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1 Introduction

Designed, but naturalistic, perennial herbaceous vegetation involving either, or both, native and non-native species is increasingly in vogue in the urban landscapes of Europe and North America (Oudolf and Kingsbury, 2013; Rainer and West, 2015). This change is significantly due to the value people place on the experience of flowers in urban landscapes (Todorova, et al., 2004; Lindemann-Matthies and Bose, 2007; Southon, et al., 2017) and their capacity to evoke emotionally powerful memories of, and relationships with nature (Lindemann-Matthies, 2002; Clayton, 2007). The functionality of herbaceous vegetation in the delivery of ecosystem services, for example, habitat and food for fauna (Salisbury, et al., 2015; Hicks et al., 2016) is also important. There is a growing awareness amongst urban people of the importance of flowers to invertebrate pollinators and associated faunal food-webs (Southon, et al., 2017). Ecological research (Baldock, et al., 2015) shows that species undertaking these roles may be drawn from both native and non-native floras; current geographical distribution of species is often not the critical factor in maximizing functional effectiveness (Salisbury et al., 2015).

As flower-rich, forb-dominated vegetation is used on a large scale, long-term manageability becomes a critical concern; individual forb species need to be able to compete, resist colonization and persist. These functional requirements pose a dilemma to designers of naturalistic herbaceous vegetation, as public support for its inherently disordered appearance is heavily reliant on it being exceptionally flowery (Hoyle, 2015; Lindemann-Matthies and Bose, 2007). This requires forbs to be more dominant than grasses, but in semi-natural “meadow” vegetation the opposite is the norm (del-Val and Crawley, 2005). Bjørn, et al. (2016) ask whether it is possible to use design and management to establish and maintain forb-rich vegetation with low grass content that is also resistant to weed invasion at low maintenance levels? Evidence from purely ecological perspectives grounded in naturally occurring vegetation suggests that forb-rich vegetation can only be maintained over a limited period. In acid grassland, grasses regained their former dominance over forbs within as little as three years post cessation of graminicide use (Del Val and Crawley, 2005). However, acid grasslands tend to be relatively forb-poor (Rodwell, 1992), and in this particular instance, the return to a grass-dominated vegetation was hastened by high levels of rabbit grazing (Del Val and Crawley, 2005). On the other hand, in restored prairie grassland sown with forb-only mixtures, sizeable amounts of prairie forbs persisted for at least eight years after sowing, with priority effects limiting colonization by unsown grasses (Werner et al., 2016). These results suggest that while forb-rich sown vegetation cannot be maintained indefinitely without additional intervention, it can nonetheless persist for quite some time.

The percentage forb biomass in meadow communities varies greatly, depending on cutting regime, leaf phenology, soil productivity and climatic factors (Robertson and Jefferson, 2000), from >90% in unproductive meadows with summer drought to <10% in meadows on highly productive soil in maritime climates. Under favourable climatic and edaphic conditions, grasses highly competitive, resulting in meadows that tend to be insufficiently flowery to cue public support (Southon, et al., 2017). Grasses do however play an important functional role in meadows, with evergreen species in particular suppressing weed invasion in winter when standing biomass is at its lowest and the community most open. Hence, while grassy meadows may be an attractive model in terms of functionality, their anticipated low flower density on typically productive urban soils tends to limit aesthetic success.

An alternative model for designed urban landscapes are tall-forb communities such as North American Prairie whose peak growth and flowering occur in summer and autumn. These communities cannot be managed by cutting in summer, and with most species being winter-deciduous, they are subject to weed seedling colonisation in winter, particularly in maritime climates. These seedling weeds can be controlled by annual flash burning in spring (Hitchmough and de la Fleur, 2006). This practice has fewer benefits for prairie persistence in continental climates (Schmithals and Kühn, 2014) and is energy and time intensive.

An alternative would be to reduce weed colonization by incorporating forbs into the mix that are functionally equivalent to grasses in terms of their winter-green phenology, thus resulting in similar benefits in terms of weed suppression (Young et al., 2009). For example, in the context of designed tall-forb Prairie communities, this could be achieved by adding an under-canopy layer of forb species that are leafy in winter, thus closing the gaps created by the deciduous habit of the taller prairie forbs. On productive soils, competition for light exerted by dominant canopy species is intense (Keddy, et al., 1997) leading to the elimination of shade-intolerant under-canopy species. In productive semi-natural prairie communities, survival of the latter is often contingent on patches of unproductive soil where biomass accumulation of the shade-casting species is restricted (Curtis, 1959). In designed vegetation, incorporating shade tolerant under-canopy species appears more promising than encouraging patchiness.

Temperate shade-tolerant forb species are most numerous in deciduous woodland. Taylor and Pearcy (1975) identify three main ecological strategies for woodland under-story species to persist in their habitats; (1) early growing, slightly shade-tolerant; (2) intermediate, shade-tolerant; and (3) late growing, highly shade-tolerant. The latter group are characterized by low to very low growth rates, often in combination with drought-tolerant, evergreen foliage, for example; Hepatica nobilis and Asarum europaeum, whose photosynthetic activity peaks in spring and late autumn when trees are leafless (Overdieck, 1985). The majority of woodland understory forbs belong to the intermediate, shade-tolerant group, for example, Anemone nemorosa, Primula elatior and Primula vulgaris. Growth occurs while the tree canopy is leafless, with dormancy entered by mid-summer.

To use woodland forbs as under-canopy to tall forbs in designed herbaceous vegetation requires their light requirements to be met. Hirose and Werger (1995) found approximately 80% of photosynthetic photon flux density (PPFD) incident on a tall, wet meadow was intercepted by the canopy on an overcast day in late July. McCain et al. (2010) record a mean PPFD extinction of 70% for prairie-grass dominated vegetation. Extinction ranges are similar for woodland (Holmes, 1995; Le Duc and Havill, 1998). The duration of the shade-free window is also important. Routhier and Lapointe (2002) found the biomass of the under-canopy forb Trillium erectum to be positively correlated with number of days from Trillium emergence to woodland leaf emergence.

To be sustainable, forbs used in designed two-layer plantings need to be relatively unpalatable. Herbivory, in combination with competition for light can have a major influence on forb persistence (Edwards and Crawley, 1999; del-Val and Crawley, 2005); forbs are typically more palatable than grasses. Many European woodland forbs are relatively unpalatable (Whale, 1984) however their basal foliage provides shaded refugia for slugs, thus potentially increasing grazing pressure (Nystrand and Granström, 1997), disproportionately affecting the more palatable forbs (Hitchmough and Wagner, 2011).

This paper investigates the utility of a novel, designed community including both a tall over-canopy of North American forbs and an under-canopy of woodland forbs native to Europe and North America, in creating flower-rich designed vegetation of high persistence that is resistant to weed invasion. It also looks at how the various experimental factors influenced the composition and properties of this novel vegetation over a four year period. It is the first published study to explicitly look at whether designed vegetation performance and functionality, can be improved by utilizing phenological understanding and adding extra canopy layers. Key research questions were as follows:

- Was the combination of a summer-growing over-canopy and winter/spring-growing under-canopy effective in inhibiting weed biomass over a four year period?

