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RESEARCH ARTICLE

Floral resources in Swedish grasslands remain relatively stable under an experimental drought and are enhanced by soil amendments if regularly mown

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Abstract

1. One of the main reasons why insect pollinators are declining is a lack of floral resources. In agricultural landscapes, remaining seminatural grasslands play a key role for providing such resources. However, droughts pose an increasing threat to the abundance and continuity of flowers. Soil amendments are a novel management tool for Swedish grasslands aiming to increase carbon sequestration and soil water holding capacity. In this study, we examined how drought is affecting floral resources (i.e. floral units, nectar quantity and nectar continuity) in grasslands with different mowing regimes, and if soil amendments could mitigate potential negative drought effects.
2. In summer 2019, we set up an experiment combining rain-out shelters ('drought'), soil amendments ('compost') and different mowing regimes ('mown' vs. 'abandoned') in four extensively managed Swedish grasslands (48 plots, size 2 m^2). Between May and August 2021, we counted the floral units nine times in each plot. We derived values for the nectar sugar production per floral unit from an existing database.
3. We observed a decrease in floral units under drought in the mown, but not in the abandoned plots. Nectar quantity and continuity over the season were not significantly affected by drought across both mowing regimes—in the abandoned plots the nectar provision even extended slightly in duration (towards late summer). The compost treatment had positive effects on the floral units, nectar quantity and continuity (extending it towards early summer) in the mown, but not in the abandoned plots. The plant species in our study reacted differently to the treatments. Most of the nectar was provided by only few species (mainly *Lathyrus pratensis*, *Vicia cracca* and *Anthriscus sylvestris*).
4. The results are species specific, thus other plant communities might respond differently. However, our experiment shows that nectar provision (based on database values) in grasslands with a native plant community and natural soil conditions

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remains relatively stable under drought. We also found that soil amendments increase floral resources in managed grasslands.

KEYWORDS
compost, drought, floral resources, grassland management, insect pollinators, mowing, nectar, soil amendments

1 | INTRODUCTION

1.1 | Insect pollinators and floral resources

In recent decades, numerous studies have revealed a dramatic decrease in diversity and abundance of insect pollinators (Biesmeijer et al., 2006; Hallmann et al., 2017; Ollerton, 2017; Potts, Roberts, et al., 2010). This leads to subsequent negative effects on plant diversity and crop yields, since more than 80% of all wild plant species (Potts, Biesmeijer, et al., 2010) and almost 75% of all cultivated plant species (Klein et al., 2007) are dependent on insect pollination for seed and fruit set.

One of the main reasons insect pollinators are declining is thought to be a lack of floral resources (nectar and pollen) due to land use change (Carvell et al., 2006; Dicks et al., 2021; Goulson et al., 2015). Continued habitat loss throughout the 20th century has caused floral resources to decrease both in abundance and diversity (Goulson et al., 2015). For example seminatural grasslands, a flower-rich habitat type, have been reduced to ca. 3%–4% of their original extent in large parts of Northern Europe over the last century (Cousins et al., 2015; Hooftman & Bullock, 2012). Hence, remaining seminatural grasslands provide a vital supply of floral resources and nesting sites for pollinating insects, especially in landscapes dominated by intensive agriculture (Bugin et al., 2022; Cole et al., 2017; Öckinger & Smith, 2007). Although agricultural crops such as oilseed rape *Brassica napus* can flower abundantly, the fact that they flower only within a limited timeframe causes resource gaps, especially in late summer (Rundlöf et al., 2014; Timberlake et al., 2019). This resource gap coincides with the period when most pollinator species have their peak flight activity (Balfour et al., 2018). For example for bumblebees it is crucial to have a continuous supply of floral resources throughout the season (Carvell et al., 2006; Rundlöf et al., 2014; Timberlake et al., 2019). Even just a short timeframe without enough floral resources can be problematic, since bumblebees store only a few days' worth of reserves (Carvell et al., 2006). Another reason why intensive agriculture cannot compensate for the loss of seminatural grasslands is that agricultural crops are often treated with pesticides and grown in monocultures with low floral trait diversity (González-Varo et al., 2013). Pollinator diversity is positively correlated with plant diversity (Fründ et al., 2010; Nicholls & Altieri, 2013), and pollinators are often highly specialized (Blüthgen & Klein, 2011; Fründ et al., 2010).

1.2 | Effects of drought, mowing and soil amendments on floral resources

Droughts have been identified as one of the major future threats to pollinators globally (Brown et al., 2016). Droughts can cause both direct effects on pollinators (less food provisioning) and plants (less pollination success) as well as indirect effects via plant–pollinator interactions (changing floral signal and reward traits) (Descamps et al., 2021; Gallagher & Campbell, 2017). Flowers are a main source of water loss during droughts due to transpiration (Bourbia et al., 2020) and plants have been found to produce fewer flowers per plant when they are water stressed (Burkle & Runyon, 2016; Descamps et al., 2021; Kuppler & Kotowska, 2021; Rering et al., 2020; Thomson, 2016, but see Turner, 1993). Moreover, flowers tend to become smaller in size (Descamps et al., 2021; Kuppler & Kotowska, 2021), bloom for shorter periods (Turner, 1993) and contain less nectar (Gallagher & Campbell, 2017; Phillips et al., 2018; Rering et al., 2020). Kuppler and Kotowska (2021), however, found no consistent pattern: the nectar volume declined in indoor, but not in outdoor studies. Drought-induced changes in floral traits can subsequently reduce pollinator attraction, that is, pollinator visits (Descamps et al., 2021; Kuppler et al., 2021; Rering et al., 2020; Walter, 2018, but see Kuppler & Kotowska, 2021), which can cause cascading negative effects on the reproduction of plants. Under drought, plants have been found to produce fewer seeds and have a lower seed mass per plant, which decreases their reproductive success (Rering et al., 2020; Zeiter et al., 2016).

