

Effect of mulch type, seed size, and plant adaptive strategies on germination and species composition in newly established perennial wildflower meadows

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Abstract

Ecological information about plant communities can contribute to better landscape design. Grime's CSR model, which categorises plant species as competitors (C), stress-tolerators (S), and ruderals (R), is fundamental to understanding plant community assembly. Seed size is a crucial trait that influences germination success and species establishment, especially when seeds are sown *in situ*. In landscape architecture, mulches are commonly used for sowing because they help retain soil moisture and suppress weed growth. This study investigates two main aspects in combination with different mulching substrates: (1) how CSR (competitor–stress-tolerator–ruderal) strategies influence species composition, and (2) how seed size affects initial germination. It also examines which adaptive strategies are associated with species that become dominant under specific mulch conditions. An experimental study was conducted using two types of mulch – organic (compost) and mineral (sand) – and three different seed mixtures containing perennial herbaceous plants. Species cover was assessed in the third year after sowing. Additional data on seed weight, adaptive strategy, and maximum species height were retrieved from published databases. The statistical analyses were performed using generalised linear models. The findings highlight the role of adaptive strategy in determining species dominance. The type of mulch affects the dominant adaptive strategy. Dominant plants in sand mulch had a higher R-score. In compost, the C-score was the highest, whereas in plots without mulch, the S-score prevails. Seed size also played a significant role in germination across various substrates. These results have important implications for species selection in wildflower meadow design. Understanding the interaction between adaptive strategy and mulch type can enhance the success of perennial plant communities by optimising species compositions. Planning the management of established wildflower meadows can also be aided.

Key words: CSR strategies, landscape architecture, perennial meadow, sand garden, seed size, urban biodiversity.

Introduction

Wildflower meadows, which include both annual and perennial species, have become a popular trend in landscape design as an alternative model of greenspace that avoids low biodiversity of monoculture and block planting (Hitchmough 2004; Kuneva et al. 2008, 2009). Designing flower meadows as nature-like plant communities is a challenge for landscape architects and designers (Hitchmough 2017). Urban wildflower meadows have a positive impact on citizens (Hitchmough 2016). They are a strong tool for the mitigation of the urban island effect (Alizadeh and Hitchmough 2020). Ecologically based plant design is a way of reducing resources to maintain green areas (Hitchmough 2010).

Ecological theories have practical implications for the management of grasslands (Grime 1980, p. 21), and in this term could be useful for the management of established (artificial) wildflower meadows. Grime (1974, 1977, 2001) explains the CSR theory, which includes three main strategies that show how plants compete, deal with environmental limits, or recover from damage. Pierce et al.'s (2017) global method for calculating CSR strategy reveals the linkage between leaf traits and basic plant rates. This method and strategy–environment relationship helps to predict plant assemblage in response to changes in biogeochemical cycles, climate, and land use. The CSR model could assist in designing herbaceous communities in urban environments, selecting cultivar species, and predicting the effects of climate change (Wang et al. 2024b).

According to Grime (1980, p. 21), plant strategies can be understood as clusters of analogous genetic traits that consistently occur across various species or

populations, leading to recurring patterns in their ecological behaviour. He argues that in the context of grassland management, a functional understanding of these strategies may prove more beneficial than traditional taxonomic knowledge. Specifically, Grime (1980, p. 25) identifies three primary strategies: the competitive strategy, which is dominant in nutrient-rich and stable environments; the stress-tolerant strategy, associated with habitats characterized by persistent resource limitations; and the ruderal strategy, which prevails in ecosystems subject to frequent disturbance yet capable of high productivity. Furthermore, sources of ecological information are not only established grasslands but also recently disturbed areas that are in different phases of recolonization (Grime 1980, p. 14).

The CSR plant strategy of the dominant species is the primary factor that determines how habitat affects plant composition (Wang et al. 2024a). Some authors have investigated the strategies of natural plant communities and identified differences among various habitats (Dudova et al. 2019, Han et al. 2021, Wang et al. 2024a). CSR strategy theory based on leaf traits (Pierce et al. 2017) could be a useful tool in garden design for planning the right plants in certain environments (Wang et al. 2024b). For example, Fenzl and Kircher (2009) added to the work of Messer (2008) and Borchardt (1998) by suggesting five types of plant groups to use for mixing different perennial plants, focusing on their structure and main ways they compete. They are divided into structural plants (C, C-S, S), companion plants (C, C-S, S), groundcover (up to 30 cm) (C, C-S, S), filler (R, R-S, C-R), and scattered plants, which are described as 'plants with a short growth period that do not require much space'. These recommendations

are made for meadows established by plugs, eventually combined with sowing, but not only with sowing.

Management can be more economic and useful if it is informed by ecological methods and theories. The major aim of understanding ecological processes is to seek to manipulate them. (Grime 1980, p. 13). For example, rare mowing in productive habitats leads to 'expansion of large perennial grasses, tall forbs and shrubs' (Grime 1980, p. 22). Management during the peak of biomass, may be most effective for suppressing competitive plants. Also, reduction of productivity may be done by removing grass clippings.

There are two main factors that reduce plant biomass – stress and disturbance (Grime 1980, p. 22). Grime (1977) suggests that in environments with extremely low productivity, the ruderal stage may be entirely absent from the successional sequence, resulting instead in a gradual transition marked by the development of increasingly larger stress-tolerant plant forms. Accordingly, creating an environment for stress-tolerant plant species will decrease the abundance of competitive and ruderal plants, and also reduce the overall plant biomass. Since disturbances do not correlate with stress-tolerant plants, the mowing regime must be reduced (Grime 1980, p. 31).

In this context, designing an unproductive wildflower meadow within an urban environment offers economic advantages. Less biomass means less expenses for removal and disposal of mown parts (Grime 1980, p. 31; Hoyle et al. 2017). However, creating harsh conditions for stress-tolerant plants may result in an overall reduction in seed germination.

