Urban Ecosystems (2024) 27:591–600
https://doi.org/10.1007/s11252-023-01479-w

Stress tolerant species are keys to plant communities success on extensive green roof: an experimental test of CSR strategy dynamic

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Abstract

Selecting appropriate native plant species to ensure the resilience of plant communities and ecosystem services on extensive green roofs is a challenge. Plant functional strategy models provide a useful framework for identifying plant characteristics that promote plant success on green roofs, and for generalizing results obtained with a limited number of species to a global flora. We analysed the dynamics of floristic composition and CSR strategies of seeded plant communities on experimental extensive green roofs under different stress conditions (substrate depths and fertilization treatments) at early establishment (4 years). Floristic composition evolved strongly over four years, with a significant reduction in species richness and equitability due to the increasing dominance of the stress-tolerant *Sedum album*. CSR strategies shifted from initial communities co-dominated by C and R strategies to communities largely dominated by S strategy four years later. Changes in plant communities strategy were modulated by substrate depth, with a higher increase in S strategy under more stressful conditions. At the installation of vegetation, the dominant factor discriminating CSR composition was fertilization supply. Substrate depth emerged as the primary factor determining CSR strategy after four years of plant community establishment. Our study supports the pattern that stress-tolerant species tend to rapidly dominate plant communities on extensive green roofs and suggests that native species selection for implementing analogous habitat on extensive green roofs, in a temperate climate, should primarily focus on natural habitats composed of stress-tolerant species. A mix of different functional strategies can be favourable to vegetation success on green roofs with environmental heterogeneity.

Keywords Plant selection · Substrate depth · Fertilization · Analogous habitat

Introduction

Green roofs provide a diversity of ecosystem services in urban environments, including support for urban biodiversity, water and climate regulation, aesthetics, and well-being (Madre et al. 2014; Gonsalves et al. 2022; Czemiel Berndtsson 2010; Nguyen Dang et al. 2022). Plant communities (in terms of composition and diversity) play a key role in the provision of ecosystem services on green roofs (Farrell et al. 2022). Hence, plant community resistance and resilience to environmental conditions and disturbances are crucial factors influencing the efficiency of green roofs in delivering ecosystem services (Shahmohammad et al. 2022). Extensive green roofs, which are characterized by shallow substrate depth and low weight load, are a popular choice due to their lower constraints on building structures compared to intensive green roofs (Getter and Rowe 2006). However, plant communities on extensive green roofs face limitations concerning their ability to withstand drought conditions depending on substrate depth, extreme temperature fluctuations (Oberndorfer et al. 2007) and nutrient content (FLL 2008). Studies on the dynamics of green roof plant communities have shown that species composition shifts over time, with some desired species becoming extirpated from the system (Rivière et al. 2022; Brown and Lundholm 2015). To ensure the long-term persistence of vegetation on green roofs and the provision of multiple ecosystem services, green roof ecologists advocate increasingly for extending the diversity of plant selection beyond the traditional succulent *Sedum* species, typical of extensive green roofs (Nagase

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and Dunnett 2010; Madre et al. 2014; Brown and Lundholm 2015).

The success of plant species and the evolution of plant communities depend on the microenvironmental conditions of green roofs (MacIvor and Lundholm 2011; Brown and Lundholm 2015; Rivière et al. 2022). Plant species selection for green roofs should consider specific conditions present on the roof, including factors such as substrate depth, sun exposure, building insulation, nutrient content, etc. (Brown and Lundholm 2015; Rivière et al. 2022). The analogous habitats hypothesis proposes that species adapted to similar conditions on the ground can also be successful on green roofs (Lundholm 2006). While this approach has successfully identified local sets of species that can tolerate the conditions of extensive green roofs (Ksiazek-Mikenas et al. 2021; Rivière et al. 2022), it rarely allows generalizations to other situations. In temperate climate, extensive green roofs are generally considered analogous to rocky and dry grasslands habitats (Rivière et al. 2022), but the dynamics of plant communities may also make extensive green roofs prone to the development of ruderal species typical of fallow habitats (Lundholm et al. 2014; Thuring and Dunnett 2019).

Natural habitats provide an immense reservoir of plant species that can be used on extensive green roofs. Individually testing each candidate species is impossible. Using plant functional strategy to understand plant characteristics promoting success on green roofs allows us to generalize results from studies with a limited number of species to a global flora. The theory of functional ecology allows for studying the variations of functional traits in response to variation and changes in environmental conditions, as well as understanding the temporal dynamics of plant communities (Grime 1988; Garnier, Navas, and Grigulis 2016; Violle et al. 2007). To better understand the success and dynamics of plant communities on green roofs, the functional response of these plant communities to environmental stressors can be studied with the CSR strategies model (Lundholm et al. 2014; Thuring and Dunnett 2019). The CSR strategies integrate plant anatomical, morphological, and physiological characteristics (functional traits) into general syndromes (C-S-R) that represent different evolutionary responses to biotic and abiotic constraints. According to the CSR model, plant species are classified into different strategies based on their survival and reproduction in response to environmental stress and disturbance intensity. Competitors (C) exploit conditions of low stress and low disturbance; stress-tolerants (S) exploit high stress, low disturbance habitats; and ruderals (R) exploit low stress, high-disturbance situations (Grime 1974). There are also intermediate strategies among these three main strategies (Grime 1977) which, together with stress tolerant, commonly occur in plant communities found on older green roofs (Thuring and Dunnett 2019). These strategies can be seen as responses to gradients of environmental stress and disturbances, which are characteristics of an extensive green roof environment (Nagase and Dunnett 2010).