In addition to natural disturbances such as droughts, grassland management like mowing or grazing can alter the amount of floral resources. Grassland management in general encourages vegetative growth and enhances flower production (Bullock, 1996). Carvell (2002) found that regularly grazed grasslands had a higher amount of floral resources compared to areas that had not been grazed for 2 years. On a landscape scale, a mosaic of different mowing/grazing regimes (or a rotating scheme) works best to promote a continuous supply of floral resources over the entire growing season (Johansen et al., 2019; Noordijk et al., 2009; Pywell et al., 2011). Late-mown meadows can then provide floral resources around midsummer, and early-mown meadows can re-flower again in late summer (Johansen et al., 2019; Noordijk et al., 2009). The mown biomass should be removed to promote forbs such as *Trifolium* spp. (Pywell et al., 2011).

Another management option, which remains uncommon in Scandinavian grasslands, is to use soil amendments such as compost or biochar in order to increase soil carbon sequestration (i.e. the mitigation of rising atmospheric carbon dioxide concentrations via carbon storage in biomass and soil organic matter) and yields. The Marin Carbon Project in northern California found that only a one-time application of compost on grasslands doubled the soil carbon sequestration and biomass production (Ryals & Silver, 2013). Four years after the compost application in California, the abundance of forbs had slightly (not significantly) decreased compared to graminoids (Ryals et al., 2016), which might imply a decrease in floral resources. If soil amendments favour mainly competitive graminoid species, their application might have negative consequences for biodiversity. On the other hand, biochar has been found to lead to a shift from graminoids to forbs (Schimmelpfennig et al., 2014), which would imply an increase in floral resources. Also Oram et al. (2014) found that biochar had a beneficial effect on *Trifolium pratense* and the authors suggest that biochar could help to maintain legumes in agricultural pastures and seminatural grasslands. Regarding nectar production, Baude et al. (2011) concluded that plant litter amendments increased the nectar sugar content of one plant species, but not that of two other species. Soil amendments in general are known to improve the soil aggregate stability, water infiltration rate, water holding capacity and microbial biomass (Harden et al., 2018; Paustian et al., 2016; Smith, 2012), which could buffer potential negative drought effects on floral resources.

In July 2019, we set up a drought and soil amendment experiment in grasslands in southern Sweden. The main aim of this experiment is to test the interactive effects of soil amendments (i.e. compost), drought and mowing on (i) carbon sequestration, (ii) yield and (iii) biodiversity.

1.3 | Knowledge gaps and hypotheses

Drought effects on floral resources have been of growing research interest in recent years. However, most of those studies have been conducted in arid to semiarid regions or in laboratories/greenhouses, and there have been only few natural experiments in temperate regions (Kuppler & Kotowska, 2021; Phillips et al., 2018). Moreover, those studies often focus on crop species, and are imposing only a single drought event—Descamps et al. (2021) therefore suggest to measure the effects of repeated droughts on wild herbaceous plant species, as we do in our study. To our knowledge, no study has yet investigated the effects of soil amendments (i.e. compost) on floral resources in grasslands. In this study, we examine how drought and soil amendments affect floral resources (i.e. floral units, nectar quantity and nectar continuity) in grasslands with different mowing regimes. On one hand, mown plots should have less water loss because the above ground biomass has been removed. On the other hand, management is known to increase flower production and could therefore increase the water loss of plants. The net effect is hard to predict, but we expect mowing to have an effect on the provision of floral resources. We hypothesize that

H1: the quantity and continuity of floral resources will decrease under drought, and
H2: increase with soil amendments.

2 | MATERIALS AND METHODS

2.1 | Experimental set-up and treatments

Our four experimental sites are located in southern Sweden. The mean annual precipitation between 1991 and 2020 in our study area was ca. 500 mm and the mean annual temperature ca. 6.5°C (Swedish Meteorological and Hydrological Institute, 2022). In southern Sweden, the growing season, that is, when the daily average temperature is above 5°C, starts at the beginning of April and lasts until the end of October (Swedish Meteorological and Hydrological Institute, 2021). The grasslands of our experiment were chosen to represent typical Swedish grasslands regarding their current and historic land use and their vegetation characteristics. They are former arable fields that have been converted into grasslands in the early 1990s and since then have been extensively managed for hay and grazing. All field work for this study was done with permission of the land owners. The soil in all sites is silty clay.

For the drought treatment, we set up 12 rain-out shelters in July 2019, according to the protocol of the Drought-Net Research Coordination Network (Knapp et al., 2017; Yahdjian & Sala, 2002). These rain-out shelters are designed to reproduce the first quantile of the local 100-year precipitation record (i.e. a 1-in-100-year drought), which means in our case that they exclude 58% of the precipitation. Each rain-out shelter measures 5.5 × 3.0 m and is covered by sixteen 20-cm-wide polycarbonate strips that cover ca. 58% of the roof's surface. Pictures and sketches of our study sites and experimental set-up can be found in Supporting Information 1. Two plots are placed under each rain-out shelter, including a 50 cm buffer area around each plot to minimize edge effects. Water from the roofs is collected in gutters and led away from the plots in plastic tubes. Around each rain-out shelter, we placed a rubber sheet into the soil down to ca. 40 cm depth, in order to avoid lateral water inflow. Since our focus is on drought effects during the growing season, the rain-out shelters are in place only between early April and late October each year (roofs are taken off over the winter). Under the rain-out shelters, the volumetric soil water content decreased by 7.2% (compared to the control plots), measured every 15 min between 2019 and 2021 during the growing seasons with 24 TOMST TMS-4 loggers (TOMST®) in the centre of 12 rain-out shelters and in 12 control plots (spread evenly across our four sites) at ca. 10 cm soil depth.