- Did the design of the five plant communities (i.e. sowing mix and density variables) affect the longer-term characteristics (species richness, abundance, persistence, and biomass) of the vegetation?

- Was species richness, abundance, persistence, and biomass affected by mulch type and soil productivity?

- Are two-layer communities visually successful models for future urban planting design?

2 Methods

The experiment was conducted in Sheffield (53˚N24', 1˚W30'), United Kingdom, on an old field previously used for research on prairie vegetation. The topsoil consisted of a well-drained clay loam. Physical and chemical analyses for the soil materials used in the study, plus site climate data are given in Hitchmough et al. (2004).

In September 2005, all standing vegetation was eliminated from the site using a glyphosate-based herbicide. In December 2005 a fully factorial, randomised split-split-plot design involving 4 replicates of each treatment combination was set-up. A total of 16 treatment main plots of 3 m x 2 m, were randomly selected from a 3 x 6 rectangular arrangement, leaving two positions un-assigned. Of the selected plots, eight were allocated at random to a ‘productive’ soil treatment with the original soil profile intact. The remaining eight plots were allocated to an ‘unproductive’ treatment achieved by inverting the 300 mm upper layer of topsoil under an excavated 300 mm layer of the site’s subsoil. Four of the productive ‘topsoil’ main plots were then sown with the plant community mixes at low density (approximately 100 seedlings m^{-2}), while the other four were sown at high density (i.e. approximately 200 seedlings/m^{-2}). The same process was applied to less productive ‘subsoil’ main plots.

Prior to sowing, each main plot was randomly split into two split-plots, one of which was covered with a 50 mm deep mulch of coarse sand, and the other with a 50 mm layer of site subsoil. These split-plots were further split into five; 1000mm x 600 mm split-split-plots to be over-sown with one of five randomly assigned seed mixtures designed to result in target communities characterized by different ratios of over-canopy (tall:medium) and under-canopy(low species); T1 (tall dominated = 3:1:1), T4 (tall and medium dominated =3:3:1) T3 (no dominance =1:1:1), T2 (low dominated =1:1:3), T5 (medium and low dominated = (1:3:3).

All five target communities included the same twenty-six species (nine taller over-canopy, nine shorter over-canopy, and eight under-canopy species) (Table 1). Over-canopy species were selected on the basis of past studies on establishment and management of prairie species in northern Britain (Hitchmough et al., 2004; Hitchmough and de la Fleur, 2006), germination and emergence characteristics of woodland under-storey forbs (Ahmad and Hitchmough, 2007) and palatability to slugs (Hitchmough and Wagner, 2011).

Over-canopy forbs were North American prairie and woodland edge species, selected to flower between summer and autumn, and provide food for native pollinators (Garbuzov and Ratnieks, 2015). Under-canopy forbs were Western European or North American woodland species. Phlox pilosa was included because it is subject to shading within its prairie habitat. Species selection was used to build in gradients of tolerance towards shading, and palatability to molluscs (Table 1). Seed was obtained from Jelitto Seeds (Germany) and Prairie Moon Nursery (MN, USA). Sowing was completed by January 12th 2006.

Seed mix portions for the 160 split-split-plots were made up individually to ensure equivalent sown composition. Composition of seed mixtures was based on target number of seedlings for each species (ranging from 1-9 seedlings per split-split-plot, depending on sowing density and canopy layer ratios). Within each target community field emergence data (Ahmad and Hitchmough, 2007) was used to ensure species within a given canopy height group were present at approximately the same density. After initial emergence in 2006, seedlings of each species within central 800 x 400 mm permanent quadrats within the 1000 x 600 mm split-split-plots were identified and counted. Seedlings in excess of the target were removed. Where seedlings were below target, additional seedlings were transplanted into the permanent quadrats to achieve species level target densities. This process was completed by 30th July 2006, resulting in 56 seedlings per quadrat (≈170 seedlings m^{-2}) for low-density treatments, and 84 seedlings per quadrat (≈260 seedlings m^{-2}) for high-density treatments. Between 2007 and 2010, all plots were cut annually in early January and the cut material raked up and removed. No weeding was undertaken beyond September 2006.

2.1 Experimental management and data recording

Immediately after thinning/transplanting at the end of July 2006, seedling numbers per quadrat were counted to provide a baseline measurement. In September 2009, a final count of individuals was carried out for species from the tall- and mid-canopy layers, with all counted individuals cut off at ground level and individually bagged labelled, and dried prior to weighing standing biomass. Weed biomass per quadrat was also harvested and treated in the same way. Under-canopy species were harvested in the same way in early May 2010 close to peak biomass. Due to the large volume of biomass, it was impracticable to oven-dry samples; instead, they were air-dried in a sealed glasshouse, then stored in a warm room for one year, with final dry weight determined at equilibrium with the atmosphere.

2.2 Statistical analysis

For all analyses, species were grouped in two, rather than three layers. We dispensed with the distinction between taller over-canopy species and shorter over-canopy species, as the latter were characterized by poor persistence. We constructed GLMMs (Generalised Linear Mixed Models) using Poisson errors to analyse treatment effects on sown species richness (Table 2), both pooled across the two main layers, and individually for over-canopy and the under-canopy layer, as well as on plant densities of the six most abundant individual species (Table 4). Treatments included; soil, mulch, sowing density, seed mix, and all possible interactions between these factors as fixed effects. Blocks, main plots nested within blocks, and split-plots nested within main plots were included as random effects (Schabenberger and Pierce, 2002). In spite of focusing just on these most abundant species, no convergence was achieved for GLMM models for Lathyrus vernus. Consequently, count data for this species was Box-Cox-transformed using the MASS package 7.3-43 in R 3.2.1 (R Foundation for Statistical Computing, Vienna, AT), and then analysed with a LMM (Linear Mixed Models), using the same effects specifications as before. Similar LMMs were constructed for various biomass parameters (Table 4), over-canopy biomass and total weed biomass in autumn 2009, and under-canopy biomass in spring 2010 (Table 5), as well as biomass of the same six most abundant species as before (Table 6). Again, data was Box-Cox transformed prior to LMM analyses. All mixed model analyses were performed with SAS 9.3 (SAS Institute, Cary, NC, US), using PROC MIXED for LMMs and PROC GLIMMIX for GLMMs.

3 Results

3.1 Species richness

Mulching had a significant effect ($F_{1,12} = 6.91$; $P = 0.022$) on overall species richness within communities after four years, with sand mulching resulting in higher richness (Fig. 1A). We also found a weakly significant soil productivity x seedling density interaction effect on richness ($F_{1,12} = 4.81$; $P = 0.049$), with richness levels in 2009/10 highest in productive topsoil treatment plots sown at the lower density (Table 2). Over-canopy species richness was more responsive to experimental treatments than under-canopy species richness, for which there were no significant effects. Over-canopy species richness was significantly affected by sowing density ($F_{1,12} = 6.18$; $P = 0.029$), with higher levels of richness associated with low-density sowing, and by type of mulch ($F_{1,12} = 7.79$; $P = 0.016$), with higher richness being associated with sand-mulching (Fig. 1B).