CSR strategies also provide a framework for understanding the temporal dynamics of plant communities. Extensive green roof vegetation can be considered as a form of primary succession, as the bare substrate develops into a plant community through seeding or spontaneous colonization (Brown and Lundholm 2015). Based on a literature review, Grime (2001) suggested that, in general, life strategies of dominant species shift during the course of primary succession from stress-tolerating pioneers to more competitive strategists. This hypothesis has been disputed on various time scales by those who have observed different patterns of primary succession at glacier retreat fronts (Caccianiga et al. 2006), on land along uplifted coasts (Ecke and Rydin 1999), and on mineral substrates of abandoned quarries (Pitz et al. 2018). Thuring and Dunnett (2019) suggested that long-term floristic diversity on extensive green roofs may be facilitated by ensuring a diversity of traits and species at the time of installation. However, little is known about the dynamics of CSR strategies on extensive green roofs, even during the installation and early establishment period, which is crucial for determining the trajectory of vegetation development. The stressful environmental conditions of extensive green roofs may favour stress-tolerant species, depending on the local environmental conditions. In less stressful conditions, such as higher nutrient availability or deeper substrate depth with less drought conditions, ruderal or competitive strategies may dominate the plant community. In this context, the habitat analogous hypothesis can be extended to other (semi-) natural habitats than dry grassland that share similar environmental conditions, such as meadows or urban fallow. Generalist species may also be suitable for extensive green roofs (Thuring and Dunnett 2019).

The objective of this study is to analyse, through an experimental approach, the early dynamics of floristic composition and CSR composition of plant communities under different stress situations (substrate depth and initial fertilization) on extensive green roofs, both at the time of installation and after a 4-year period.

Material and methods

Study site and experimental design

The experiment was conducted at Gembloux Agro-Bio-Tech, Belgium (50°33’48” N 4°41’52” E). The climate in the region is a temperate oceanic climate (Cfb - Köppen climate classification) (Service fédéral belge 2022).

The experiment consisted of 32 mini extensive green roof trays with dimensions of 100 cm X 80 cm X 20 cm (hereafter designated as GR). Each GR was composed of a drainage layer (Floraset® FS 50, Zinco©), a filter layer (Filter system SF, Zinco©) and a substrate typically used on European green roofs provided by a green roof manufacturer (lightweight substrate for extensive green roofs 6.6%clay −20.7%silt −72.7%sand, Zinco©). Two substrate depth modalities (10 or 15 cm), providing two levels of hydric stress (Ladani et al. 2019), were crossed with two fertilization modalities (fertilized or not fertilized). Fertilization consisted of a one-time application of 20 g of fertilizer for green roofs (Pflanzenfit 4 M NPK 23-5-10, Zinco©) at the time of seeding. GR were placed on the ground on an urban mineral zone with a random assignment of substrate X fertilization modalities, without any shade.

According to their habitat, seven native herbaceous species were selected per CSR strategy (Fig. 1). Competitive strategy species (C) were selected from a pool of characteristic meadow species. Ruderal strategy species (R) were selected from a pool of characteristic urban fallow species. Stress-tolerant strategy species (S) were selected from a pool of characteristic dry grassland species. Intermediate strategy species (CSR) were selected from a pool of local native generalist species. The database from Hunt et al. (2004) was used to determine the strategy of each species. For each GR, all seeds of the 28 species were mixed together before being sown by hand. One hundred seeds per square metre per species were seeded in April 2019, followed by a 2 L watering per tray.

Data collection and analysis

For each species, vegetative cover was visually estimated based on a continuous scale in each GR in June 2019 (year1) and in May 2022 (year4). For both years, C-S-R plant community scores – CSR signatures sensu Hunt et al. (2004) (sum of individual species C-S-R scores weighted by the relative mean cover of species) were calculated for the plant community of each GR using the spreadsheet-based tools from Hunt et al. (2004).

In a first step, floristic composition and CSR strategy were analysed over the entire data set, considering together time since GR installation (year1 – year4) and environmental factors (substrate depth and fertilization). The mean relative cover of each species per GR was calculated for year1 and year4 to identify the dominant species and their succession between years.