Seed mass and other seed production traits can affect plant survival independently of primary strategy (Pierce et

al. 2014). Seed size has a significant influence on the seedling survival and height growth rate. Larger seeds have a significantly higher chance to survive (Fang et al. 2013). Large seeds, which are over 5.0 mm, demonstrate significantly higher seedling germination than intermediate (2.0–5.0 mm) or small seeds (< 2.0 mm). Larger seeds absorb 100 times more water than small seeds (Hitchmough and de la Fleur 2006, Hitchmough et al. 2008, Fang et al. 2013).

Soil parameters primarily align shifts in CSR plant strategies among different environments. Soil and climate variables significantly correlate with the dominant strategy (Rafiee et al. 2024). Mulching is a widely used technique in landscape design changes soil characteristic. Water retaining is one of the most important characteristics of the mulch. The other is inhibiting weed germination. There are some techniques for decreasing weeds from soil seed bank. Removing the top 15 cm of soil and applying 5 cm of sand mulch before sowing greatly reduces weed competition in the first growing season (Gao et al. 2012, Bretzel et al. 2024). Applying 7.5 cm of mulch sand while removing only the existing vegetation also has a positive impact (Hitchmough 2017, Hristova 2024b).

However, organic mulch has a negative impact on species richness (Hristova 2024b). It suppresses seeds in two ways: mechanically – through the thickness of the mulch layer – and physiologically – by releasing phytotoxins, which act as growth inhibitors (Waldron and Nichols 2009). The quantitative ratio of carbon to nitrogen leads to the formation of different compounds. Higher carbon levels lead to organic acids, while higher nitrogen levels lead to ammonia. Both, in high amounts, inhibit seed germination (Waldron and

Nichols 2009, Acharya et al. 2018). When mulch is used for sowing, it alters the germination environment in the topsoil layer where it is applied. In addition to modifying soil conditions, mulch can influence plant growth and species establishment.

The aim of this study is to explore how different mulching substrates influence early stages of plant community assembly. Specifically, it examines two main aspects: first, how species' CSR (competitor–stress-tolerator–ruderal) strategies relate to resulting species composition; and second, whether seed size affects initial germination success. In addition, the study considers which adaptive strategies are associated with species that become dominant under particular mulch conditions.

Material and Methods

Experiment establishment and field studies

The experimental plots were established at the Vrazhdebna Educational and Experimental Field, located in the northeastern part of Sofia, Bulgaria (42°42'26.4" N, 23°26'12.0" E) in a moderate continental climate with highest precipitation in May, June, and July (Koleva and Peneva 1990). The soil is mostly sandy with a low quantity of loam, rich in phosphorus and with neutral acidity. Climatic and soil conditions at the site are described in detail in Hristova (2024a).

First, the soil was manipulated with a rotary tiller, and all plant parts were removed. Two types of mulch were applied over the topsoil in a 75 mm layer: mineral mulch (sand, 0–4 mm fraction) and organic mulch (compost processed at Sofia's MBT municipal waste plant 'Han Bogrov'

facility, 0–10 mm fraction; C: N = 13.7, pH = 7.06, water content 42.5 %, moisture 657.9 g·L⁻¹ and 100% germination coefficient according to the Institute for Sustainable Plant Production 2022). A control condition without mulch was also included. Each mulch type was assigned to three replicate plots 1.5 × 1.5 m, each containing a different seed mixture. Seed mixtures are based on semi-natural habitats used for pastures or hay meadows, usually the alliance *Arrhenatherion elatioris* Koch (1926). The seeds are used for landscape design. Both economic and aesthetic factors influence their production (Mainz and Wieden 2019). Restoration projects, which are more specific tasks than general landscape design projects, are not the focus of this research.

In early December 2021, seeds from perennial herbaceous plants – previously used in an earlier experiment (Hristova 2024a, 2024b) – were sown in the experimental plots (Appendix A, Table A1). Due to an initial period of drought followed by prolonged rainfall, the seeds were sown during winter under suboptimal conditions, specifically onto slightly waterlogged soil that remained overly moist at the surface. They were applied over the mulching substrates, raked and compacted with a plank. No additional irrigation was provided after sowing.

During the first growing season, all plots were weeded, although some annual weeds with ornamental value (e.g., *Consolida regalis* Gray) were left intact. In June of the third year, two assessments were conducted to measure the projected cover of each species in every plot.

Plant identification was done according to Yordanov (1963), Fetovadzhieva (1973), and Delipavlov et al. (2011). Non-native species were identified based on seed mix specifications.

Data analysis

'A field-portable list of CSR strategies' (Pierce et al. 2017) was used for determining the adaptive strategies of the species. If some species were not presented, the nearest taxonomic species values were used. To assess relative importance, the methods from Wang et al. (2024a) were applied. The importance value (I_v) and dominance (D) were calculated using the formulas from Ohsawa (1984) – formulas (1) and (2), respectively.

$$I_v = H \cdot C, \quad (1)$$

$$D = \frac{I_v}{\sum (I_v \cdot 100)}, \quad (2)$$

where: I_v is the species' importance; H is the maximum height, m; C is the species' projected cover; and D is the value of dominance of a species within a plot.

The relative importance (RI) of a species was classified into five categories: dominant species ($D \geq 20$), subdominant species ($10 \leq D < 20$), companion species ($5 \leq D < 10$), rare species ($1 \leq D < 5$), and extremely rare species ($D < 1$).

The C-S-R scores were classified into 19 groups based on the dominant strategy (Hodgson 1999). The community weighted means (CWMs) for each plot were calculated using the dominance (D) to compute a weighted average.

Descriptive statistics were calculated for the weighted mean scores of C (competitor), S (stress-tolerator), and R (ruderal) strategies across the three mulch types.

The influence of mulch type and seed size on germination was examined. The maximum species height and air-dry weight of 1000 seeds were extracted from the published 'LEDA traitbase' (Kleyer et

al. 2008). Seed size is defined by seed mass of 1000 air-dry seeds (M), which was categorised as follows: $0 \text{ g} \leq M < 1 \text{ g}$ (small), $1 \text{ g} \leq M < 5 \text{ g}$ (medium), and $M \geq 5 \text{ g}$ (large).