3.2 Species abundance and dominance

Of 26 species sown in 2006, 22 persisted into the final year of the experiment (Table 2), some only as sporadic occurrences. Species-level analysis using the more appropriate GLMM approach was only possible for the five most common species (Table 4). In all five, plant numbers in the final year of the experiment were significantly related to seed mix (A. gerardii: $F_{4,96} = 3.21$; $P = 0.016$; $P = 0.006$; P. elatior: $F_{4,96} = 9.62$; $P < 0.001$; P. vulgaris: $F_{4,96} = 5.77$; $P < 0.001$; S. novae-angliae: $F_{4,96} = 3.81$; S. integrifolium: $F_{4,96} = 7.91$; $P < 0.001$) and specifically amount of seed sown in the different mixes. This relationship was weakest in A. gerardii and S. novae-angliae, and strongest in P. elatior (Fig. 2A). Plant numbers in S. integrifolium also varied with mulch ($F_{1,12} = 28.90$; $P < 0.001$), with sand mulch having a positive effect ($F_{1,12} = 28.90$; $P < 0.001$) on numbers of plants still present in 2009/10 (Fig. 2A).

For the sixth species, L. vernus, LMM analysis of transformed plant counts (Table 4) indicated that density of this species, was similarly affected by seed mix ($F_{4,96}$; 5.85; $P < 0.001$). A significant interaction between seed mix and sowing density ($F_{4,96} = 4.06$; $P = 0.004$) appeared to be due to numbers being reduced at the higher sowing density particularly in mix T4 (low canopy dominated ; see Fig. 2B). The highest numbers of L. vernus were found on sand mulch (Fig. 2B).

3.3 Community biomass

Mean standing biomass (±SE; N=160) of the sown components in the vegetation in 2009/10 was 856 (±55) g m^{-2} (2009) for the over-canopy in autumn 2009 and 144 (±8) g m^{-2} for the under-canopy in spring 2010, respectively. Weeds contributed just 42 (±5) g m^{-2} in autumn 2009 and about 13 (±3) g m^{-2} in spring 2010 to these biomass totals. Treatment factors interacted in a complex manner in determining community biomass, with significant second and third-order interactions in statistical models (Table 5) resulting in complex and difficult to interpret patterns across treatment combinations.

In the case of over-canopy biomass, a significant second-order interaction between mulch and seed mix ($F_{4,96}$ = 3.52; P = 0.010) was indicative of a reduced over-canopy in the case of seed mix T1 (tall dominated) when sown onto sand rather than subsoil mulch. The biomass of the under-canopy layer was higher on subsoil mulch ($F_{1,12}$ = 14.02; P = 0.003), with, the size of the effect varying between different combinations of experimental treatments (see higher order interactions involving mulch in Table 5). A significant interaction between sowing density and sowing mix ($F_{4,96}$ = 16.25; P < 0.001) was indicative of a much higher under-canopy biomass in mix T1, (tall dominated) when sowing density was low.

3.4 Species biomass and dominance

In terms of biomass the most dominant species at the 2009/10 final census were; Silphium integrifolium (mean biomass: 375 g m^{-2}), Symphyotrichum novae-angliae (312 g m^{-2}), Primula vulgaris (84 g m^{-2}), Andropogon gerardii (84 g m^{-2}), Primula elatior (49 g m^{-2}) and Helianthus mollis (33g m^{-2}) (Table 3). Biomass patterns across treatments are shown for S. integrifolium, the dominant over-canopy species in Fig. 3A, and P. vulgaris, the dominant under-canopy species, in Fig. 3B.

The biomass of S. integrifolium, was significantly affected by three-way interactions involving sowing density × mulch × seed mix ($F_{4,96} = 10.96$; $P < 0.001$). On sand mulch, for example, at low sowing density, Silphium biomass was highest with seed mixes containing a low to medium proportion of over-canopy species (mixes T2, T5, T3), whereas at high sowing density, the highest biomass was with T3 and T4, with medium to high proportion of seeds of over canopy species (Fig. 3A). Biomass of Symphyotrichum novae-angliae, was unaffected by experimental treatments, and Andropogon gerardii we only found a significant two-way interaction between sowing density and seed mix ($F_{4,96} = 3.05$; $P = 0.020$).

In the under-canopy layer, both Primula elatior and P. vulgaris, showed highly significant two-way interactions between sowing density × seed mix (P. elatior: $F_{4,96} = 7.37$; $P < 0.001$; P. vulgaris: $F_{4,96} = 7.47$; $P < 0.001$) due to higher Primula biomass in low-density sowings in some mixes (Fig. 3B). In the case of P. elatior, mulch had a significant main effect ($F_{4,96} = 8.94$; $P = 0.011$), with slightly higher biomass levels on subsoil mulch.

4 Discussion

4.1 Was the combination of a summer-growing over-canopy and winter/spring growing under-canopy effective in inhibiting weed biomass over a 4 year period?

Initial weed invasion was low due to the use of weed seed free sowing mulches and plot weeding in the first year. Despite no weeding post 2006, and seed rain from the surrounding brown field vegetation, by September 2009, weed biomass was still very small by September 2009, at only 4% of the total biomass of sown species. In a previous experiment on the same site with a similar prairie plant community, but without an under-canopy layer, mean weed cover values after three years without weeding averaged 45.6% when management involved only cutting and removal of the vegetation in spring, and 12.3% with the optimal weed management treatment of spring burning (Hitchmough and de La Fleur, 2006). This suggests that the combination of a winter green understory layer and a summer green upper canopy layer was efficacious in reducing weed colonization. To explore the underlying mechanism further, a series of two-sided Spearman correlation tests were carried out to explore the relationships between weed biomass and other biomass components (over-canopy biomass, under-canopy biomass, and also biomass individually of the two most dominant species in the over-canopy, Silphium integrifolium and Symphyotrichum novae-angliae), as well as with sown species richness (all tests with N = 160). The strongest associations of weed biomass were with total sown biomass (i.e. under-canopy plus over-canopy), with Spearman's rho $r_S = -0.375$, with over-canopy biomass at $r_S = -0.363$, and with biomass of Silphium integrifolium at $r_S = -0.388$ (all three at $P < 0.001$). No significant correlations were found between weed biomass and under-canopy biomass ($r_S = -0.10$; $P = 0.214$), and between weed biomass and biomass of Symphotrichum novae-angliae ($r_S = -0.07$; $P = 0.354$). Neither was there a significant correlation between weed biomass and sown species richness ($r_S = -0.07$; $P = 0.721$). Without a significant relationship between weed biomass and biomass of the sown under-canopy, we were not able to establish any correlational evidence for a weed-suppressive role of the added understory. However, this does not necessarily prove that this layer does not contribute to weed suppression. To explicitly test for such a contribution, we would have had to specifically include suitable control treatments involving the sowing only of the prairie over-canopy on its own, looking at weed establishment both in the presence as well as in the absence of a sown understory.