For the compost treatment, we applied compost made of maize (*Zea mays*) as a single (one-time) application. The maize was

harvested in September 2019 and composted until late January 2020. In mid-February 2020, we applied ca. 11 kg wet compost per m^2 as a thin layer on the grasslands, following the same procedure as in the Marin Carbon Project (Ryals & Silver, 2013).

In each of our four experimental sites, we replicated the four treatments (i.e. control, drought, drought and compost and compost) three times, resulting in 12 plots per treatment and 48 plots in total. For this study, each plot measures 2 m^2 and is split into two subplots: 1 m^2 was left untouched since the start of the experiment, that is, three growing seasons without mowing (hereafter called 'abandoned'). The other 1 m^2 was cut every year at the end of July/beginning of August with removal of the biomass to mimic typical Swedish grassland management for hey/silage harvest (hereafter called 'mown'). There were slight differences to the typical mowing management however, that is, we cut the biomass at ground level and removed litter and bryophytes, in order to measure biomass changes. The mown plots were not cut during the sampling year in order to allow us to count the floral units throughout the entire flowering season.

2.2 | Floral resources

To assess how floral resources respond to our treatments, we counted the floral units in all 48 plots nine times during the 2021 flowering season: monthly between mid-May until mid-July and weekly between mid-July until mid-August. The sampling frequency increased at the end of the summer because this period is of higher importance for pollinating insects (see Section 1.1). Floral units are defined as one or multiple flowers that can be visited by a small pollinator (ca. 1 cm long) without having to fly in-between (Carvalheiro et al., 2008), and it is the common entity to work with in pollination ecology. In total, we found 37 flowering forb species, of which 13 species have floral units that consist of only one flower per unit. For the remaining 24 species, we counted the number of flowers per floral unit in the field (mean number of open flowers of 10 floral units per species). All plant species were named after Mossberg and Stenberg (2003).

We derived the amount of nectar that plant communities provide for pollinating insects based on an existing database (Baude et al., 2016). Although both nectar and pollen are important floral resources for pollinating insects, we focused only on nectar because it is the main energy source for pollinators and it can be quantitatively compared between plant species (Baude et al., 2016; Descamps et al., 2021). Values for the nectar sugar production per flower were taken from Baude et al. (2016) who measured and modelled those values for 260 common plant species in Great Britain. Since those nectar values were obtained under average climatic conditions, they may overestimate nectar sugar production under drought conditions. For 22 of our 37 flowering forb species, nectar sugar production per flower had been empirically measured in that database (mean of nectar sugar content collected in flowers that were bagged for 24 h (µg/flower/day)). For the remaining 15 plant species, we gathered the nectar value from a species that presumably has a similar value (i.e. a species from the same plant family, with the same flower shape and a similar flower size). A full list with all nectar values and flowers per floral unit can be found in Supporting Information 2. By multiplying the nectar value per flower with the mean number of flowers per floral unit, we calculated the mean nectar sugar production per floral unit (µg/floral unit/day).

2.3 | Analysis

To compare the number of floral units between our treatments, we fitted a linear mixed model (LMM) using the function 'lmer' from the R package 'LME4' (Bates et al., 2015) and checked diagnostic plots to ensure that the assumptions of heteroscedasticity and normality of residuals are fulfilled. Our LMM contained as response variable the square root of the 'mean number of floral units per m^2' ($n = 96$), as fixed effects 'drought' (two levels: drought, no drought), 'compost' (two levels: compost, no compost) and 'mowing' (two levels: mown, abandoned) including their interactions, and as random effects 'plot' (48 levels) nested within 'site' (four levels). We fitted the LMM using the maximum likelihood (ML) method. *p*-values for the fixed effects were obtained from a Chi-square test using the function 'Anova' from the R package 'CAR' (Fox & Weisberg, 2019). To calculate pairwise differences in floral resources between treatments, we applied the post-hoc Tukey's test, using the R function 'lsmeans' from the R package 'LSMEANS' (Lenth, 2016). An adjusted pseudo *R*-squared was derived through the R function 'rsq' from the R package 'RSQ' (Zhang, 2021). To analyse nectar quantity, we performed the same analysis as described above, but using the square root of the 'mean nectar sugar production (µg/day/m^2)' ($n = 96$) as response variable instead.

To investigate nectar continuity over the growing season, we fitted two generalized additive models (GAMs), one for each mowing regime, using the R function 'gam' from the R package 'MGCV' (Wood, 2011). GAMs are suitable for fitting smooth curves to non-linear data. Based on the shapes of these curves we could interpret how the nectar quantity developed over time, and how it differed between treatments. Our GAMs contained as response variable the square root of the 'nectar sugar production (µg/day/m^2)' ($n = 432$), as smoothed fixed effect 'Date' (9 sampling days) with different smooths per 'Treatment' (four levels: control, compost, drought and compost, drought), as fixed effect 'Treatment' and as random effect 'Plot' nested within 'Date'. We fitted the GAMs using the restricted maximum likelihood (REML) method and checked diagnostic plots to validate models against the assumptions of heteroscedasticity and normality of residuals using the gam.check function from the R package 'MGCV' (Wood, 2011).

All analyses and figures were performed using R v.4.1.3 (R Core Team, 2022).