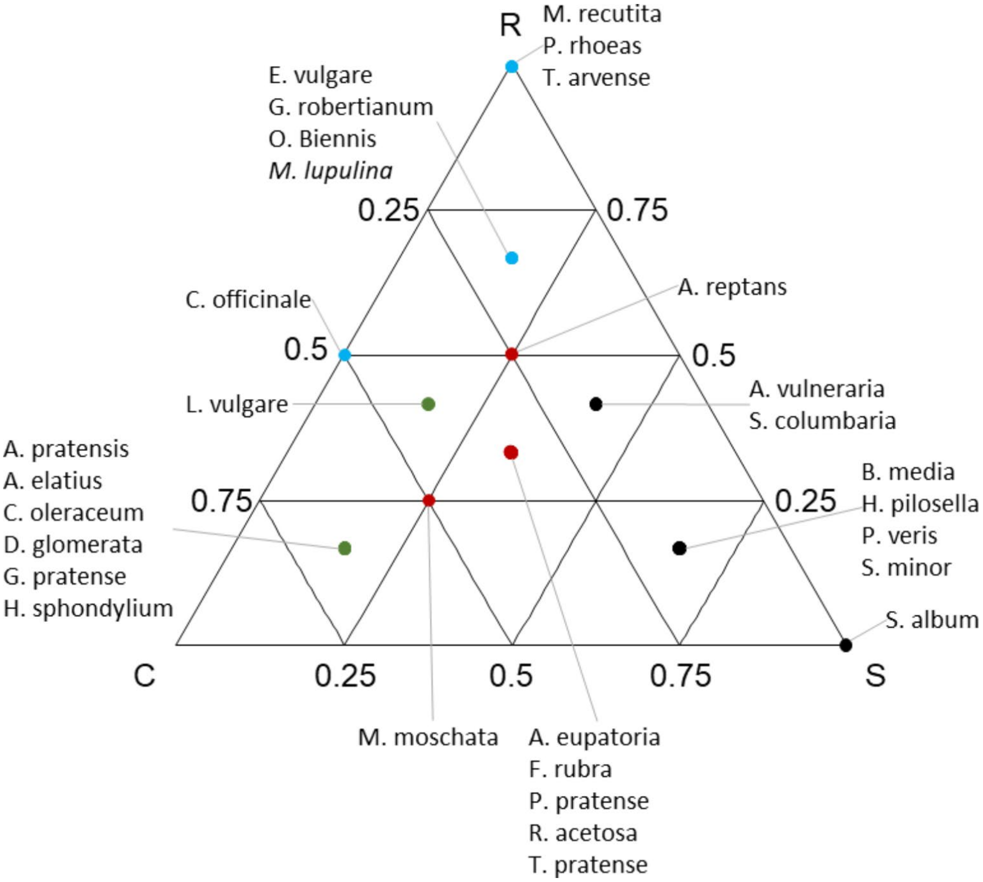

Fig. 1 Position of seeded and spontaneous species in the Grime's CSR triangle. Dot colour indicates the strategy of the species retained for species selection: green – C, black - S, Blue - R, red - CSR. The spontaneous species is shown in italics

To study the influence of time since installation (year1 – year4), substrate depth and fertilizer supply on the species richness of each GR, we performed a linear mixed model analysis with repeated measures. We used the lmer function (lme4) (Bates et al. 2020) and the Anova function (car) (Fox et al. 2020). To evaluate the diversity of plant communities of each GR, equitability (evenness) was estimated with the Pielou index ("diversity" and "specnumber", vegan) (Pielou 1966). To study the influence of time since installation (year1 – year4), substrate depth and fertilizer supply on the Pielou index, we performed a linear mixed model analysis with repeated measures. We used the lmer function (lme4) and the Anova function (car). All residuals were visually examined for heteroscedasticity, and logarithmic transformations were applied as needed to fulfil the model assumptions.

Table 1 Mean percentage of relative cover per species (+/- Sd) per GR in year1 and year4, species code and species CSR strategy. Bold species are dominant species. Number of species per strategy are indicated for both years

Species	Code	CSR strategy	Year1	Year4
Alopecurus pratensis L.	Alo_pra	C	10 ± 4	7 ± 6
Anthyllis vulneraria L.	Ant_vul	S	< 1	2 ± 6
Echium vulgare L.	Ech_vul	R	3 ± 3	< 1
Geranium pratense L.	Ger_pra	C	< 1	2 ± 3
Geranium robertianum L.	Ger_rob	R	4 ± 3	< 1
Hieracium pilosella L.	Hie_pil	S	6 ± 4	< 1
Leucanthemum vulgare Lamk.	Leu_vul	C	9 ± 4	1 ± 4
Malva moschata L.	Mal_mos	CSR	1 ± 3	< 1
Sanguisorba minor Scop.	San_min	S	3 ± 2	2 ± 4
***Sedum album*L.**	Sed_alb	S	< 1	
***Trifolium pratense*L.**	Tri_pra	CSR	**23 ± 9**	
Cirsium oleraceum (L.) Scop.	Cir_ole	C	< 1	0
Dactylis glomerata L.	Dac_glo	C	16 ± 7	0
Festuca rubra L.	Fes_rub	CSR	5 ± 4	0
Matricaria recutita L.	Mat_rec	R	7 ± 5	0
Papaver rhoeas L.	Pap_rho	R	5 ± 3	0
Phleum pratense L.	Phl_pra	CSR	6 ± 3	0
Rumex acetosa L.	Rum_ace	CSR	< 1	0
Thlaspi arvense L.	Thl_arv	R	< 1	0
Agrimonia eupatoria L.	Agr_eup	CSR	0	< 1
Cynoglossum officinale L.	Cyn_off	R	0	< 1
***Medicago lupulina*L.**	Med_lup	R	0	
Scabiosa columbaria L.	Sca_col	S	0	< 1
Ajuga reptans L.	Aju_rep	CSR	0	0
Arrhenatherum elatius (L.) P.Beauv.	Arr_ela	C	0	0
Briza media L.	Bri_med	S	0	0
Heracleum sphondylium L.	Her_sph	C	0	0
Oenothera biennis L.	Oen_bie	R	0	0
Primula veris L.	Pri_ver	S	0	0
CSR Strategy			**Nb species**	
			Year1	**Year4**
C			5	3
S			4	5
R			5	4
CSR			5	3

