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Drought response and urban-pollinator attractiveness of ornamental plant species

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ABSTRACT

Faced with pollinator declines, cities could serve as refuges for biodiversity conservation by managing floral resources in public green spaces. Ornamental plants could play an important role in attracting pollinators because they form part of urban floral management. However, knowledge of how their floral traits respond to drought is lacking, and it is unknown whether they will be suitable for pollinators under future climates. The main objective of this study was to determine the covariation of floral traits of ornamental plant species and effects of drought on them. To this end, in a city greenhouse we measured floral traits of eight ornamental species commonly used in urban green spaces in France. We subjected the plants to a control treatment or a drought treatment, reducing the volume and frequency of watering. We observed interspecific variability in floral traits among these species and a change in covariation between the traits pollen quantity and nectar quantity in the drought treatment. Drought influenced morphological traits related to floral display more than other floral traits, with mean decreases of 28 % in floral height, 35 % in floral area and 58 % in the number of floral units. Ornamental plants seemed attractive to different morphotypes of pollinators depending on their floral unit number, nectar sugar concentration or nectar tube depth, with most visits made by Hymenoptera. These results are expected to encourage green-space managers to select urban plants according to their functional characteristics and adapt their choice of plants to climate change.

Introduction

Pollination is an important ecosystem service that ensures the reproduction of flowering plants by allowing the transfer of pollen from stamens to stigmas. In temperate regions, 78 % of plants depend on animals for pollination (Ollerton et al., 2011), while at the global level, 70 % of crops used to feed humans depend on insects for pollination (i.e., 35 % of the world's food production) (Klein et al., 2006). A loss of pollinator biodiversity, at both genetic and community levels, has been observed since 1990, particularly among bees, butterflies and flies in Europe and the USA (Vasiliev & Greenwood, 2021), as well as in Australia, Asia and Africa (Brown & Paxton, 2009). For solitary bees, honeybees and bumblebees, this decline is due to fragmentation and loss of habitats and degradation of available resources (Brown & Paxton, 2009; Potts et al., 2010) but also to the introduction of invasive species and climate change (Kevan & Viana, 2003; Kluser & Peduzzi, 2007; Potts et al., 2010).

Faced with this decline, cities can act as refuges for pollinators if they are well managed. A recent review found contrasting effects of

urbanization on pollinators (negative, positive or no effects for 24 %, 37 % and 39 % of studies, respectively) (Wenzel et al., 2020). Among negative effects, higher temperatures caused by urban heat islands could reduce pollinator diversity, with a 41 % decrease in wild bee abundance for every 1 °C increase in Raleigh, North Carolina, USA (Hamblin et al., 2018). Moreover, urbanization leads to high proportions of impervious surfaces and depletion of floral resources, which could decrease the abundance and diversity of wild bees (Fauviau et al., 2022; Hamblin et al., 2018). Among positive effects, several studies have found higher abundance and diversity of wild bees and species richness of bumblebees in urban environments than in rural landscapes, due in particular to the presence of more varied nesting sites and less pesticide use in the former (Baldock et al., 2015; Hall et al., 2017; Matteson et al., 2008; Osborne et al., 2008). Cities with open areas of residential housing are favorable nesting and foraging areas, as are gardens, parks and extensive green areas with a high degree of connectivity (Baldock et al., 2019; Wenzel et al., 2020). Urban green spaces tend to favor generalist pollinators (Deguines et al., 2016) and social bees (Silva et al., 2023). Floral resources, which are dependent upon flowering plant abundance, richness

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and composition, favor diversity in pollinator communities (Ahrné et al., 2009; Somme et al., 2016; Wenzel et al., 2020; Wojcik et al., 2008). Majewska and Altizer (2020) observed that local garden characteristics (i.e., plant species diversity, presence of woody vegetation, size, and sun exposure) influenced urban pollinators more than surrounding landscape characteristics did. Thus, one strategy to help conserve pollinators in cities could be to increase the number and quality of floral resources in publicly managed green spaces, as highlighted by Baldock et al. (2019).