3 | RESULTS

3.1 | Floral units

The model revealed moderate evidence that the number of floral units was affected by drought (LMM: Chi-square = 5.25; $p = 0.02$) as well as by compost (LMM: Chi-square = 5.27; $p = 0.02$), and very strong evidence for the interaction between drought and mowing (LMM: Chi-square = 14.30; $p < 0.001$). However, for mowing itself there was little to no evidence of it affecting the number of floral units (LMM: Chi-square = 0.33; $p = 0.57$). As stated above (see Section 2.1), mowing refers to the previous mowing regime—during the sampling year no plots were mown. Looking at the two mowing regimes separately, we could see that in the mown plots, there was very strong evidence for the drought treatment having a negative effect on the number of floral units, and moderate evidence for compost treatment having a positive effect on the number of floral units, see Figure 1a. In the abandoned plots, there was little to no evidence of a treatment effect on floral units, see Figure 1b. The adjusted pseudo *R*-squared for this model was 0.75. A list with all LMM results can be found in Supporting Information 3.

Of the 37 flowering forb species in our study, only 15 were found flowering across the four treatments control, compost, drought and compost and drought, see Figure 2. Those species reacted very differently to the treatments. For example *Anthriscus sylvestris* and *Cerastium fontanum*—species associated with nutrient-rich grasslands and not providing much nectar per flower—strongly increased their flower production with the compost treatment, whereas other species produced fewer flowers (e.g. *Vicia cracca* and *Vicia tetrasperma* (both legumes)). Under the drought treatment, species like *Lathyrus pratensis* and *V. tetrasperma* (both legumes) increased their flower production, whereas for example, *Hypericum maculatum*, *Leontodon autumnalis*, *Ranunculus acris* and *V. cracca* decreased it.

3.2 | Nectar quantity

In contrast to the number of floral units, the model revealed little to no evidence that the nectar sugar production (µg/day/m^2) was affected by drought (LMM: Chi-square = 0.82; $p = 0.36$), compost (LMM: Chi-square = 0.76; $p = 0.38$) or mowing (LMM: Chi-square = 0.91; $p = 0.34$). It should be noted that nectar values per flower were derived from a database and not directly measured in our study. For the interaction between compost and mowing we found moderate evidence of it affecting the nectar sugar production (LMM: Chi-square = 4.36; $p = 0.04$), indicating that in the mown plots, the compost treatment increased the nectar sugar production. The adjusted pseudo *R*-squared for this model was 0.58.

Most of the inferred nectar supply in our study was provided by only few species, see Figure 3, with legumes contributing about half of all nectar (mainly *L. pratensis*, *V. cracca*, *Trifolium medium* and *Trifolium repens*).

3.3 | Nectar continuity

The peak nectar sugar production around mid-summer was higher in the abandoned than in the mown plots, comparing the blue lines (i.e.

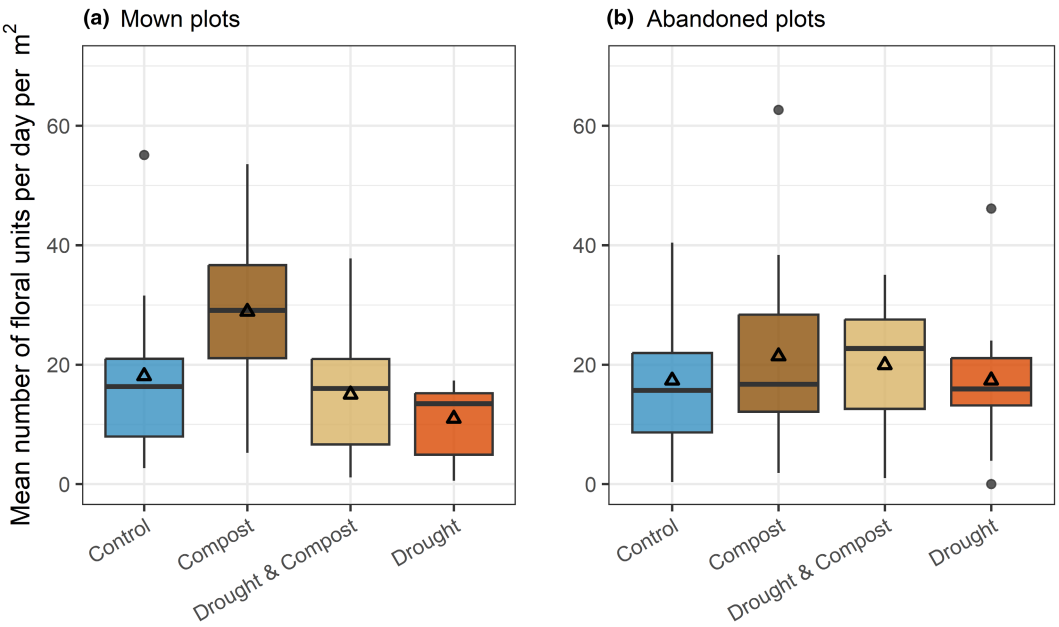


FIGURE 1 Results from four experimental sites in Swedish grasslands, studying the effects of drought, compost and mowing on floral resources. Box and whisker plots are showing the mean number of floral units found per m^2 per day (mean of 9 sampling days during the flowering season 2021) in the (a) mown and (b) abandoned plots. Each box represents 12 experimental subplots (size 1 m^2). The horizontal lines inside the boxes are indicating medians and the triangles are showing means.