Efficacy of light extinction depends on canopy depth (McCain, et al., 2015) and density (Suzaki, et al., 2003). The leaf canopies of Silphium integrifolium and Symphotrichum novae-angliae and were 900-1200mm tall, and dense, with a mean combined dry biomass of 687g m^{-2} in September 2009. Weed biomass was mostly restricted to plot edges, and composed of Holcus lanatus and ruderal Epilobium. The longevity of these effects is potentially considerable. Sown prairie vegetation on productive soils in Sheffield parks with biomass levels similar to those described in this study, was largely weed free after thirteen years (Hitchmough, 2017).

In the present study, the winter-green foliage of the two Primula dominants (approximately 16 plants per m^2; see Fig. 5) may have contributed to weed suppression by restricting light availability to any weeds present in gaps between the Primula rosettes during winter and spring. Alternatively the main contribution of this layer may simply have been to add additional biomass to that of the upper canopy.

4.2 Did the design of the five plant communities (i.e. sowing mix and density) affect the longer-term characteristics (species diversity, abundance, persistence, and biomass) of the vegetation?

We had expected the starting ratio of over-canopy to under-canopy species to have a clearer effect on community development than the statistical analysis suggests. One explanation for these relatively small effects may have been that the same species were present in all plots (albeit in differing initial ratios), and from the second year, the dominant over-canopy species were shading all plots irrespective of the mix originally sown. Seed mix starting point did however affect numerical abundance of the six most common species after four years , but not their biomasses. At higher densities, individuals of a species were smaller. This is consistent with Farrer and Goldberg (2011) who showed that adult biomass in prairie species tends to be more negatively affected by neighbours of the same species rather than other species. Although " species" was not an experimental variable (all sub-plots had the same species) the study does show the criticality of species selection as a design decision. Had the six most successful species not been selected, outcomes would have been radically different.

We had anticipated that increasing sowing density would increase inter- and intra-specific competition thus reducing weed colonization, but also persistence of smaller or shade intolerant sown species. This latter was partly supported by the data; richness of sown over-canopy species was highest on plots sown at the lower density. In terms of the density of individual species, statistically detectable density effects on abundance of the six dominant species were limited to a single interaction between density and seed mix for L. vernus. This indicates that this species is suppressed by over-canopy forbs when these are sown at high density. This species emerges into growth in March, and is hence more sensitive to competition for light with the over-canopy species.

Irrespective of initial sowing density the two most abundant and productive over-canopy species (S. novae-angliae and S. integrifolium), were able to maintain dominance, increasing the resilience of the community to weed invasion, but causing the decline of many of the shorter over-canopy species. Reduced sowing rates of these types of tall species may, at least in the short term, improve survival of shorter over-canopy species. While occurrence was too sporadic for formal statistical analysis, in the 2009/10 census, Echinacea purpurea and Gillenia trifoliata were most abundant in low-density sowings on sand mulch.

4.3 Was species richness, abundance, persistence, and biomass affected by mulch type and soil productivity?

Abundance of two of the six most successful species, S. integrifolium and L. vernus was significantly higher on sand mulch. Sand mulch also resulted in a richer over-canopy. It seems likely that this was an indirect effect of reduced levels of slug grazing both of established plants and self-sown seedlings. In contrast, no mulch-related patterns were observed for the two unpalatable Primula species (Jennings and Barkham, 1975) that dominated the under-canopy layer. Under-canopy biomass was higher on plots with subsoil mulch. This may be due to either reduced light competition with the over-canopy dominant S. integrifolium on subsoil mulch, or to lower moisture stress.

Our assumptions that community biomass, and hence competitive displacement effects within the community (Buckland and Grime, 2000), would be greater on the more productive topsoil than on the subsoil plots were not confirmed. As no biomass harvests were made prior to 2009, it is possible that these effects did occur transiently, but as the roots of species grew into the topsoil buried 300mm beneath the surface, productivity on the subsoil became indistinguishable from the topsoil.

In terms of urban landscape practice, these are constructive findings. Communities of highly productive over-canopy species and highly shade-tolerant under-canopy species, when combined with each other, were able to persist and function effectively under highly productive conditions that would subject shorter, more unproductive meadow-like communities to invasion and decline. The soil at the experimental site was typically moisture-retentive, but probably too dry for species of wet habitats, such as Eupatorium maculatum, Phlox glaberrima and P. maculata, particularly under competition from taller over-canopy species as in the present study.

Fig. 5 shows the leaves of the dominant S. integrifolium well emerged on the 6th March in 2010. Roberts, et al., (2015) report an average leafing up date for Quercus robur, a dominant woodland tree in Britain, as 23rd April, although in Sheffield, leafing up more typically occurs in early May. Whilst leaf phenology varies from year to year, intense shading at ground level occurred earlier in the year in this study than in woodland, potentially restricting the range of under-canopy species that can persist.

4.4 Are two-layer communities visually successful models for future urban planting design?

Whilst our experimental design does not allow us to discern whether the impact of the under-canopy had a significant effect on weed suppression, the presence of this layer was valuable from an aesthetic perspective, providing greenery during winter when otherwise winter dormant prairie vegetation is unattractive. It also greatly increased the duration of the flowering season, with under-canopy species flowering from March to May (Fig. 5), and over canopy species from July to October (Fig. 4 and 6). This long flowering season makes this vegetation potentially attractive both to people and to generalist invertebrate pollinators. Aesthetic and biodiversity potential were however gradually undermined by the decline in species richness that led to fewer flowers in early summer, and a simplification of community structure.

As a model for practice, the prototype discussed in this paper could be improved by extending the range of over and under-canopy forbs. In this study, we restricted ourselves to under-canopy species that could be established by sowing seed in situ, thereby excluding many of the most shade tolerant species including many woodland species with complex seed dormancy (Baskin and Baskin, 2001). Where resources allow, evergreen species with equivalent shade tolerance to the two Primula species used in this study, for example; Ajuga reptans, Omphalodes, and Pulmonaria, could be established by planting.

Because the over-canopy species used in this study were North American that could be established by sowing seed in situ, capacity for resilience was limited, as many of these species are palatable to slugs (Hahn, et al., 2011; Hitchmough and Wagner, 2011). Although we did not have the resources to monitor slug populations and slug grazing impacts directly in this in this study, we knew from previous studies on this site (Hitchmough and Wagner, 2011) that it supports a large slug population. Our species selection process gave us a range of taxa that varied in their demonstrated palatability to slugs. All of the species that declined are palatable to slugs, whilst the species that were largely extant in 2009/10 are less palatable to slugs (Tables 7 and 8). Sand mulches reduce the frequency of slug grazing on emergent shoots in spring (Hitchmough and Wagner, 2011), by restricting slug mobility to wet nights. On large-scale plots sand-mulching restricts slug grazing to the plot edges, but our experimental plots were too small to achieve this.