For each RI and CSR class, species from the seed mixes that were found in the plots were counted; if a species was not found, it was assigned a value of 0. The Shapiro-Wilk test show that the data was not normally distributed. There are too many zeros for conducting ANOVA. Therefore, a zero-inflated negative binomial (ZINB) regression was conducted to examine the effects of mulch, relative importance (RI) and CSR strategies, including their interactions on the quantity of species in each group.

Binary logistic regression was applied to analyse the effect of mulch substrates and seed weight on germination success and their interactions. Since the response variable (germination) is binary – coded as 1 if the species germinated, and 0 if it did not – logistic regression is an appropriate method for modelling the probability of germination based on categorical and continuous predictors.

The zero-inflated negative binomial (ZINB) regression and the binary logistic regression were conducted using the R package *pscl* (Jackman 2024) and *ggplot2* (Wickham 2016). The R package *dplyr* (Wickham et al. 2023) was used for means and standard deviations. Also 'ggtern' (Hamilton and Ferry 2018) an extension to *ggplot2*, for the creation of ternary diagrams.

Dispersion was calculated using the sum of squared Pearson residuals divided by the residual degrees of freedom in the generalized linear model.

Results

CWMs of C-, S-, R-scores in different mulch types

In sand mulch, the C strategy showed a mean of 31.00 (SD = 2.35), the S strategy had a mean of 25.30 (SD = 5.13), and the R strategy had the highest mean at 43.70 (SD = 7.48). There was a lowest dispersion for C- and S-scores in the sand (figs 1 and 2).

For control plots (bare soil), the C strategy has the lowest mean ($M = 25.50$, $SD = 11.60$), while the S strategy was higher ($M = 34.80$, $SD = 9.35$), and the R strategy remained relatively high ($M = 39.70$, $SD = 2.75$) (figs 1 and 2).

In compost, the C strategy reached its highest mean ($M = 35.10$, $SD = 12.90$), the S strategy dropped to its lowest ($M = 18.10$, $SD = 13.90$), and the R strategy had the lowest mean ($M = 46.90$, $SD = 24.10$) but the highest variation and the highest R scores (figs 1 and 2).

CSR strategy of dominant species

A zero-inflated negative binomial (ZINB) regression showed that the number of species in each RI group was noticeably different ($SE = 0.28$, $p < 0.001$), and a higher RI score was associated with fewer species. Furthermore, there was significant interaction between RI groups and C-, S-, and R- groups ($SE = 0.02$, $p = .045$). Mulch ($SE = 0.44$, $p = 0.098$) and CSR ($SE = 0.09$, $p = 0.103$) showed trends but were not significant main effects. The model showed a satisfactory fit (dispersion = 1.34) (Table 1).

In sand mulch, species predominantly exhibited ruderal strategies. The sandy substrate, which is characterised by low nutrient content and poor water retention, favours plants that invest in rapid growth and have high reproductive outputs. Competitive and stress-tolerant traits were expressed to a lesser extent, suggesting that survival in this environment depends more on rapid colonisation than long-term

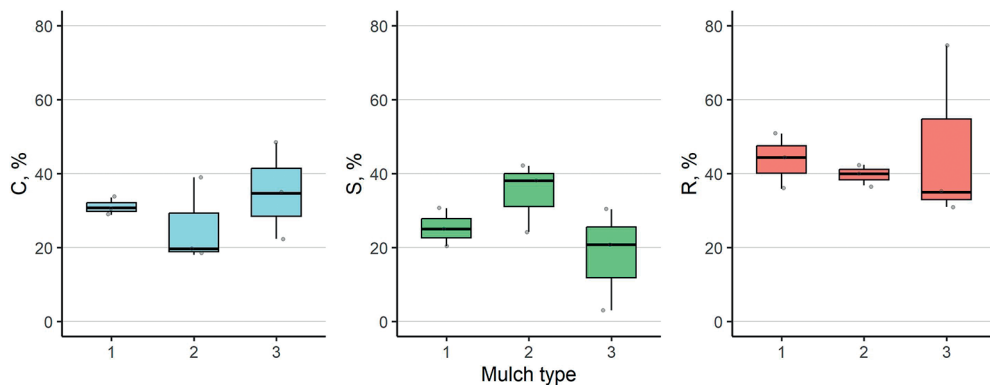


Fig. 1. Mean values and standard deviations of community-weighted means (CWMs) of C-, S-, and R-strategy values across different mulch types.

Note: 1 – sand, 2 – control (bare soil), 3 – compost.

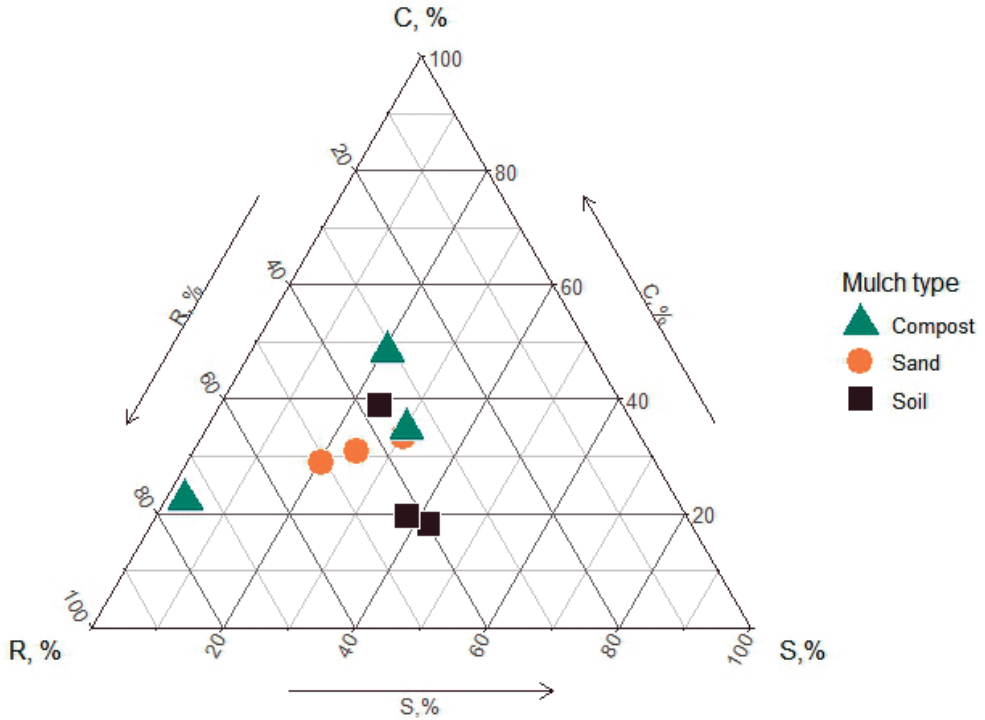


Fig. 2. Community weighted means (CWMs) of C-, S-, and R-scores in sand, bare soil and compost.