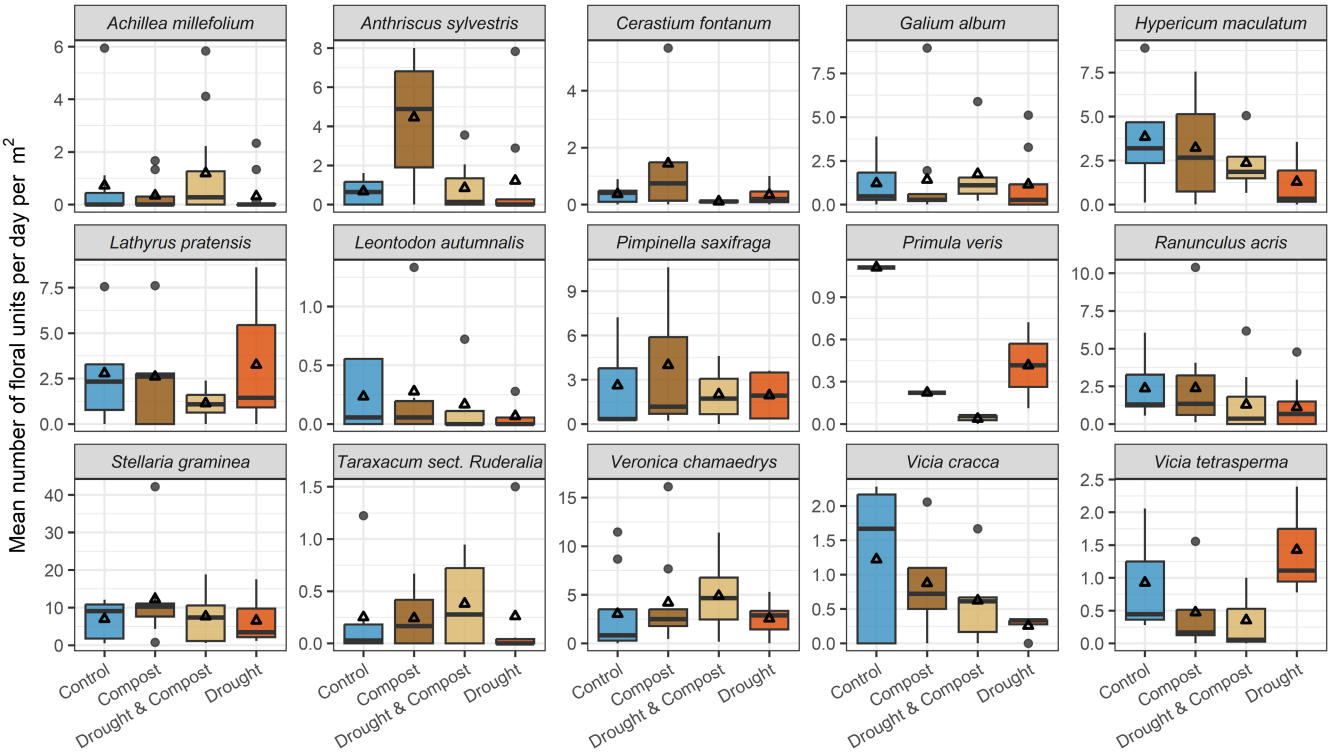


FIGURE 2 Results from four experimental sites in Swedish grasslands, studying the effects of drought, compost and mowing on floral resources. Box and whisker plots are showing the mean number of floral units found per m^2 per day (mean of 9 sampling days during the flowering season 2021). Each box represents 12 experimental plots (size 2 m^2). The horizontal lines inside the boxes are indicating medians and the triangles are showing means. Only those plant species that were found flowering in all four treatments 'control', 'compost', 'drought and compost' and 'drought' are shown.

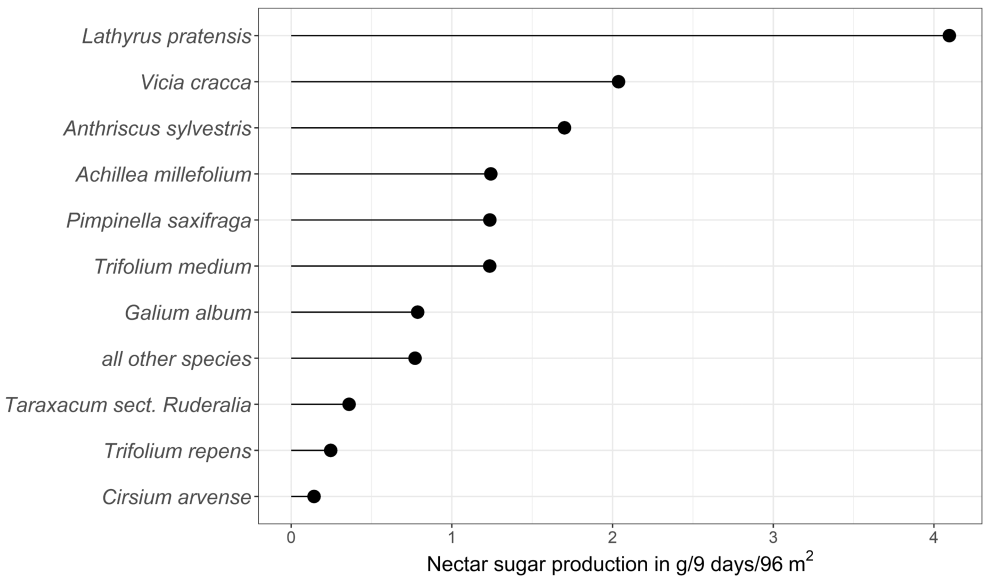


FIGURE 3 Results from four experimental sites in Swedish grasslands, studying the effects of drought, compost and mowing on floral resources. Sum of nectar sugar production across all 48 experimental plots (size 2 m^2) and 9 sampling days (during the flowering season 2021). Values for the 10 most nectar-producing species are shown separately.