To order the variation of taxonomic species composition according to sampling period (year1 – year 4), substrate depth and fertilizer supply, we performed a global Principal Coordinate Analysis (PCoA) ("cmdscale", stats) on species abundance (cover) for all mini GR. To identify the species correlated with the axes of this PCoA in a correlation circle, we calculated a Pearson correlation for each species ("cor", stats).

To study the influence of substrate depth and fertilizer supply on the evolution of CSR strategy between year1 and year4, a two-ways ANOVA ("aov", stats) was performed on C-S-R scores of GR plant communities. No transformation was necessary to meet the assumptions of statistical analyses.

In a second step, to identify the specific effect of environmental factors independently of time effect, floristic composition and CSR strategy were analysed in relation to environmental factors (substrate depth and fertilization) separately for year1 and year4.

To study the influence of substrate depth and fertilizer supply on taxonomic species composition for each year (year1 and year4), we performed a global Principal Coordinate Analysis (PCoA) ("cmdscale", stats) on all GR for each year independently. To identify the species correlated with the axes of this PCoA in a correlation circle, we calculated a Pearson correlation for each species ("cor", stats).

To study the influence of substrate depth and fertilizer supply on the C-S-R scores of GR plant communities, we performed a Kruskal-Wallis test ("kruskal.test", car (R Core Team 2022) for each year independently.

All data analyses were performed in R.4.0.2 (R Core Team 2022).

Results

Over the entire experiment, 20 out of 28 seeded species grew in year1 compared to 15 in year4 (Table 1). The mean plant cover per GR evolved from 62 ± 21% in year1 to 92 ± 23% in year4. The number of species per strategy was rather similar in year1 (C: 5, S: 4, R: 5, CSR: 3). At the end of experiment, the variation in species richness per strategy was limited, but more marked for C and CSR strategies (C: -2, S: +1, R: -1, CSR: -2) (Table 1).

The result of the repeated ANOVA (year, substrate depth and fertiliser supply) on the species richness showed no significant interactions between substrate depth and fertiliser supply (Supplementary materials). The mean species richness per GR decreased significantly from 12.53 ± 1.52 in year1 to 9.09 ± 3.06 in year2 (P < 0.001). Substrate depth (P = 0.53) and fertiliser supply (P = 0.40) did not significantly influence mean species richness per GR. The result of the repeated ANOVA (year, substrate depth and fertiliser supply) on the Pielou equitability index showed no significant interactions between substrate depth and fertiliser supply (Supplementary materials). The mean evenness (Pielou equitability index) per GR decreased significantly from 0.88 ± 0.04 in year1 to 0.72 ± 0.14 in year2 (P < 0.001). Substrate depth (P = 0.44) and fertiliser supply (P = 0.66) did not significantly influence the mean Pielou equitability index per GR.

The first and second axes of PCoA (Fig. 2) based on the species composition of GR for year1 and year4 explained 46.84% of global floristic variation (PCoA1 = 39.62%, PCoA2 = 7,22%). The PCoA clearly discriminated GR vegetation from year1 and year4 and indicated more homogeneous vegetation across GR in year1 than in year4. Time since seeding discriminated more GR plant communities than substrate depth or fertilizer supply. However, in year4, substrate depth tended to differentiate plant communities along axis 2.

The plant community was dominated in year1 by *Trifolium pratense* L., a seeded CSR strategy species (mean relative cover = 23 ± 9%) and in year4 by *Sedum album* L., a seeded S strategy species (mean relative cover = 44 ± 16%) and the spontaneous colonizing species *Medicago lupulina* L., a R strategy species (mean relative cover = 25 ± 17%) (Table 1). The only non-seeded species observed was *M. lupulina*.

Plant community strategy shifted through time, with initial communities co-dominated by C strategy (mean C-score year1: 0.36 ± 0.04) and R strategy (mean R-score year1: 0.38 ± 0.05), with a lower contribution of S strategy (mean S-score year1: 0.25 ± 0.03), to communities largely dominated by S strategy four years later (mean S-score year4: 0.59 ± 0.12). This was due to a strong increase in S strategy (+ 136.4 ± 63.9%), a strong decrease in C strategy (year4: 0.15 ± 0.06, -54.4 ± 17.8%) and a decrease in R strategy (year4: 0.26 ± 0.08, -30.4 ± 25.4%) (Table 2).