Table 1. Count model coefficients (ZINB).

Predictor	Estimate	Std. Error	p-value
Intercept	1.714	1.128	0.129
Mulch type	-0.725	0.438	0.098
RI	-1.087	0.278	<0.001 ***
CSR strategy	-0.141	0.086	0.103
Mulch type × CSR strategy	0.045	0.034	0.191
RI × CSR strategy	0.040	0.020	0.045 *

Note: ZINB model; dispersion = 1.34, * $p < 0.05$, *** $p < 0.001$.

resource monopolisation or physiological resilience (Fig. 3).

There were dominant species, including *Centaurea jacea* L., *Leucanthemum vulgare* Lam. (C:S:R = 20.85:0:79.15 %),

Festuca trichophylla (Duval-Jouve) C.E.Hubb. (C:S:R = 10.41:35.7:53.89 %), *Sanguisorba minor* Scop. (C:S:R = 25.53:43.98:30.48 %) and *Anthemis tinctoria* L. (C:S:R = 15.6:43.45:40.95 %) (Table 2).

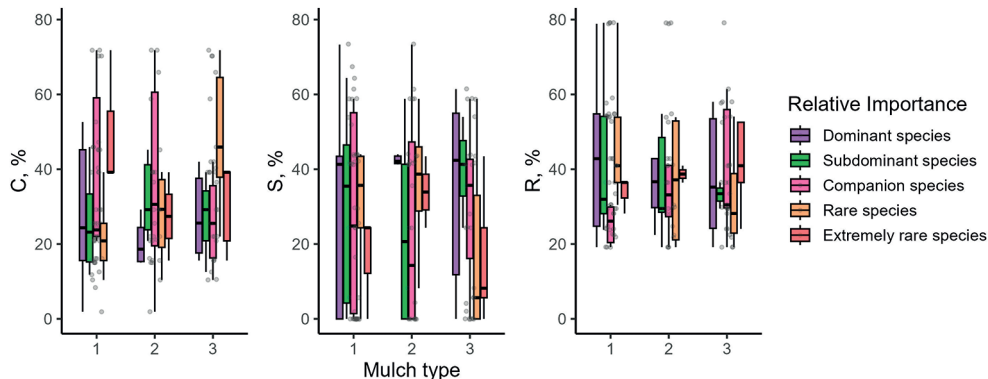


Fig. 3. C-, S-, R-scores of RI groups across different mulch types: 1 – sand, 2 – bare soil, 3 – compost.

Table 2. Dominant species and their C-, S-, R-strategy values among different mulch types.

Species	Tertiary CSR strategy	C-, S-, R-strategy values			Mulch type		
		C, %	S, %	R, %	Sand	Soil	Com-post
<i>Achillea millefolium</i> L.	S/CSR	22.02	58.81	19.18			+
<i>Anthemis tinctoria</i> L.	SR/CSR	15.60	43.45	40.95	+	+	
<i>Centaurea jacea</i> L.	CR/CSR	39.19	24.35	36.46	+	+	+
<i>Cichorium intybus</i> L.	CS/CSR	36.55	41.68	21.77			+
<i>Consolida regalis</i> Gray	SR/CSR	20.39	36.93	42.68		+	
<i>Festuca trichophylla</i> (Duval-Jouve) C.E.Hubb.	SR	10.41	35.70	53.89	+		
<i>Knautia arvensis</i> (L.) Coult.	C/CR	70.27	5.66	24.07			+
<i>Leucanthemum vulgare</i> Lam.	R/CR	20.85	0	79.15	+		+
<i>Sanguisorba minor</i> Scop.	S/CSR	25.53	43.98	30.48	+		

In soil without mulch, species tend to adopt stress-tolerant strategies. Soil provides more stable but moderately challenging environment, possibly due to variations in moisture, temperature, or other stress factors. In this context, species prioritise traits that support resilience and structural persistence. Competitive and ruderal traits were still present but not as dominant, indicating a balanced strategic profile shaped by moderate abiotic stress (Fig. 3).

Anthemis tinctoria (C:S:R = 15.6:43.45:40.95 %) and *Centaurea jacea* (C:S:R = 39.19:24.35:36.46 %) were dominant species in control plots. *Consolida regalis* (C:S:R = 20.39:36.93:42.68 %) was also dominant in the same plots (Table 2).

In compost mulch, species show a mix of competitive and ruderal strategies. The high nutrient availability and improved moisture conditions promote both resource acquisition and rapid growth. This environment supports a wider vari-

ety of strategic behaviours, allowing both dominant competitors and opportunistic colonisers to thrive. Stress tolerance is less pronounced, reflecting the relatively benign conditions created by the compost substrate (Fig. 3).

There were also more than one dominant species in compost: *Centaurea jacea*, *Cichorium intybus* L. (C:S:R = 36.55:41.68:21.77 %), *Knautia arvensis* (L.) Coult. (C:S:R = 70.27:5.66:24.07 %), *Achillea millefolium* L. (C:S:R = 22.02:58.81:19.18 %), and *Leucanthemum vulgare* (C:S:R = 20.85:0:79.15 %). *Centaurea jacea* was a dominant species in all mulch types (Table 2). Appendix B (Fig. B1 and Table B1) presents the remaining RI groups across substrates.

The influence of a mulch type and seed size on germination

The overall binary logistic regression model was statistically significant, with a residual deviance of 665.29. A chi-square test was performed to evaluate whether the inclusion of eight predictors significantly improved the model's fit compared to the null model. The test yielded a chi-square value of 25.97 with 8 degrees of freedom, resulting in a p -value below 0.05 (χ^2 (8)

= 25.97, $p < 0.05$). The model demonstrated an acceptable fit, as reflected by the Akaike Information Criterion (AIC = 683.29) and a dispersion parameter close to 1 (dispersion = 1.02) (Table 3).