In contrast to most prairie species, many Eurasian, Eastern Temperate Asian and Eastern South African species are much less palatable and potentially more persistent in multi-layer communities, for example; Aconitum, Actaea, Agapanthus, Dierama, Filipendula, Geranium, Knautia, Kniphofia, Leucanthemum, Persicaria, Veronica, and Veronicastrum (Asian and North American) (Hitchmough, 2017). However, many of the species in these genera establish too slowly or unreliably from in situ sowing, thus requiring planting, and incurring additional establishment costs. Aesthetics and functionality could be further improved by reducing dominance in the over-canopy by selecting species with more equivalent growth rates, height and ecological fitness. Sowing or planting over-canopy species at densities that are inversely proportional to their dominance potential is an effective means of reducing extirpation of the slowest-growing, most shade-intolerant species (Hitchmough, 2017).

5 Conclusion

The combination of a shade-tolerant forb under-canopy with a tall forb over-canopy was effective in restricting weed invasion under a low-maintenance regime in a Western European climate. Our study was not designed to separate the effects of these two layers, and a future study is warranted to more clearly unpick these relationships. Addition of a winter-green under-canopy layer increased the attractiveness of the vegetation during this time of year and extended the flowering season, with peaks in spring and late summer to autumn. It seems likely that this combination of layers can potentially be applied to a diversity of designed herbaceous plant communities, to close seasonal gaps when the over-canopy species are either dormant or have reduced canopy cover. This application of phenology to design is likely to become more important as the combination of urban heat islands and climate change increase the capacity for weed invasion over-winter in designed herbaceous vegetation. The study highlights how artificial, designed plant communities can utilize species that do not naturally co-occur to provide increased urban functionality by combining complementary ecological traits.

6 References

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Table 1. Ecological characteristics of the species used (from Curtis 1959; Ellenberg, et al., 1991; Hitchmough and Wagner, 2011; Spira, 2011; USDA Plant Database http://plants.usda.gov

Table 2. Effects of experimental treatments on sown species richness, both pooled across the two layers and individually for each separate layer. Analyses were based on plant counts in autumn 2009 (over-canopy layer) and spring 2010 (under-canopy layer). Mixed model F-values and significance levels are given. Significant model terms ($P < 0.05$) in bold.

Table 3. Overall abundance and biomass of sown over-canopy species in autumn 2009 and sown under-canopy species in spring 2010, respectively. Species are listed in order of declining biomass. Plant densities across the experiment are expressed as mean ± SE (N=160), and as a percentage of baseline densities in 2006, and finally in terms of split-split-plot occupancy (Maximum = 160). Phlox divaricata, P. pilosa, Zizia aptera and Helenium autumnale were not found in 2009/10.

Table 4. Effects of experimental treatments on plant densities of the six most abundant species at the 2009/10 census. Mixed model F-values and significance levels are given. Significant model terms ($P < 0.05$) in bold.

Table 5. Effects of experimental treatments on biomass of canopy components in the final year of the experiment. Analyses were based on biomass harvests in autumn 2009 (over-canopy layer and weeds) and spring 2010 (under-canopy layer). Mixed model F-values and significance levels are given. Significant model terms ($P < 0.05$) in bold.

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Table 7. Palatability and shade tolerance of species that by September 2009/May 2010, were effectively extinct. Location within the grid is based on observation within this and past experiments (Hitchmough and Woudstra, 1999; Hitchmough and Wagner, 2011), and in cultivation in the UK.

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Species	Distribution/habitat	Relative growth productivity	Soil moisture stress tolerance	Shade tolerance	Palatability to slugs
Under-canopy 300-450mm					
Dodecatheon meadia	Eastern USA, prairie-woodland	low	medium	high	low
Lathyrus vernus	Eurasia, woodland-woodland edge	low	medium	high	Low-medium
Phlox divaricata	Eastern USA/Canada, woodland-woodland edge	low	medium	medium	high
Phlox pilosa	Eastern USA, prairie-woodland edge	low	medium-high	medium-low	high-medium
Polemonium reptans	Eastern USA, woodland - woodland edge	low-medium	medium	medium	low
Primula elatior	Eurasia, woodland	low	low-medium	high	low
Primula vulgaris	Eurasia, woodland	low	low-medium	high	low
Zizia aptera	Eastern USA, woodland-woodland edge	low-medium	medium	medium-low	medium-low
Shorter over-canopy 750-900mm					
Echinacea purpurea	Eastern USA, prairie-woodland edge	medium	medium-low	medium	high
Gillenia trifoliata	Eastern USA/Canada, woodland-woodland edge	medium	medium-high	high-medium	medium
Phlox glaberrima	Eastern USA, prairie to woodland edge	medium	low	medium	medium
Penstemon digitalis	Eastern USA, prairie	medium	medium	low	medium
Phlox maculata	Eastern USA, prairie to woodland edge	medium	low	medium	medium
Rudbeckia fulgida var. speciosa	Eastern USA, prairie to woodland edge	medium	low	medium	high
Silene regia	Eastern USA, prairie to woodland edge	medium	medium	low	medium
Solidago speciosa	Eastern USA, prairie	medium	medium-high	low	medium
Symphyotrichum oolentangiense	Eastern USA, prairie	medium	medium-high	low	low
Taller over-canopy, >900mm					
Andropogon gerardii	Eastern USA, prairie	high	high	low	low
Eupatorium maculatum	Eastern USA, prairie-woodland edge	high	low	medium-low	medium-low
Helianthus mollis	Eastern USA, prairie	high	high	low	low
Helenium autumnale	Eastern USA, prairie-woodland edge	medium-high	medium	low	medium-high
Phlox amplifolia	Eastern USA, prairie-woodland edge	high	low	medium	low
Rudbeckia subtomentosa	Eastern USA, prairie-woodland edge	high	medium	medium-low	low
Silphium integrifolium	Eastern USA, prairie	high	high	low	low

Symphyotrichum novae-angliae 'Septemberrubin'	Eastern USA, prairie to woodland edge	high	medium	medium-low	low
Veronicastrum virginicum	Eastern USA, prairie-woodland edge	high	low-medium	medium	low

Table 2. Effects of experimental treatments on sown species richness, both pooled across the two layers and individually for each separate layer. Analyses were based on plant counts in autumn 2009 (over-canopy layer) and spring 2010 (under-canopy layer). Mixed model F-values and significance levels are given. Treatments with significant model terms (P < 0.05) are shown in bold.