Changes in plant communities strategy were modulated by substrate depth. Increase in S strategy was significantly higher in more stressing 10 cm depth substrate (+ 165.1 ± 66.7%) than in less stressing 15 cm depth substrate (+ 107.8 ± 50.2%) (P = 0.005). Decrease in C strategy was significantly lower in lower stressing 15 cm substrate (-46.1 ± 18.4%) than in higher stressing 10 cm substrate (-68.7 ± 8.2%) (P < 0.001). Level of fertilization also significantly influenced the evolution of S and C strategies in plant communities. Increase in S strategy was significantly higher in fertilized GR (+ 162.2 ± 68.4%) than in non-fertilized GR (+ 110.7 ± 50.93%) (P = 0.011). Decrease in C strategy was significantly lower in fertilized GR (-62.7 ± 15.1%) than in non-fertilized GR (-52.1 ± 19.8%) (P = 0.03) (Table 2).

To remove the time effect and analyse in detail the influence of each factor at the time of installation and after 4 years, we ran a PCOA on species composition and analysed the effect of substrate depth and fertilisation on CSR strategies for each year independently.

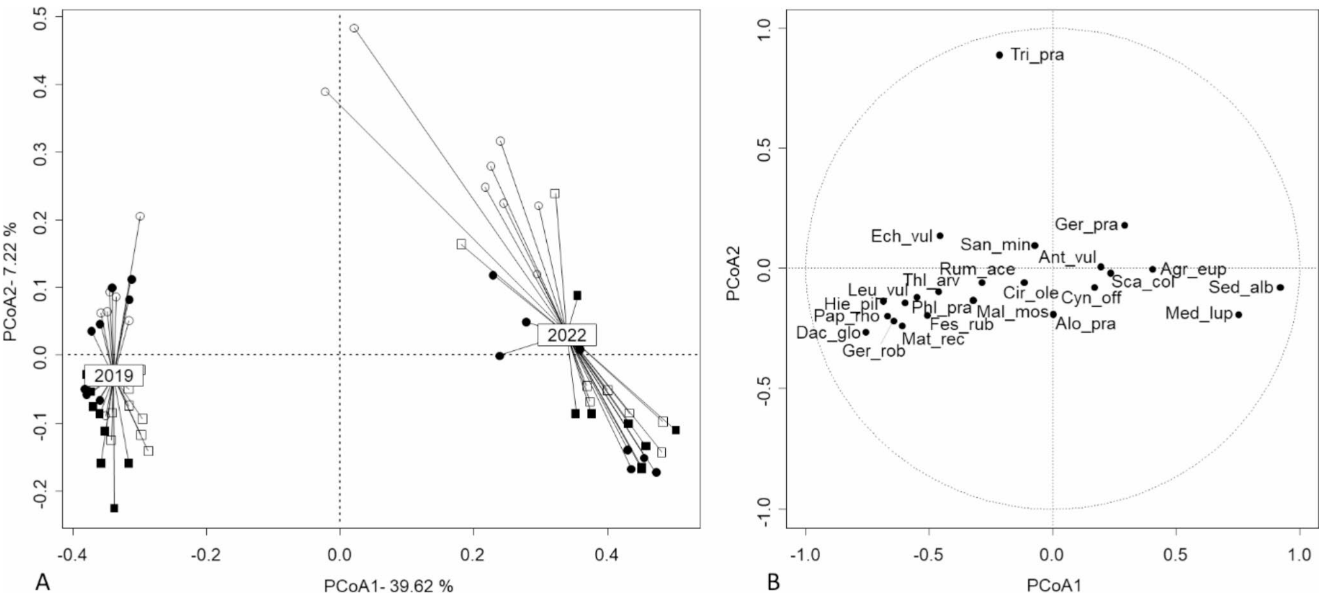

Fig. 2 PCoA based on species composition of GR (**A**) Ordispiders are pooled by year. Symbols represent substrate depth (square = 10 cm; circle = 15 cm) and fertilizer supply (white = without; black = with). (**B**) Correlation circle of species. See Table 1 for species name

Table 2 Percentage of the evolution of CSR strategy between year1 and year4 and results of two-ways ANOVA testing the influence of substrate depth (10 and 15 cm) and fertilizer supply (0: without; 1: with) on the evolution of CSR strategies (%) between year1 and year4. Positive values indicated an increase and negative values a decrease. P-values of ANOVA analysis are indicated, bold values indicated significant influence

Strategy	Evolution between year1 and year4	Interaction	Substrate depth			Fertilizer supply		
		P	10	15	P	0	1	P
C	-54.4 ±17.8	0.23	-68.7 ±8.2	-46.1 ±18.4	**< 0.001**	-52.1 ±19.8	-62.7 ±15.1	**0.030**
S	136.4 ±63.9	0.47	165.1 ±66.7	107.8 ±50.2	**0.005**	110.7 ±50.93	162.2 ±68.4	**0.011**
R	-30.4 ±25.4	0.44	-38.5 ±23.4	-22.3 ±26.2	0.073	-24.4 ±25.1	-36.4 ±25.8	0.182