A significant negative main effect was observed for compost (SE = 0.34, $p = 0.014$), suggesting lower odds of germination under compost compared to the sand and control plots (bare soil). The interaction between bare soil and large seeds was also statistically significant (SE = 1.14, $p = 0.029$), indicating a negative effect of bare soil over large seeds. There is also significant negative effect of interception between sand mulch and small seeds (SE = 0.22, $p = 0.02$). No other main effects or interactions reached significance ($p > 0.05$) (Table 3).

Discussion

CSR strategy

There was a notable difference in the CSR strategies of plants across various relative importance groups. Interactions between CSR groups and mulches indicated a trend; however, it is likely that larger plots are required for more definitive results.

Table 3. GLM Coefficients for effect of seed size on germinated specie in different mulch types.

Predictor	Estimate	SE	p -value
Intercept	-0.511	0.220	0.020*
Control plots	-0.413	0.323	0.201
Compost	-0.847	0.344	0.014*
Medium seeds	-0.251	0.318	0.429
Large seeds	0.201	0.454	0.658
Control plots × Medium seeds	-0.183	0.476	0.701
Compost × Medium seeds	0.251	0.491	0.608
Control plots × Large seeds	-2.495	1.141	0.029*
Compost × Large seeds	-0.547	0.756	0.469

Note: dispersion = 1.02, * $p < 0.05$ indicates statistical significance.

Both the type of mulch and the adaptive strategy affected plant composition. The relative importance groups exhibited varying means of C-, S-, and R-scores across different substrates.

The results align with those of Wang et al. (2024a) and reaffirm the connection between the dominant species primary strategy and the characteristics of the community. Understanding the primary strategy of dominant species sheds light on environmental conditions.

In sandy habitats dominated by ruderal (R) species, mowing should be carefully timed to coincide with periods of sufficient soil moisture. Given the low water-holding capacity of sandy substrates, moisture availability is critical for the rapid regeneration and reproductive success characteristic of R-strategists. Extreme stress and/or disturbance create an environment in which few species can survive (Grime 1980, p. 33). Mowing during dry periods can inhibit regrowth, reduce vegetative cover, ultimately undermining the persistence of ruderal species. Therefore, for management practices aiming to maintain or promote R-dominated plant communities in sandy environments, mowing is most effective when conducted during or immediately following rainfall events or within wetter seasons that support rapid post-disturbance recovery.

In bare soil, where stress-tolerant species tend to dominate, mowing should be applied with caution and at a low frequency. These species typically invest in structural stability and long-term persistence rather than rapid regrowth, making them less responsive to frequent disturbance. Intensive or poorly timed mowing may disrupt the equilibrium of such communities, reduce biomass recovery, and favour the encroachment of more ruderal or opportunistic species. To maintain the functional

integrity of stress-adapted assemblages, mowing should be limited to occasional interventions, preferably during periods of adequate soil moisture and minimal physiological stress. Low-frequency mowing – such as once per year – can benefit S-R strategists, which are adapted to moderately disturbed, unproductive habitats (Grime 1980, p. 25).

In compost-enriched environments, where both competitive and ruderal strategies are expressed, mowing should be applied at moderate frequency and timed to balance growth control with species regeneration. The high nutrient and moisture availability in compost supports rapid biomass accumulation, which, if unmanaged, can lead to competitive exclusion. The results are in agreement with the findings of Sparke et al. (2011). More than 45 % organic matter creates too fertile conditions and increases weeds. Periodic mowing – conducted two to three times per growing season and aligned with phases of active growth (Grime 1980, p. 22) – can help regulate dominant competitors while allowing ruderal species to complete their life cycles. Such a regime supports strategic diversity and maintains a dynamic, yet stable, community structure.

Seed size

Although large seeds are typically more resilient to stressful environments due to their greater energy reserves, their germination was significantly reduced under bare soil conditions. This finding contrasts with expectations based on seed size and their stress tolerance but aligns with their advantage in litter cover (Lönnerberg and Eriksson 2013, Muller-Landau 2010). Compared to sand, the probability of germination for large-seeded species was approximately 2.5 times lower in compost

and more than 11 times lower in control plots (bare soil), the latter being statistically significant. These results suggest that, under certain mulch-free conditions, even stress-tolerant traits like large seed size may not compensate for the harsher surface microclimate or soil compaction that may inhibit germination. In parallel, although large seeds typically absorb water up to 100 times faster than small seeds (Osmond et al. 1980) and generally exhibit higher germination rates in the field, excess soil moisture during winter may have triggered premature germination or caused seed damage through freezing.

Meanwhile, under sand mulch, small-seeded species were significantly more frequent. Compared to sand, the number of small-seeded species was approximately 1.5 times lower in bare soil and 2.3 times lower in compost. The harsh abiotic conditions at the soil surface – such as poor water retention – likely reduce the survival chances of both small-seeded species and slow-establishing large-seeded species, highlighting the dual vulnerability of extreme seed sizes under suboptimal mulch conditions. The highest number of small-seeded species successfully germinated in sand, suggesting that the loose, well-drained structure of this substrate provided more favourable microsite for light-dependent and surface-germinating species.

These findings are consistent with those of Hitchmough and de la Fleur (2006), who reported that sand mulch plots positively affect germination of prairie vegetation. Seed size influences germination; however, larger seeds did not exhibit a clear advantage across all substrates. This outcome diverges from the results presented by Hitchmough et al. (2008) and Fang et al. (2013) but species with large seeds are the most in sand

mulch plots. In bare soil, the lack of mulch likely led to surface crust formation and faster evaporation, which are especially detrimental to larger seeds that require more consistent moisture and stable conditions for germination. In contrast, both compost and sand mulches may have mitigated these stresses by improving surface structure, maintaining humidity, and reducing soil compaction.