Effect	D.f.	Across layers		Over-canopy		Under-canopy	
		GLMM		GLMM		GLMM	
		F	P	F	P	F	P
Soil	1, 12	0.85	0.374	0.22	0.646	0.65	0.437
Density	1, 12	3.34	0.093	**6.18**	**0.029**	1.37	0.264
Mulch	1, 12	**6.91**	**0.022**	**7.79**	**0.016**	0.72	0.414
Seed mix	4, 96	0.27	0.896	1.06	0.382	0.64	0.637
Soil × Density	1, 12	**4.81**	**0.049**	1.72	0.214	1.76	0.210
Soil × Mulch	1, 12	0.17	0.687	0.32	0.582	0.00	0.995
Soil × Seed mix	4, 96	0.23	0.924	0.24	0.916	0.14	0.968
Density × Mulch	1, 12	0.00	0.968	0.21	0.653	0.24	0.634
Density × Seed mix	4, 96	0.29	0.885	0.16	0.958	0.44	0.780
Mulch × Seed mix	4, 96	1.30	0.277	1.31	0.272	0.37	0.830
Soil × Density × Mulch	1, 12	0.00	0.950	0.01	0.929	0.06	0.816
Soil × Density × Seed mix	4, 96	0.20	0.935	0.37	0.831	0.06	0.993
Soil × Mulch × Seed mix	4, 96	0.32	0.861	0.29	0.883	0.10	0.982
Density × Mulch × Seed mix	4, 96	0.23	0.922	0.29	0.882	0.29	0.882
Soil × Density × Mulch × Seed mix	4, 96	0.36	0.837	0.48	0.750	0.22	0.927

Table 3. Overall abundance and biomass of sown over-canopy species in autumn 2009 and sown under-canopy species in spring 2010, respectively. Species are listed in order of declining biomass. Plant densities across the experiment are expressed as mean ± SE (N=160), and as a percentage of baseline densities in 2006, and finally in terms of split-split-plot occupancy (Maximum = 160). Phlox divaricata, P. pilosa, Zizia aptera and Helenium autumnale were not found in 2009/10.

Species	Layer	Biomass (g m^{-2})	Plant density (Plants m^{-2})	Percentage (baseline: 2006)	Occurrence (max.: 160)
Silphium integrifolium	Over-canopy	375.4 ± 38.2	6.74 ± 0.43	59.8	131
Symphyotrichum novae-angliae	Over-canopy	312.0 ± 34.5	4.04 ± 0.32	61.6	117
Primula vulgaris	Under-canopy	83.8 ± 4.7	9.20 ± 0.39	69.8	158
Andropogon gerardii	Over-canopy	83.8 ± 14.0	3.55 ± 0.32	36.8	97
Primula elatior	Under-canopy	49.3 ± 5.2	6.89 ± 0.42	41.1	144
Helianthus mollis	Over-canopy	32.7 ± 6.6	1.72 ± 0.28	42.7	50
Solidago speciosa	Over-canopy	13.6 ± 3.4	0.96 ± 0.16	19.4	35
Lathyrus vernus	Under-canopy	10.6 ± 1.5	3.32 ± 0.28	44.4	99
Echinacea purpurea	Over-canopy	10.1 ± 2.8	1.04 ± 0.20	9.3	35
Rudbeckia subtomentosa	Over-canopy	9.3 ± 2.0	1.54 ± 0.20	17.9	55
Veronicastrum virginicum	Over-canopy	7.4 ± 1.4	2.25 ± 0.25	22.1	73
Phlox amplifolia	Over-canopy	3.9 ± 1.5	0.41 ± 0.10	8.0	16
Gillenia trifoliata	Over-canopy	2.4 ± 0.7	1.07 ± 0.16	9.9	42
Eupatorium maculatum	Over-canopy	2.4 ± 1.5	0.23 ± 0.08	2.3	10
Symphyotrichum oolentangiensis	Over-canopy	1.1 ± 0.5	0.31 ± 0.08	7.4	14
Penstemon digitalis	Over-canopy	1.1 ± 0.4	0.20 ± 0.06	2.0	10
Rudbeckia fulgida	Over-canopy	0.60 ± 0.51	0.08 ± 0.04	0.8	4
Phlox glaberrima	Over-canopy	0.34 ± 0.23	0.06 ± 0.03	1.6	3
Polemonium reptans	Under-canopy	0.16 ± 0.05	0.33 ± 0.08	3.2	17
Phlox maculata	Over-canopy	0.07 ± 0.07	0.02 ± 0.02	0.5	1
Silene regia	Over-canopy	0.01 ± 0.01	0.02 ± 0.02	0.2	1
Dodecatheon meadia	Under-canopy	0.00 ± 0.00	0.37 ± 0.09	5.9	17

Table 4. Effects of experimental treatments on plant densities of the six most abundant species at the 2009/10 census. Mixed model F-values and significance levels are given. Only treatments with model terms significant (P < 0.05) for at least one species are shown.

		Over-canopy						Under-canopy					
		Silphium integrifolium		Symphyotrichum novae-angliae		Andropogon gerardii		Primula vulgaris		Primula elatior		Lathyrus vernus	
		GLMM		GLMM		GLMM		GLMM		GLMM		LMM	
Effect	D.f.	F	P	F	P	F	P	F	P	F	P	F	P
Mulch	1, 12	**28.90**	**< 0.001**	1.41	0.259	3.83	0.074	2.23	0.161	0.23	0.642	**17.16**	**0.001**
Seed mix	4, 96	**7.91**	**< 0.001**	**3.81**	**0.006**	**3.21**	**0.016**	**5.77**	**< 0.001**	**9.62**	**< 0.001**	**5.85**	**< 0.001**
Density × Seed mix	4, 96	0.71	0.586	0.42	0.794	0.57	0.686	1.58	0.185	0.58	0.681	**4.06**	**0.004**

Table 5. Effects of experimental treatments on biomass of canopy components in the final year of the experiment. Analyses were based on biomass harvests in autumn 2009 (over-canopy layer and weeds) and spring 2010 (under-canopy layer). Mixed model F-values and significance levels are given. Only model terms significant ($P < 0.05$) for at least one species group are shown.

		Over-canopy		Under-canopy		Weeds	
Effect	D.f.	F	P	F	P	F	P
Mulch	1, 12	4.18	0.063	**14.02**	**0.003**	0.51	0.490
Soil × Mulch	1, 12	**5.35**	**0.039**	1.91	0.192	0.05	0.833
Density × Seed mix	4, 96	1.58	0.185	**16.25**	**< 0.001**	0.24	0.917
Mulch × Seed mix	4, 96	**3.52**	**0.010**	1.19	0.318	**3.47**	**0.011**
Soil × Density × Mulch	1, 12	**7.61**	**0.017**	**17.58**	**0.001**	0.51	0.487
Density × Mulch × Seed mix	4, 96	**3.26**	**0.015**	**4.32**	**0.003**	**6.03**	**< 0.001**

Table 6. Effects of experimental treatments on biomass of the six most abundant sown species in the 2009/10 census. Analyses were based on biomass harvests in autumn 2009 (over-canopy species) and spring 2010 (under-canopy species). Mixed model F-values and significance levels are given. Only model terms significant (P < 0.05) for at least one species are shown.