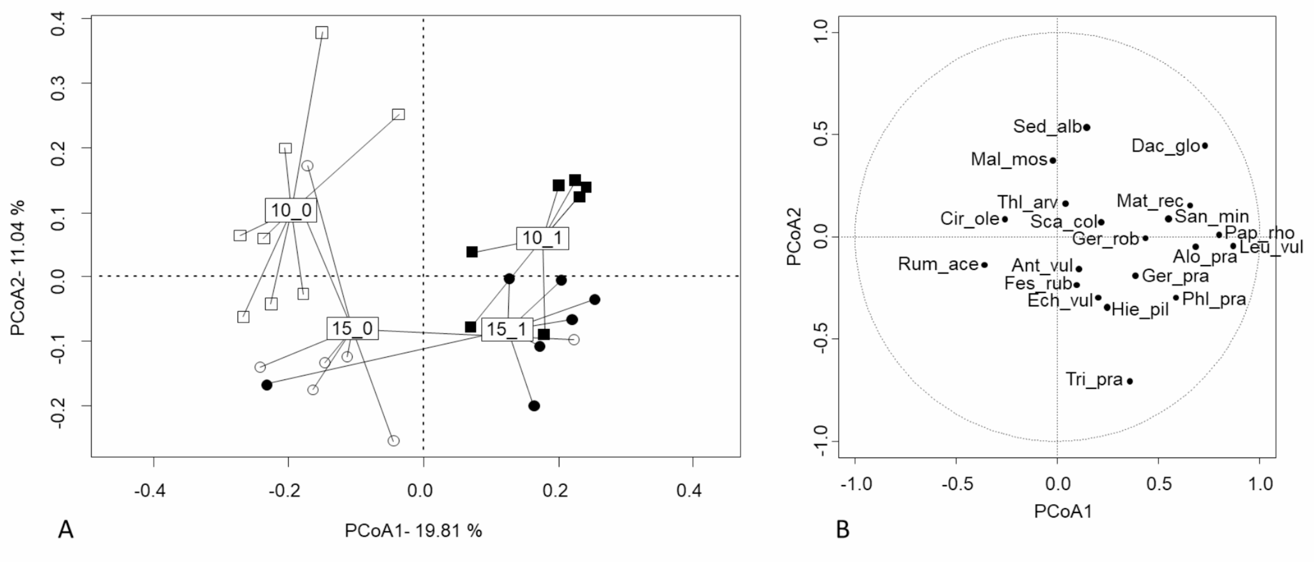

Fig. 3 PCoA based on year1 species composition of GR (**A**) Ordispiders are pooled by environmental conditions. Symbols represent substrate depth (square = 10 cm; circle = 15 cm) and fertilizer supply (white = without; black = with). (**B**) Correlation circle of species. See Table 1 for species name

In year1, the first and second axes of PCoA (Fig. 3) based on the species composition of GR plant communities explained 30.85% of global floristic variation (PCoA1 = 19.81%, PCoA2 = 11.04%). The PCoA showed that substrate depth and fertilizer supply influenced the plant community composition. Axis 1 differentiated plant communities according to fertilization with non-fertilized GR on negative coordinates and fertilized GR on positive coordinates. Axis 2 differentiated plant communities according to substrate depth with 15 cm depth substrate on negative coordinates and 10 cm depth substrate on positive coordinates. *Leucanthemum vulgare* Lamk. and *Papaver rhoeas* L. were correlated to the first axis with fertilization supply.

In year4, the first and second axes of PCoA (Fig. 4) based on species composition of GR plant communities explained 41.01% of global floristic variation (PCoA1 = 26.06%, PCoA2 = 14.97%). The PCoA showed a differentiation of GR plant communities with 15 cm substrate depth and no fertilization from the other modalities along the first axis. Correlation circle of species indicated that the three species *Trifolium pratense* L. (CSR), *Sedum album* L. (S) and *Medicago lupulina* L. (R) were most correlated to axes. *T. pratense* was correlated to GR with high substrate depth and no fertilization while *S. album* and *M. lupulina* were correlated to other GR modalities.

In year1, fertilizer supply was the only environmental factor affecting the CSR strategy of GR plant communities, with a significant influence on S and R scores. Mean plant community S-score was significantly higher in non-fertilized GR (0.27 ± 0.03) than in fertilized GR (0.24 ± 0.03) (P = 0.015), although the relative difference was limited (8%). Mean plant community R-score was significantly higher (12%) in fertilized GR (0.41 ± 0.05) than in non-fertilized GR (0.36 ± 0.04) (P = 0.002). Substrate depth did not influence CSR strategies of GR plant communities at the time of plant communities installation (year1) (Table 3).