The germination index of the experimental compost was 100 % (Institute for Sustainable Plant Production 2022), which mean that the compost is mature. However, regardless of seed size, compost mulch suppressed overall germination of the target plants. The nitrogen content in compost was a normal to slightly lower, with a C: N ratio of 13.7. By comparison, soils in Central and Eastern Europe typically exhibit C:N ratios in the range of 9–12 (Batjes 2002). The nitrogen content was much higher than the usual compost range of 20.4–40.1 (Enakiev et al. 2017, 2022). The optimal C:N ratio is between 25 and 30 (Haug 1980). Low C:N ratios under 15 can lead to the production of ammonia, a known inhibitor of seed germination (Haug 1993, Waldron and Nichols 2009). Compost with C:N = 15 has lower germination index (53–66 %) in comparison with 18 and 21. The recommended parameters for composting are an aeration rates of $0.48 \text{ L} \cdot (\text{kg DM})^{-1} \cdot \text{min}^{-1}$ and a C:N ratio of 18 with moisture contents of 65–75 % (Guo et al. 2012). While compost mulch can improve surface conditions by retaining moisture, its loose structure and lightness may also make it prone to displacement by wind or rainfall. This instability can expose germinating seeds to drying conditions or temperature fluctuations. This suggests that while mulch generally creates more favourable micro-environment for seed emergence, its spe-

cific physical properties – such as structural stability – also influence germination success. Another possible reason is the presence of soil-borne fungal or bacterial pathogens, which often grow well in nutrient-rich, organic materials and can greatly harm seed survival and seedling growth.

These results have practical implications for the design of flowering meadows, particularly in selecting appropriate mulching materials, composing effective seed mixtures, and optimizing the management of established meadows. Further experimental work is needed to better understand the underlying mechanisms and to evaluate germination outcomes across different compost formulations. Future research should also consider calculating CSR scores using leaf traits measured directly from experimental plants to improve the accuracy of strategy classification.

Conclusion

The study demonstrates that mulch type influences plant composition by shaping the dominance of different ecological strategies and affecting seed germination. Sand mulch favours species with ruderal strategy, adapted to frequent disturbances. Supporting their regeneration requires carefully timed mowing during moist periods. Under winter sowing conditions, large seeds perform well in sand mulch, but small seeds show significantly better performance in sand compared to other substrates. Bare soil significantly reduces the germination of large-seeded species and favours stress-tolerant plants that are sensitive to disturbance. Implementing low-frequency mowing may help maintain a balance among different ecological strategies. Compost significantly reduces germination regardless of seed size.

Competitive species tend to perform best in compost mulch, suggesting that more frequent mowing may be necessary to prevent their dominance and maintain species diversity. These findings highlight the importance of tailoring management practices, such as mowing regimes and mulch selection, to both abiotic conditions and the functional traits of target plant communities.

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Appendix A

Table A1. Plant species in seed mixes.

No	Species	Seed mixes		
		02	06	06a
1	<i>Achillea millefolium</i> L.	+	+	+
2	<i>Agrimonia eupatoria</i> L.		+	
3	<i>Anthemis tinctoria</i> L.		+	+
4	<i>Anthoxanthum odoratum</i> L.		+	+
5	<i>Anthriscus sylvestris</i> (L.) Hoffm.	+		
6	<i>Anthyllis vulneraria</i> L.		+	+
7	<i>Arrhenatherum elatius</i> (L.) P.Beauv.	+		
8	<i>Bellis perennis</i> L.	+		
9	<i>Briza media</i> L.			+
10	<i>Bromus erectus</i> Huds.			+
11	<i>Buphthalmum salicifolium</i> L.		+	+
12	<i>Campanula patula</i> L.	+	+	+
13	<i>Campanula rotundifolia</i> L.			+
14	<i>Carum carvi</i> L.		+	
15	<i>Centaurea jacea</i> L.	+	+	+
16	<i>Centaurea scabiosa</i> L.		+	+
17	<i>Cichorium intybus</i> L.		+	
18	<i>Crepis biennis</i> L.	+	+	
19	<i>Cynosurus cristatus</i> L.	+	+	+
20	<i>Daucus carota</i> L.	+	+	+
21	<i>Dianthus carthusianorum</i> L.		+	+
22	<i>Echium vulgare</i> L.		+	
23	<i>Festuca ovina</i> L.			+
24	<i>Festuca trichophylla</i> (Duval-Jouve) C.E.Hubb.			+
25	<i>Galium mollugo</i> L.	+	+	
26	<i>Galium verum</i> L.		+	+
27	<i>Geranium pratense</i> L.		+	
28	<i>Heracleum sphondylium</i> L.	+		
29	<i>Hypericum perforatum</i> L.		+	+
30	<i>Knautia arvensis</i> (L.) Coult.	+	+	+
31	<i>Leontodon hispidus</i> L.	+		+
32	<i>Leucanthemum vulgare</i> Lam.	+	+	+
33	<i>Lotus corniculatus</i> L.		+	+
34	<i>Malva moschata</i> L.		+	+
35	<i>Medicago lupulina</i> L.		+	+
36	<i>Onobrychis viciifolia</i> Scop.	+	+	+
37	<i>Picris hieracioides</i> L.	+		
38	<i>Pimpinella saxifraga</i> L.		+	+

No	Species	Seed mixes		
		02	06	06a
39	<i>Plantago lanceolata</i> L.	+	+	
40	<i>Potentilla recta</i> L.		+	
41	<i>Prunella grandiflora</i> (L.) Scholler	+	+	+
42	<i>Prunella vulgaris</i> L.	+	+	
43	<i>Ranunculus acris</i> L.	+		
44	<i>Ranunculus bulbosus</i> L.	+		+
45	<i>Rhinanthus alectorolophus</i> (Scop.) Pollich		+	+
46	<i>Rumex acetosa</i> L.	+		
47	<i>Salvia pratensis</i> L.	+	+	+
48	<i>Salvia verticillata</i> L.		+	
49	<i>Sanguisorba minor</i> Scop.	+	+	+
50	<i>Scabiosa columbaria</i> L.			+
51	<i>Silene nutans</i> L.		+	
52	<i>Silene vulgaris</i> (Moench) Garcke	+	+	+
53	<i>Thymus pulegioides</i> L.			+
54	<i>Tragopogon orientalis</i> Willd.		+	+
55	<i>Trisetum flavescens</i> (L.) P.Beauv.	+	+	
56	<i>Veronica teucrium</i> L.			+

Note: 02 – wet meadow seed mix, 06 – universal meadow seed mix, 06a – dry meadow seed mix.