		Over-canopy						Under-canopy					
		Silphium integrifolium		Symphyotrichum novae-angliae		Andropogon gerardii		Primula vulgaris		Primula elatior		Lathyrus vernus	
Effect	D.f.	F	P	F	P	F	P	F	P	F	P	F	P
Mulch	1, 12	3.11	0.103	1.17	0.301	3.29	0.095	3.82	0.074	**8.94**	**0.011**	**6.81**	**0.023**
Soil × Mulch	1, 12	**4.77**	**0.0496**	2.20	0.164	0.05	0.828	2.65	0.130	0.08	0.776	0.01	0.907
Density × Seed mix	4, 96	1.27	0.286	0.91	0.464	**3.05**	**0.020**	**7.47**	**< 0.001**	**7.37**	**< 0.001**	1.59	0.182
Mulch × Seed mix	4, 96	**8.82**	**< 0.001**	0.34	0.851	2.45	0.051	1.68	0.160	0.47	0.760	**5.00**	**0.001**
Soil × Density × Mulch	1, 12	3.27	0.096	2.88	0.115	0.02	0.884	**9.21**	**0.0104**	**8.66**	**0.012**	**6.27**	**0.028**
Soil × Density × Seed mix	4, 96	0.21	0.935	0.43	0.787	0.59	0.673	1.48	0.215	0.50	0.734	**3.96**	**0.005**
Density × Mulch × Seed mix	4, 96	**10.96**	**< 0.001**	0.78	0.543	0.15	0.964	**2.60**	**0.041**	**2.69**	**0.036**	**2.50**	**0.047**
Soil × Density × Mulch × Seed mix	4, 96	0.38	0.821	0.61	0.654	0.37	0.826	**3.02**	**0.022**	1.71	0.155	0.82	0.516

Table 7. Palatability and shade tolerance of species that by September 2009/May 2010 were effectively extinct. Location within the grid is based on observation within this and past experiments (Hitchmough and Woudstra, 1999; Hitchmough and Wagner, 2011), and in cultivation in the UK.

		Shade tolerance: low	Shade tolerance: intermediate	Shade tolerance: high
Palatability	Low			
	intermediate		Phlox amplifolia Phlox glaberrima Phlox maculata Ziza aptera	
	high	Helenium autumnale	Phlox divaricartus Phlox pilosa Rudbeckia fulgida var. speciosa	

Table 8. Palatability and shade tolerance of species that were extant by September 2009/May 2010. . Species that appeared most persistent are shown in bold. Location within the grid is based on observation within this and past experiments (Hitchmough and Woudstra, 1999; Hitchmough and Wagner 2011), and in cultivation in the UK.

		Shade tolerance		
		low	intermediate	high
Palatability	Low	**Andropogon gerardii** Penstemon digitalis	**Helianthus mollis** Polemonium reptans **Silphium integrifolium** **Symphyotrichum novae-angliae**	Dodecatheon meadia **Lathyrus vernus** **Primula elatior** **Primula vulgaris**
	intermediate	Symphyotrichum oolentangiense Solidago speciosa	Gillenia trifoliata Rudbeckia subtomentosa Silene regia	
	high		Echinacea purpurea Eupatorium maculatum	

Figure legends

Figure 1. Species richness in terms of number of species per 0.32 m^2 quadrat for (A) across layers, (B) for the over-canopy, and (C) for the under-canopy in autumn 2009 / spring 2010 surveys. Significance levels of experimental treatment factors: *P<0.05; **P<0.01; and ***P<0.001.

Figure 2. Plant densities per m^2 of (A) S. integrifolium, the most productive species in the over-canopy, in autumn 2009, and (B) L. vernus, the species most responsive to experimental treatments in the under-canopy, in spring 2010. Significance levels of experimental treatment factors: *P<0.05; **P<0.01; and ***P<0.001.

Figure 3. Dry biomass in g m^{-2} of (A) S. integrifolium, the most productive over-canopy species, in autumn 2009, and (B) P. vulgaris, the most productive under-canopy species, in spring 2010. Significance levels of experimental treatment factors: *P<0.05; **P<0.01; and ***P<0.001.

Figure 4. The over-canopy layer in September 2006.

Figure 5. The under-canopy species Primula elatior and P. vulgaris in flower in April 2010 prior to harvesting. The emerging leaves of Silphium integrifolium are already present between the primula.

Figure 6. The over-canopy layer in September 2009 prior to harvesting.

Figure 1. Species richness in terms of number of species per 0.32 m^2 quadrat for (A) across layers, (B) for the over-canopy, and (C) for the under-canopy in autumn 2009 / spring 2010 surveys. Significance levels of experimental treatment factors: *P<0.05; **P<0.01; and ***P<0.001.