control treatment) in Figure 4a versus b. In the mown plots, the compost treatment increased the overall nectar sugar production and shifted it towards earlier in the season (peaking in mid-June compared to early July in the control plots), see Figure 4a. The drought treatment decreased the nectar sugar production (especially around mid-summer) but the compost treatment could reverse that trend (curves are similar for the control and the drought & compost treatment). This indicates that compost could buffer negative drought

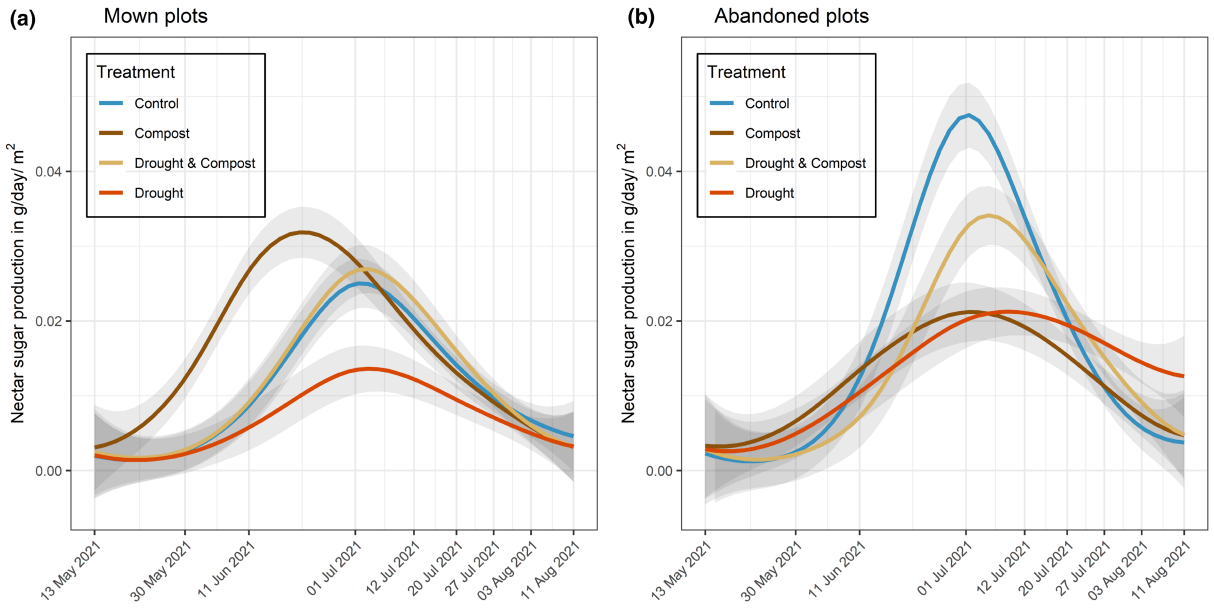


FIGURE 4 Results from four experimental sites in Swedish grasslands, studying the effects of drought, compost and mowing on floral resources. Modelled nectar sugar production (g/day/m^2) over time per treatment in the (a) mown and (b) abandoned plots. The lines and confidence intervals are smoothed with generalized additive models (GAMs).

effects on nectar provision. The adjusted pseudo *R*-squared for this model was 0.62.

In the abandoned plots, the patterns look slightly different. The compost treatment lowered the peak nectar production around mid-summer compared to the control treatment, see Figure 4b. Also the drought treatment caused a lower nectar sugar production during mid-summer compared to the control treatment, but a higher production in late summer compared to all other treatments, see Figure 4b. The curve of the compost & drought treatment is similar to the control treatment, which is the same pattern we saw in the mown plots. The adjusted pseudo *R*-squared for this model was 0.72.

Plotting the nectar sugar production on species level shows that the early nectar spike in the compost treatment was mainly driven by *A. sylvestris*, and the late nectar sugar production in the drought treatment mainly by *L. pratensis* (see Figure 5). *Taraxacum* sect. *Ruderalia* is an important nectar resource early in the season in all treatments.

4 | DISCUSSION

4.1 | Summary and discussion of our results

H1: The quantity and continuity of floral resources will decrease under drought

Contrary to our expectations (see Section 1.2), we did not observe a significant decrease in floral resources under our experimental drought treatment, apart from the number of floral units in the mown plots. The nectar provision in late summer was even prolonged under drought in the abandoned plots, which is interesting in the light of preventing resource gaps later in the season (see Section 1.1). Our results might differ from other drought studies in that we imposed only a moderate drought treatment (excluding 58% of precipitation during the growing season (early April until late October)) and it can be assumed that the effects of water deficit on floral resources are increasing with treatment severity (Kuppler & Kotowska, 2021). Also Turner (1993) found that a severe, short-term water deficit decreased the production of flowers (study species *T. repens*), while a mild, long-term water deficit even promoted it. An explanation for this could be that the balance between vegetative and reproductive plant growth changes in favour of flowering under mild water stress (Turner, 1993). Moreover, we studied a grassland in situ compared to most other studies that were performed in greenhouses under controlled conditions (Descamps et al., 2021). Floral resources in grasslands with a native plant community and natural soil conditions might therefore be more resistant to droughts than one would expect when scaling up greenhouse/single species results.