Source: (Hristova 2024a).

Appendix B

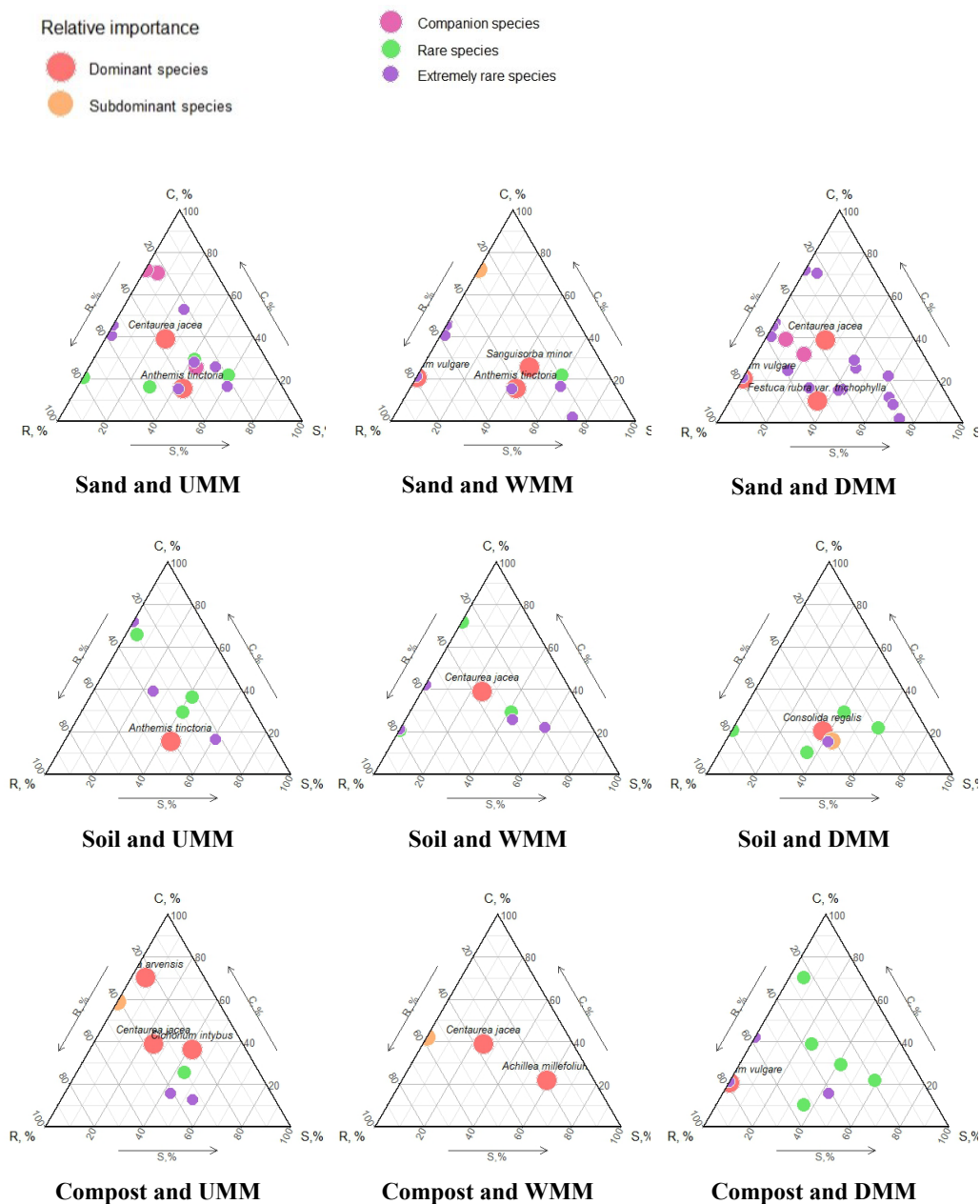


Fig. B1. C-, S-, R-strategy values and relative importance of species in each plot.
 Note: UMM – universal meadow mix, WMM – wet meadow mix, DMM – dry meadow mix.

Table B1. Relative importance and C-, S-, R-scores of indicated plants.

No	Species	C, %	S, %	R, %	Relative importance
Soil + Universal meadow mix (06)					
1	<i>Anthemis tinctoria</i> L.	15.6	43.45	40.95	5
2	<i>Cichorium intybus</i> L.	36.55	41.68	21.77	2
3	<i>Echium vulgare</i> L.	65.91	4.25	29.84	2
4	<i>Daucus carota</i> L.	29.20	41.31	29.49	2
5	<i>Centaurea jacea</i> L.	39.19	24.35	36.46	1
6	<i>Plantago lanceolata</i> L.	71.82	0	28.18	1
7	<i>Dianthus carthusianorum</i> L.	16.15	61.42	22.44	1
Soil + Wet meadow mix (02)					
1	<i>Centaurea jacea</i>	39.19	24.35	36.46	5
2	<i>Leucanthemum vulgare</i> Lam.	20.85	0	79.15	2
3	<i>Plantago lanceolata</i>	71.82	0	28.18	2
4	<i>Daucus carota</i>	29.20	41.31	29.49	2
5	<i>Achillea millefolium</i> L.	22.02	58.81	19.18	1
6	<i>Bellis perennis</i> L.	21.13	0	78.87	1
7	<i>Sanguisorba minor</i> Scop.	25.53	43.98	30.48	1
8	<i>Tragopogon orientalis</i> Willd.	42.00	0	58.00	1
Soil + Dry meadow mix (06a)					
1	<i>Consolida regalis</i> Gray	20.39	36.93	42.68	5
3	<i>Anthemis tinctoria</i>	15.6	43.45	40.95	4
4	<i>Achillea millefolium</i>	22.02	58.81	19.18	2
5	<i>Daucus carota</i>	29.2	41.31	29.49	2
2	<i>Festuca trichophylla</i> (Duval-Jouve) C.E.Hubb.	10.41	35.7	53.89	2
6	<i>Leucanthemum vulgare</i>	20.85	0	79.15	2
7	<i>Cynosurus cristatus</i> L.	15.05	42.12	42.83	1
Sand + Universal meadow mix (06)					
1	<i>Centaurea jacea</i>	39.19	24.35	36.46	5
2	<i>Anthemis tinctoria</i>	15.6	43.45	40.95	5
3	<i>Knautia arvensis</i> (L.) Coult.	70.27	5.66	24.07	3
4	<i>Plantago lanceolata</i>	71.82	0	28.18	3
5	<i>Sanguisorba minor</i>	25.53	43.98	30.48	3
6	<i>Achillea millefolium</i>	22.02	58.81	19.18	2
7	<i>Daucus carota</i>	29.20	41.31	29.49	2
8	<i>Leucanthemum vulgare</i>	20.85	0	79.15	2
9	<i>Medicago lupulina</i> L.	16.11	29.63	54.26	2
10	<i>Dianthus carthusianorum</i>	16.15	61.42	22.44	1
11	<i>Potentilla recta</i> L.	25.56	51.8	22.64	1
12	<i>Salvia verticillata</i> L.	52.62	25.51	21.87	1
13	<i>Silene nutans</i> L.	40.36	1.98	57.66	1
14	<i>Silene vulgaris</i> (Moench) Garcke	45.20	0	54.80	1
15	<i>Cynosurus cristatus</i>	15.05	42.12	42.83	1
16	<i>Scabiosa columbaria</i> L.	27.83	42.09	30.08	1

