth (e.g. Vivian-Smith, 1997).

The treatments consisted of 24 wooden planter boxes (61 cm × 61 cm); which were 15 cm high with no base. A nursery-grade weed control fabric (Quest Home & Garden, Mississauga, ON, CA) was placed under the boxes to prevent damage to the roof. To create four different substrate depth treatments, 5 cm thick concrete slabs (length and width of 60.96 cm) were placed in the wooden boxes to manipulate substrate depth. Two concrete slabs were used for the 5 cm substrate depth, one for the 10 cm depth and no concrete slabs were used for the 15 cm substrate depth. The 5/15 cm substrate depth treatment involved four concrete slabs, each 30.48 cm by 30.48 cm with a thickness of 5 cm, placed two high diagonally across from each other in a wooden box, to create two squares with a substrate depth of 5 cm and two with 15 cm. A root barrier/water retention fleece was placed in all boxes above the concrete slabs (EnkaRetain and Drain 3111®, Colbond Inc., NC, USA). The boxes were then filled to the rim with Sopraflor X substrate purchased in 2012 (Soprema Inc., Drummondville, QC, CA) (for substrate chemistry, see supplemental data).

Plant species used included *Sedum acre* and *Festuca rubra*, which were chosen due to their different drought tolerance and water usage, as observed in previous trials (MacIvor and Lundholm, 2011). Both species were harvested in May 2012 from previous experiments at Saint Mary's and the Dartmouth Commons (*S. acre* only) in Dartmouth, Nova Scotia, Canada. Once harvested, plants were transplanted directly into the planter boxes until ~25–45% cover was achieved in each quarter of the box. Initially, each quadrant contained either 1–3 individual *S. acre* plants (average height 7.4 cm) or 2–12 individual *F. rubra* plants (average height 22.6 cm). After planting, the vegetation was watered twice over a two-week period to encourage establishment. All planter boxes were divided into four quadrants, each containing plants from one of the two species (two squares per species per planter box, with duplicates of the same species arranged diagonally). In the heterogeneous treatment (5/15 cm), *S. acre* was planted in the 5 cm depth quadrants, and *F. rubra* was planted in the 15 cm depth quadrants.

Data was collected monthly throughout the 2012 and 2013 growing seasons (June–September). Cover for each species

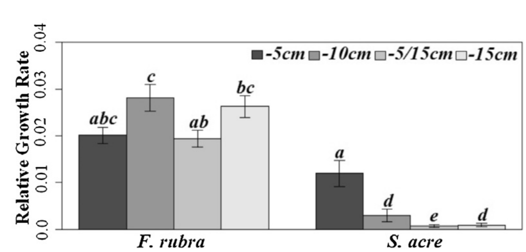

Fig. 2. The spread of *F. rubra* and *S. acre* from their original 30.48 by 30.48 cm planting by the end of the study period (September 18, 2013). The cover change was compared between both species, those bars that share a letter are not significantly different.