We also want to highlight that the individual plant species reacted differently to the experimental drought treatment (see Figure 2), which suggests that our results are not directly translatable to other plant communities with differing plant compositions. Earlier studies have concluded as well that responses of floral resources to droughts are species specific (Descamps et al., 2021; Kuppler & Kotowska, 2021; Phillips et al., 2018). This shows the need to know species identity in such natural experiments—particularly since most of the nectar is usually provided by only few species (Baude et al., 2016; Tew et al., 2021; Timberlake et al., 2019). In line with that, we also found that a small number of species provided disproportionally much nectar (see Figure 3). This indicates that the responses of plant communities to droughts or soil amendments may largely depend on a few key species. In our case, the stable nectar

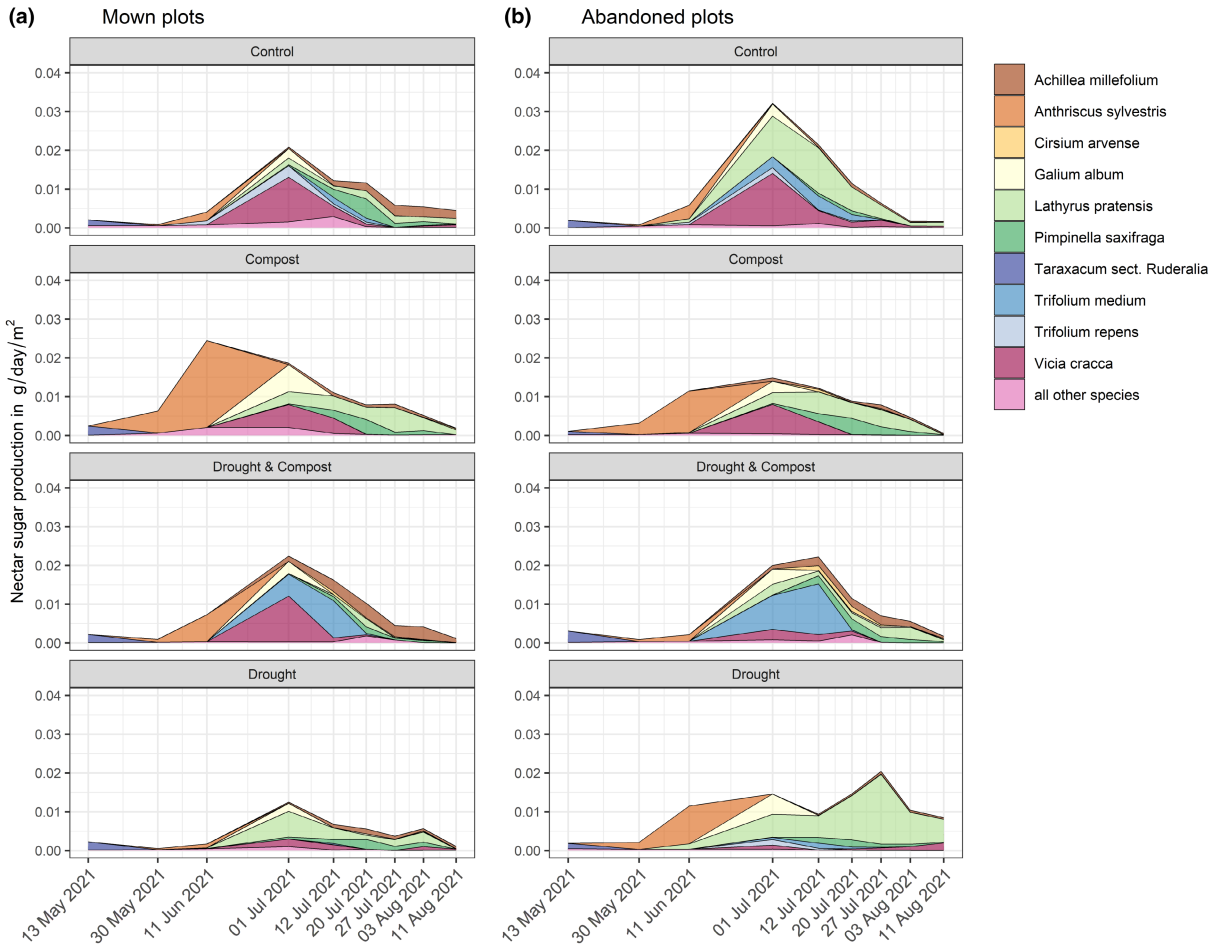


FIGURE 5 Results from four experimental sites in Swedish grasslands, studying the effects of drought, compost and mowing on floral resources. Nectar sugar production (g/day/m^2) over time per treatment in the (a) mown and (b) abandoned plots. The 10 most nectar-producing species are shown separately.

sugar production under drought was mainly driven by *L. pratensis*, which contributed a high nectar supply even in late summer (see Figure 5b). So even though the total number of floral units (across all species) decreased under drought in the mown plots, it was mainly those species with a low nectar production per floral unit that decreased whereas a few key species with a high nectar production per floral unit remained stable or even increased, which resulted in an overall relatively stable nectar provision under drought.

H2: The quantity and continuity of floral resources will increase with soil amendments

We found a positive effect of our compost treatment on floral resources (floral units, nectar quantity and nectar continuity) in the mown, but not in the abandoned plots. This might be due to a time-lag in the uptake of the compost in the abandoned plots, caused by two reasons. First, the vegetative growth rate of plants is slower when management is lacking, which might delay the effects of soil amendments. Second, there was a rather dense litter and moss layer in the abandoned plots, compared to the mown plots where all above-ground biomass had been removed yearly for the previous 3 years. That layer might have slowed down the uptake of the compost. Regarding nectar continuity, we could see that the compost treatment shifted the peak nectar production to earlier in the season by ca. 2 weeks in the mown plots (Figure 4a). Although one study in the United Kingdom found that the most crucial resource gaps for pollinators are in early spring and in late summer, there can be also short gaps in June (Timberlake et al., 2019), which this compost treatment might help to alleviate. In both the mown and abandoned plots, the curves for the combined drought and compost treatment were more similar to the control treatment than the curves for drought or compost treatment separately. This could indicate that under drought, compost might keep the phenological continuity relatively stable at levels similar to the control. An explanation could be a higher water holding capacity of the soils with the compost treatment, but this was not measured here.