No	Species	C, %	S, %	R, %	Relative importance
Sand + Wet meadow mix (02)					
1	<i>Sanguisorba minor</i>	25.53	43.98	30.48	5
2	<i>Anthemis tinctoria</i>	15.60	43.45	40.95	5
3	<i>Leucanthemum vulgare</i>	20.85	0	79.15	5
4	<i>Plantago lanceolata</i>	71.82	0	28.18	4
5	<i>Achillea millefolium</i>	22.02	58.81	19.18	2
6	<i>Leontodon hispidus</i> L.	45.93	0	54.07	1
7	<i>Bellis perennis</i>	21.13	0	78.87	1
8	<i>Silene vulgaris</i>	45.20	0	54.8	1
9	<i>Cynosurus cristatus</i>	15.05	42.12	42.83	1
10	<i>Dianthus carthusianorum</i>	16.15	61.42	22.44	1
11	<i>Silene nutans</i>	40.36	1.98	57.66	1
12	<i>Festuca ovina</i> L.	1.91	73.32	24.77	1
Sand + Dry meadow mix (06a)					
1	<i>Centaurea jacea</i>	39.19	24.35	36.46	5
2	<i>Leucanthemum vulgare</i>	20.85	0	79.15	5
3	<i>Festuca trichophylla</i>	10.41	35.7	53.89	5
4	<i>Stachys recta</i> L.	32.14	19.12	48.74	3
5	<i>Picris hieracioides</i> L.	39.24	8.20	52.56	3
6	<i>Knautia arvensis</i>	70.27	5.66	24.07	1
7	<i>Sanguisorba minor</i>	25.53	43.98	30.48	1
8	<i>Bromus erectus</i> Huds.	11.81	64.39	23.8	1
9	<i>Achillea millefolium</i>	22.02	58.81	19.18	1
10	<i>Anthemis tinctoria</i>	15.60	43.45	40.95	1
11	<i>Buphthalmum salicifolium</i> L.	24.35	16.62	59.03	1
12	<i>Daucus carota</i>	29.2	41.31	29.49	1
13	<i>Leontodon hispidus</i>	45.93	0	54.07	1
14	<i>Medicago lupulina</i>	16.11	29.63	54.26	1
15	<i>Salvia pratensis</i> L.	47.24	0	52.76	1
16	<i>Silene vulgaris</i>	45.20	0	54.80	1
17	<i>Anthoxanthum odoratum</i> L.	8.36	67.45	24.19	1
18	<i>Cynosurus cristatus</i>	15.05	42.12	42.83	1
19	<i>Festuca ovina</i>	1.91	73.32	24.77	1
20	<i>Silene nutans</i>	40.36	1.98	57.66	1
21	<i>Bellis perennis</i>	21.13	0	78.87	1
22	<i>Plantago lanceolata</i>	71.82	0	28.18	1
Compost + Universal meadow mix (06)					
1	<i>Centaurea jacea</i>	39.19	24.35	36.46	5
2	<i>Cichorium intybus</i>	36.55	41.68	21.77	5
3	<i>Knautia arvensis</i>	70.27	5.66	24.07	5
4	<i>Crepis biennis</i> L.	58.80	0	41.20	4
5	<i>Sanguisorba minor</i>	25.53	43.98	30.48	2
6	<i>Prunella vulgaris</i> L.	12.55	53.99	33.47	1
7	<i>Anthemis tinctoria</i>	15.6	43.45	40.95	1

No	Species	C, %	S, %	R, %	Relative importance
Compost + Wet meadow mix (02)					
1	<i>Achillea millefolium</i>	22.02	58.81	19.18	5
2	<i>Centaurea jacea</i>	39.19	24.35	36.46	5
3	<i>Tragopogon orientalis</i>	42.00	0	58.00	4
Compost + Dry meadow mix (06a)					
1	<i>Leucanthemum vulgare</i>	20.85	0	79.15	5
2	<i>Knautia arvensis</i>	70.27	5.66	24.07	2
3	<i>Centaurea jacea</i>	39.19	24.35	36.46	2
4	<i>Festuca trichophylla</i>	10.41	35.70	53.89	2
5	<i>Achillea millefolium</i>	22.02	58.81	19.18	2
6	<i>Daucus carota</i>	29.20	41.31	29.49	2
7	<i>Anthemis tinctoria</i>	15.60	43.45	40.95	1
8	<i>Tragopogon orientalis</i>	42.00	0	58.00	1
9	<i>Bellis perennis</i>	21.13	0	78.87	1