As part of this strategy, ornamental flowering plants could play an important role for pollinator conservation because they form part of the floral management in public parks. These plants are usually exotic species that come from a wide variety of regions, such as southern Africa, Australia, Latin America, Asia, and eastern Europe (Hentig, 1995). Some ornamental plants could be attractive to several groups of pollinators, as demonstrated in several studies (Garbuzov & Ratnieks, 2014; Mougá et al., 2015; Schindler et al., 2005; Udy et al., 2020). In urban habitats, the flowers of ornamental plants are mostly visited by Hymenoptera, with a dominance of wild bees (55 % of total visits over two years) and honeybees (27 %; Marquardt et al., 2021) or of honeybees (48 % of total visits over five years) and bumblebees (33 %; Rollings & Goulson, 2019). In this way, non-native plants may act as mutualists and help maintain pollinator populations (Salisbury et al., 2017; Zaninotto et al., 2020, 2023). Indeed, exotic plants extend the flowering season and provide resources of particular value to pollinators when the abundance of flowers on native plants is low at the end of summer (Salisbury et al., 2017). However, exotic flowers could also repel highly specialized pollinator species (Chrobock et al., 2013; Fukase & Simons, 2016; Rocha-Filho et al., 2018), and varietal selections of ornamental flowers may be unattractive to pollinators (e.g., double corolla described by Corbet et al., 2001).

Selecting ornamental plants for public green spaces thus requires a functional approach. Indeed, entomophilous plants have developed several strategies to attract insects through the co-evolution of flower characteristics (i.e., “floral traits”), which can be measured (Larue et al., 2016). There are several types of floral traits: morphological related to floral display (e.g., plant height, floral area, number of flowers); barrier, which characterize flower accessibility to pollinators (e.g., nectar tube depth, pistil and stamen lengths) and resource (e.g., nectar and pollen quantity or quality). For example, open flowers are visited mainly by pollinators with short tongues, while tubular flowers are visited mainly by pollinators with long tongues, such as some wild bees (Hegland & Totland, 2005). Pollinators are attracted to flowers by a combination of their traits (Dellinger, 2020; Goulnik et al., 2021; Junker & Parachnowitsch, 2015), although some traits have more influence on pollinator abundance at the community level, such as plant height (Fornoff et al., 2017; Junker et al., 2013), flower color and shape (Fornoff et al., 2017; Jersáková et al., 2012; Junker et al., 2013), nectar tube depth (Junker et al., 2013) and nectar sugar concentration (Fornoff et al., 2017; Goulnik et al., 2020).

Currently, urban areas are constantly expanding, creating heat islands that accentuate the droughts induced by climate change (Potts et al., 2010; Wenzel et al., 2020). In this context, plant watering management need to be reconsidered to limit the amounts of water used. Presently, some ornamental plants are grown as annuals and require multiple waterings per week. Moreover, it seems essential to choose ornamental flowering plants that are both nutritious and attractive to pollinators, but also drought-resistant, since drought tends to change floral traits. A recent review found that plants can grow 10–20 % shorter and produce 30–50 % fewer flowers during drought (Descamps et al., 2021). To a lesser degree, a lack of water changes nectar quantity and decreases pollen quality. Modifying these floral traits makes plants less attractive to pollinators, which decreases the number of plant-pollinator interactions (Al-Ghazawi et al., 2009; Burkle & Runyon, 2016; Descamps et al., 2021; Glenny et al., 2018). Drought also changes pollinator phenology and shortens the periods when it matches plant phenology

(Hegland et al., 2009).

Existing data on ornamental plants are related to their attractiveness mainly by counting pollinator visits to flowers, without recording their floral traits, and studies that have measured the combination of floral traits for different ornamental species in response to drought are lacking. Green-space managers wonder which ornamental plants will be suitable for pollinators in cities in the future. The aim of our study was thus to use a functional approach to analyze ornamental plant traits for pollinators in urban areas. To this end, we measured floral traits of eight ornamental flowering plant species commonly used in urban green spaces in France and tested their response to drought in a greenhouse. We also observed pollinator visits on six of these species *in situ*, within a flower bed regularly watered. Our research questions were: (i) How do floral traits covary among species? (ii) What effects does drought have on floral traits? and (iii) Which ornamental plants are attractive to pollinators? We expected that drought would modify floral traits of ornamental plants, especially morphological traits, as observed for native plants. We hypothesize that plants cultivated as perennials exhibit less response of floral traits to drought due to receiving less watering in the city’s flower beds compared to annual plants. We assumed that ornamental flowering plants are preferentially visited by Hymenoptera, since these insects are the most common in urban areas.