Again, as for the drought treatment, the responses to the compost treatment were species specific. For example the shift in nectar provision towards earlier in the season was mainly driven by *A. sylvestris* (see Figure 5a,b). In general, we observed that species associated with more nutrient-rich grasslands and not providing much nectar per flower such as *A. sylvestris* and *C. fontanum* increased their

flower production, whereas legumes like *V. cracca* and *V. tetrasperma* decreased it (see Figure 2). Although the overall nectar quantity in our plant communities increased with soil amendments, this could be an early warning sign that the compost treatment might shift the plant community composition in the long run (contrary to what Ryals et al. (2016) found), promoting mainly competitive species and decreasing plant diversity. This could affect pollinating insects in terms of, for example, floral diversity, pollen provision or food plants for larvae. Thus, more studies on the effects of soil amendments on plant communities and longer time series are needed.

4.2 | Methodological aspects to consider

For each species, we assumed the same number of flowers per floral units and the same amount of sugar nectar production per flower across all treatments. While counting all flowers and measuring the nectar sugar production would have provided more accurate data, we do not expect that this would have reversed the patterns we found, but rather intensified the slight decrease we observed under drought and the increase we observed with compost. We assume that under the drought treatment, plants produce fewer flowers per floral unit (Kuppler & Kotowska, 2021; Phillips et al., 2018) that are smaller in size (Descamps et al., 2021; Kuppler & Kotowska, 2021) and contain less nectar (Phillips et al., 2018; Rering et al., 2020, but see Kuppler & Kotowska, 2021) compared to the control treatment. One of the study species of Phillips et al. (2018) was *L. pratensis* and they found that under drought, the proportion of flowers containing nectar decreased. With the compost treatment, we assume the opposite trend due to improved soil water and nutrient conditions. Therefore, we might be underestimating the real drought and compost effects on floral units and nectar quantity.

The species composition varies strongly between our plots, even if they are spatially adjacent (grasslands can be very heterogeneous on a small scale). Species with a large number of floral units or high nectar content that naturally occurred in different abundances in our treatments (or not at all in some treatments) might obscure effects caused by our treatments.

We considered only one level of drought treatment and one type of soil amendment. A different timing and intensity of drought (Turner, 1993; Zeiter et al., 2016), and other types of soil amendments might cause different effects on floral resources in grasslands. Moreover, as mentioned above, the results are depending on the local species composition. Therefore, our results should be generalized only with great caution.

4.3 | Implications for grassland management to promote floral resources

Based on our results, we can highlight two management schemes that are likely to promote floral resources for pollinators in grasslands in the light of climate change. First, if compost would be applied on yearly mown/grazed grasslands (in Sweden, this would be mainly pastures grazed by livestock and meadows mown for hay/silage harvest) with the primary goal of increasing yield and/or carbon sequestration (Ryals & Silver, 2013), this would likely also increase the amount of floral units, nectar quantity and shift the peak nectar production towards earlier in the season. However, we need to understand more about potential shifts in species composition before recommending the application of soil amendments on a large scale, and soil amendments should be strictly avoided in high nature value grasslands. Second, some grasslands should be managed less frequently (e.g. every 3–5 years) to stabilize the nectar supply in late summer in the event of a drought. This could be applied for example on road verges. Moreover, such a scheme where part of the vegetation is spared from mowing/grazing would increase the survival of other life stages of pollinating insects, such as larva and pupa (Noordijk et al., 2009). In general, maintaining the remaining seminatural grasslands and applying a mosaic of different grassland management regimes (different cutting/mowing times and frequencies) could promote a high, diverse and continuous supply of floral resources in the landscape.

If species-knowledge and management possibilities allow for it, it would be beneficial to adjust management regimes to the local species composition. The main focus should then be on promoting species that contribute the highest amounts of nectar overall (in our case *L. pratensis*, *V. cracca*, and *A. sylvestris*), on species that might be less productive overall but that are flowering during periods of nectar deficit, that is, in early spring or late summer (in our case e.g. *Taraxacum* sect. *Ruderalia* and *L. pratensis*) and on species that increase the local floral diversity.

5 | CONCLUSIONS

We found that nectar provision for pollinating insects in Swedish grasslands remained relatively stable during an experimental drought. Soil amendments increased the floral resources (i.e. floral units, nectar quantity and continuity) in yearly mown but not in abandoned grassland plots. It should be noted that nectar production was not measured in the field, but values were obtained from a database. Overall, the 37 flowering plant species in our study reacted differently to the treatments (increase vs. decrease in floral resources) and most of the nectar was provided by only few species.

AUTHOR CONTRIBUTIONS

Gustaf Hugelius, Sara Cousins, Daniela Guasconi and Nina Roth designed the experimental set-up; Nina Roth conceived the ideas and designed the methodology for this study; Nina Roth collected the data; Nina Roth and Adam Kimberley analysed the data; Nina Roth led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no known conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The dataset on the floral unit counts and nectar values used in this manuscript is available from the figshare repository https://doi.org/10.6084/m9.figshare.22362874 (Roth et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting information 1: Study sites and experimental set-up.

Supporting information 2: Flower and nectar values per species.

Supporting information 3: Linear mixed models (LMMs).

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