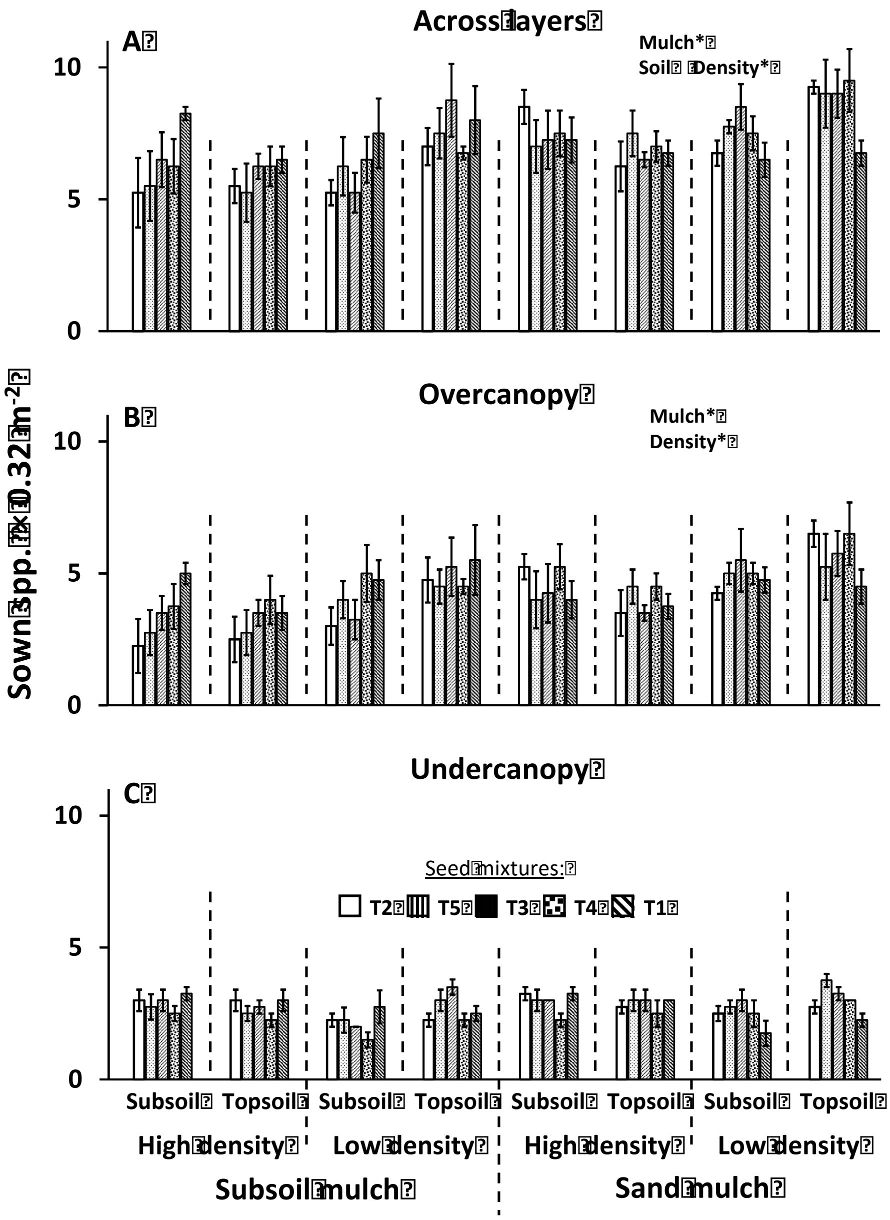

Figure 2. Plant densities per m^2 of (A) S. integrifolium, the most productive species in the over-canopy, in autumn 2009, and (B) L. vernus, the species most responsive to experimental treatments in the under-canopy, in spring 2010. Significance levels of experimental treatment factors: *P<0.05; **P<0.01; and ***P<0.001.

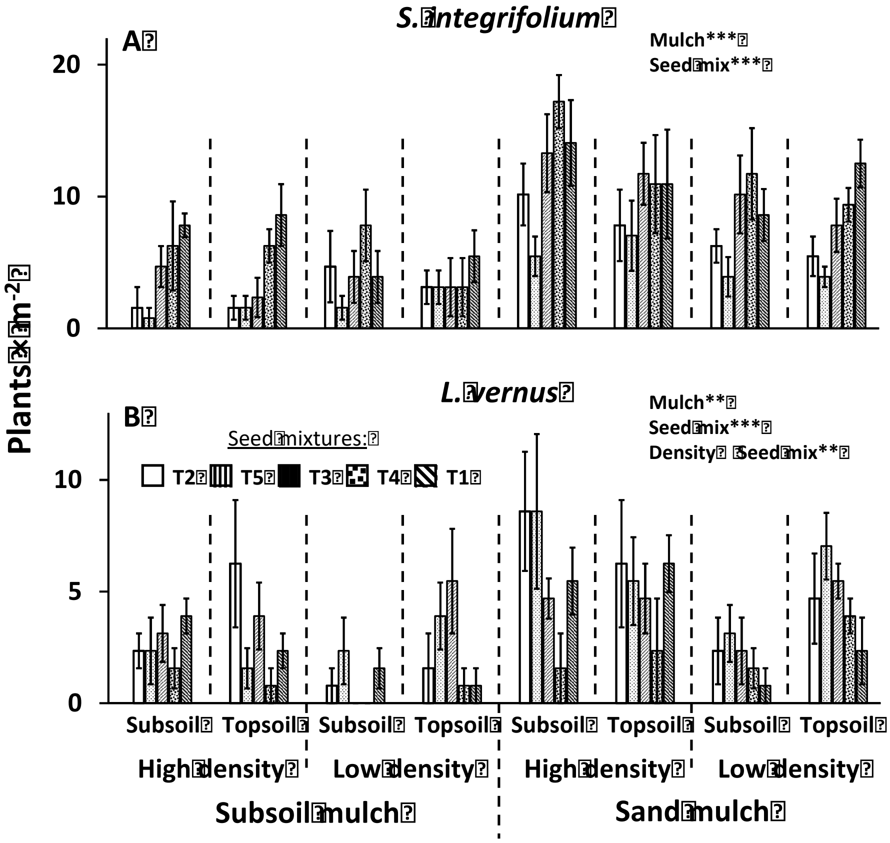

Figure 3. Dry biomass in g m^{-2} of (A) S. integrifolium, the most productive over-canopy species, in autumn 2009, and (B) P. vulgaris, the most productive under-canopy species, in spring 2010. Significance levels of experimental treatment factors: *P<0.05; **P<0.01; and ***P<0.001.

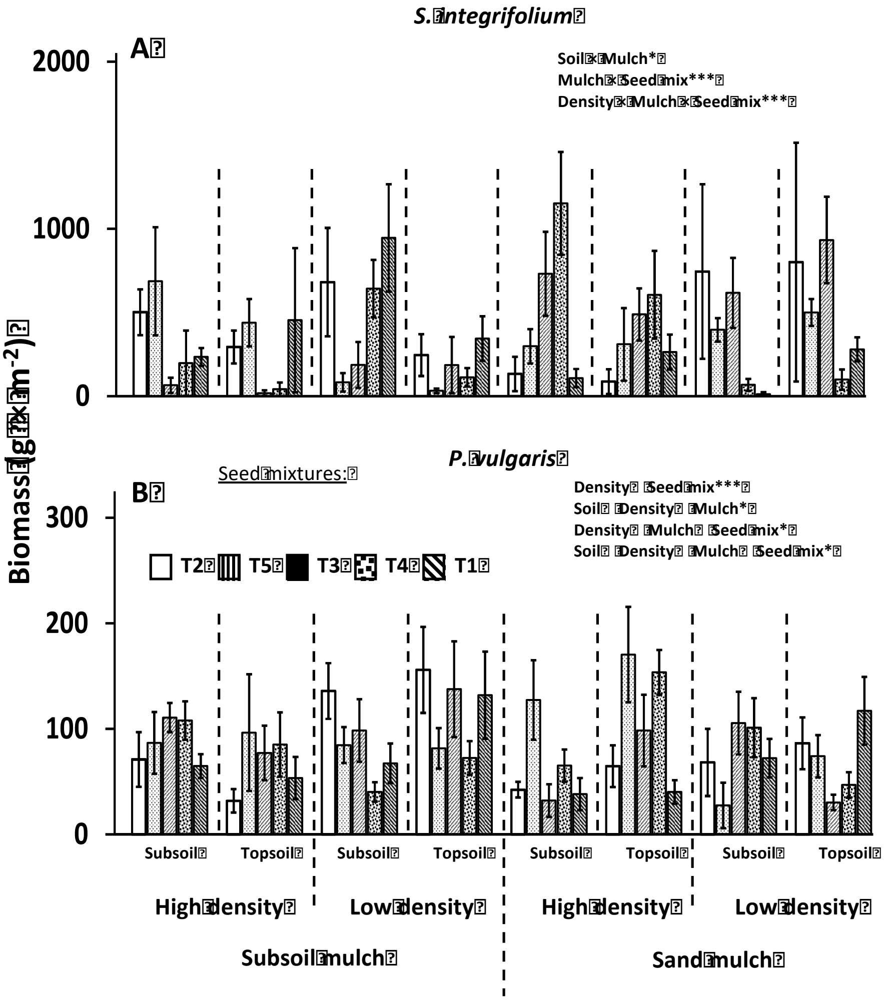

Figure 4. The over-canopy layer in September 2006.

Figure 5. The under-canopy species Primula elatior and P. vulgaris in flower in April 2010 prior to harvesting. The emerging leaves of Silphium integrifolium are already present between the primula.

Figure 6. The over-canopy layer in September 2009 prior to harvesting.