In contrast, in year4, substrate depth significantly influenced means scores of C, S, and R strategies for GR plant communities. Mean S score was significantly higher (21%) for plant communities on 10 cm substrate depth (0.66 ± 0.08)

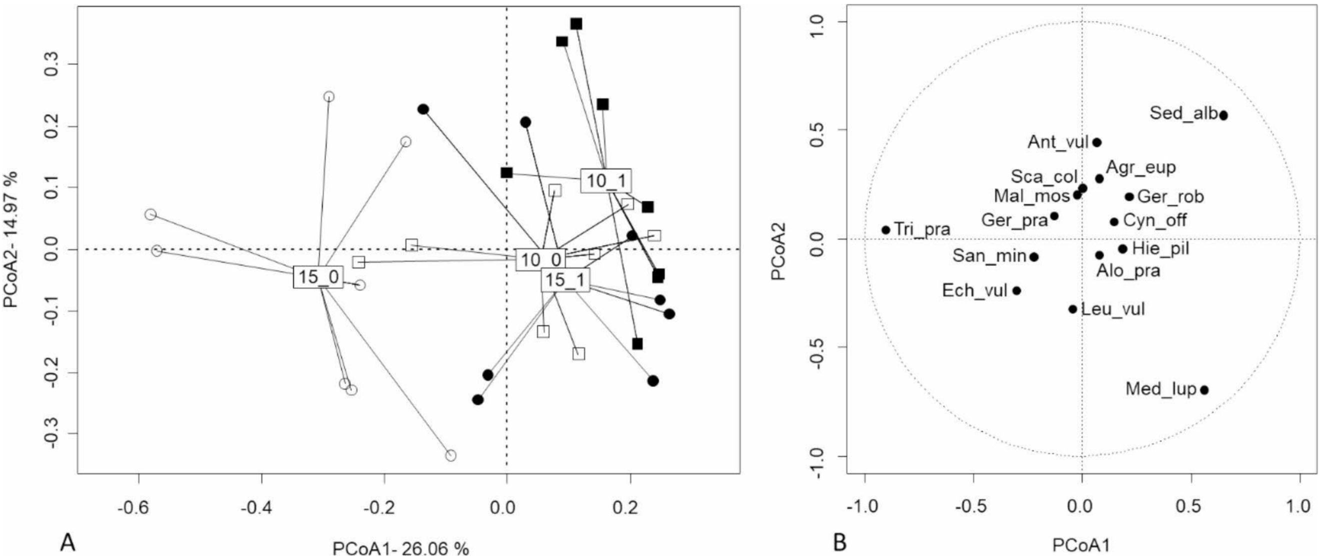

Fig. 4 PCoA based on year4 species composition of GR (**A**) Ordispiders are pooled by environmental conditions. Symbols represented substrate depth modalities (square = 10 cm; circle = 15 cm) and fertilizer supply (white = without; black = with). (**B**) Correlation circle of species. See Table 1 for species name

Table 3 Results of Kruskal- Wallis teststesting the influence of substrate depth (10 and 15 cm) and fertilizer supply (0 : without ; 1 : with) on CSR strategies scores of year1 and year4 plant community. P-values of Kruskal- Wallis tests are indicated, bold values indicated significant influence

	Substrate depth			Fertilizer supply		
Year1	10	15	P	0	1	P
C	0.36 ±0.04	0.36 ±0.04	0.57	0.38 ±0.04	0.35 ±0.03	0.08
S	0.26 ±0.04	0.25 ±0.03	0.46	0.27 ±0.03	0.24 ±0.03	**0.015**
R	0.38 ±0.05	0.39 ±0.05	0.98	0.36 ±0.04	0.41 ±0.05	**0.004**
Year4	10	15	P	0	1	P
C	0.11 ±0.03	0.19 ±0.06	**< 0.001**	0.18 ±0.07	0.13 ±0.04	**0.03**
S	0.66 ±0.08	0.52 ±0.10	**< 0.001**	0.56 ±0.11	0.62 ±0.12	0.33
R	0.23 ±0.07	0.29 ±0.08	**0.03**	0.26 ±0.07	0.25 ±0.09	0.88

than on 15 cm substrate depth (0.52 ± 0.10) (P < 0.001). The opposite pattern was observed for C and R strategies. Mean C score was significantly lower (42%) for plant communities on 10 cm depth substrate (0.11 ± 0.03) than on 15 cm depth substrate (0.19 ± 0.06) (P < 0.001). Mean R score was also significantly lower (21%) for plant communities on 10 cm depth substrate (0.23 ± 0.07) than on 15 cm depth substrate (0.29 ± 0.08) (P = 0.03) (Table 3).

Discussion

In this experimentally controlled study, we demonstrated that plant communities on extensive green roofs are subject to strong selection during their first steps of establishment, both in terms of floristic and functional composition.

Over four years, the floristic composition of experimental green roof trays evolved drastically with a decrease in species richness and equitability and a change in species dominance. At the end of the experiment, GR were largely dominated by the succulent, native *Sedum album* L. and the spontaneously colonizing species *Medicago lupulina* L., independently of the substrate depth or fertilization modalities. *Sedum* species are the main species used on extensive green roofs due to their ability to tolerate harsh environmental conditions (Vanstockem et al. 2019) and can facilitate the development of others species (Heim and Lundholm 2014; Butler and Orians 2011). In this study, we observed that native *Sedum* species can exhibit a dominant cover in the plant community, while the plant community composition often evolves over time (Köhler 2006; Aloisio et al. 2019; Ksiazek-Mikenas et al. 2021). Overall, the differences in floristic composition were higher between years than between different experimental environmental conditions, as observed by Rivière et al. (2022) in an in situ extensive green roof. However, the variation in floristic composition among the GR increased with time, but this increase was not directly related to environmental conditions. While environmental conditions, such as substrate depth and fertiliser supply, initially had a discernible effect on the species composition of plant communities in year1, with different plant communities identified for the combination of substrate X fertilization environments, the relationship became less clear in year4. The decrease in species richness and the dominance of *S. album* led to a high variability in the composition of other species between experimental green roof trays, resulting in a reduced influence of the experimental environmental conditions. The change in species richness over time and the dominance of a few species with the effects of microclimate are often observed on extensive green roofs (Bates et al. 2013; Brown and Lundholm 2015; Thuring and Dunnett 2019). These changes are generally more pronounced during the initial years following the installation of green roofs (Dunnett et al. 2008).

Changes in flora composition and differences in plant communities among the experimental environmental conditions were related to changes and differences in functional composition. Although our experimental GR were sown with a set of species representative of different CSR strategies and, hence, different traits, they rapidly evolved towards dominance of S strategy. At the time of vegetation installation, on first year, plant communities were co-dominated by C and R strategies with a lower but still significant proportion of S strategy, as observed by Lundholm et al. (2014) and by Buffam and Michell (2015). In contrast, after four years, stress tolerant strategy dominated the functional composition of plant communities, across all depth and fertilization conditions. This increase in the S strategy component over time can be attributed to the increase and dominance of *Sedum album* L. The other strategies, particularly the C strategy, declined over time across all environmental conditions. Our results contrast with the observation by Lundholm et al. (2014) that the growth of ruderals may be predominant over stress-tolerant species in the first four years following the establishment of vegetation on experimental extensive green roofs. However, an increase in S strategy has been observed on mature green roofs associated to ruderal species, maintained mainly by repeated replenishment from dispersal (Catalano et al. 2016; Ksiazek-Mikenas and Köhler 2018; Thuring and Dunnett 2019). The decline of C strategy is often observed in the succession of plant community on green roofs (Buffam and Mitchell 2015; Catalano et al. 2016; Ksiazek-Mikenas and Köhler 2018; Thuring and Dunnett 2019). The evolution over time of R strategy in plant community on green roofs remains less clear. In this study, the R strategy decreased over time, as observed over a long period of time by Thuring and Dunnett (2019). Conversely, Ksiazek-Mikenas and Köhler (2018) reported an increase of R strategy over time. A decrease in R strategy in our study can be explained by a lack of disturbance on the studied green roof and/or plant responses to more intense competition with intra- or interspecific neighbors (Lundholm et al. 2014; Dunnett 2015; Thuring and Dunnett 2019).

Besides temporal patterns, changes in functional composition were modulated by environmental conditions. At the installation of vegetation in the first year, the dominant factor discriminating the functional CSR composition of communities was fertilization supply, with a lower contribution of S strategy on fertilized GR and a higher contribution of R strategy on fertilized soil. Those patterns are expected under the CSR strategy model as, under natural conditions, S species are characteristics of low nutrient conditions, while R species can benefit from nutrient boosts linked to disturbances (Grime 1977). After four years, we observed a shift in the effect of the two environmental factors (substrate depth and fertilization) on the functional plant community composition. The effect of fertilization on S and R strategies was not detected anymore which can be due to homogenization of nutrient conditions among GR in the absence of repeated fertilization during plant communities development. It has been observed that most of the nutrient content of substrate decreases during the first year following the installation of green roofs (Lim 2023). In contrast, substrate depth emerged as the primary factor determining the distribution of CSR strategy in the community (Kelly Ksiazek-Mikenas and Köhler 2018). Specifically, the proportion of stress-tolerant strategy was higher in communities facing more stressful conditions, such as low substrate depth. In contrast, in less stressful conditions characterized by deeper substrate depth or fertilization supply, the proportion of competitive strategy was higher than in more stressful environments.

In conclusion, our study supports the general pattern that stress tolerant species, particularly *Sedum* species, tend to dominate plant communities on extensive green roofs. We showed that, even with an initial diversified mix of functional types, a shift toward stress tolerant species may occur very rapidly in the first step of plant community establishment. Therefore, native species selection for implementing analogous habitat on extensive green roofs, in a temperate climate, should focus primarily on natural habitats composed of stress-tolerant species, such as pioneer environments, dry grasslands or xeric habitats. However, we also demonstrated that microenvironmental variations, specifically small differences in substrate depth, influenced significantly the functional strategy of plant communities in the first step of establishment. Hence, in more heterogeneous situations with higher microenvironmental variations, a mix of different functional types in the initial mix of species may be favourable to vegetation success, as environmental heterogeneity will naturally direct the vegetation towards the best suited assemblages, in dynamic process (Thuring and Dunnett 2019).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11252-023-01479-w.

Author Contributions GM and SM contributed to the design of the experimental. SM and LR collected the vegetation data. LR performed the statistical analysis. All authors contributed to the manuscript writing and approved the submitted version.

Funding This work was supported by ARC CityRoof project from University of Liège.

Data Availability The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Declarations

Ethics approval Not applicable.

Competing interests The authors declare no competing interests.

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