Materials and methods

Species selected

The species studied were selected from the catalog of ornamental plants used by green-space managers in France to create their flower beds. The species were selected in part based on scores attributed to ornamental plants by managers as a function of their nectar production, pollen production and attractiveness to pollinators. The nectar and pollen production scores are derived from an internet search conducted by green-space managers across multiple nursery websites indicating the melliferous value of plants. The score of attractiveness to pollinators was determined by *in-situ* observations of pollinator visits in ornamental beds by managers in different green spaces of Nancy during the previous years (Table 1). In addition to this score-based criterion, plants were selected to obtain a variety of flowering periods, botanical families and floral trait values. Eventually, eight species (Fig. 1) from four families were selected: *Ageratum houstonianum* “Aloha Bleu” (AGEALO) and *Coreopsis tinctoria* “Mahogany Midget” (CORTIN) belonging to the Asteraceae family; *Agastache urticifolia* “Coerulea Bleu” (AGAURT), *Nepeta mussinii faessenii* (NEPFAA), *Salvia coccinea* “Snow Nymph” (SALCOC) and *Salvia farinacea* “Epi Bleu” (SALFAR) from the Lamiaceae; *Gaura lindheimeri* (GAULIN) from the Onagraceae and *Verbena × hybrida* “Muriel” (VERMUR) from the Verbenaceae. These plants are generally native from America (see details in Table 1). AGEHOU, CORTIN, AGAURT, SALCOC, SALFAR and VERMUR are cultivated as annual species and are traditionally watered three times a week from May 15 to the end of September with a volume of at least 40Lm⁻² of water by the green space managers of Nancy. GAULIN and NEPFAA are cultivated as perennial species that are watered twice during summer in the year following planting ($N + 1$) with 30 Lm⁻². The following year ($N + 2$), these plants are watered once during summer with 30 Lm⁻².

Experimental design

The experiment was performed in the city greenhouse of Nancy, in northeastern France, which was maintained at a mean daily temperature of 21.7–28.1 °C from 23 May to 22 July 2022. Plants were sown by Nancy’s green space managers using the same method as for the city’s flower beds. They were sown in seedbeds from late February to early March, using a seed compost covered with vermiculite and sprinkled with water, for an overall germination time average seven to ten days. They were then repotted into 3 L pots with a diameter of 19 cm. Plants

Table 1

Cultivation practice, native range, watering management and scores attributed to each ornamental plant species by green-space managers as a function of their nectar production, pollen production and attractiveness to pollinators. NA: not provided by green-space managers. Source of native range: (POWO, 2024).

Species	Cultivation practice	Native range	Watering management	Nectar (/3)	Pollen (/3)	Attractiveness (/6)
<i>Agastache urticifolia</i> “Coerulea Bleu”	Annual	SW. Canada to W. U.S.A	3x/week, $\geq 40 \text{ Lm}^{-2}$	3	3	6
<i>Ageratum houstonianum</i> “Aloha Bleu”	Annual	Mexico to Central America	3x/week, $\geq 40 \text{ Lm}^{-2}$	NA	NA	2
<i>Coreopsis tinctoria</i> “Mahogany Midget”	Annual	Canada to E. Mexico	3x/week, $\geq 40 \text{ Lm}^{-2}$	NA	NA	2
<i>Gaura lindheimeri</i>	Perennial	SE. Texas to SW. Louisiana	$2 \times 30 \text{ Lm}^{-2}$ year $N + 1$, $1 \times 30 \text{ Lm}^{-2}$ year $N + 2$	0	1	3
<i>Nepeta mussinii faaessinii</i>	Perennial	E. Türkiye to NW. Iran	$2 \times 30 \text{ Lm}^{-2}$ year $N + 1$, $1 \times 30 \text{ Lm}^{-2}$ year $N + 2$	2	2	4
<i>Salvia coccinea</i> “Snow Nymph”	Annual	SE. U.S.A. to N. Argentina	3x/week, $\geq 40 \text{ Lm}^{-2}$	NA	NA	3
<i>Salvia farinacea</i> “Epi Bleu”	Annual	S. Central U.S.A. to NE. Mexico	3x/week, $\geq 40 \text{ Lm}^{-2}$	3	2	5
<i>Verbena × hybrida</i> “Muriel”	Annual	South America	3x/week, $\geq 40 \text{ Lm}^{-2}$	0	2	2

Asteraceae

(A)
Ageratum houstonianum
“Aloha Bleu”
(AGEALO)



Chiehliangchen CC BY-NC

(B)
Coreopsis tinctoria
“Mahogany Midget”
(CORTIN)



Randyshonkwiler CC BY-NC

Lamiaceae

(C)
Agastache urticifolia
“Coerulea Bleu”
(AGAURT)



w-pearce-plants CC BY-NC

(D)
Nepeta mussinii faaessinii
(NEPFAA)



(E)
Salvia coccinea
“Snow Nymph”
(SALCOC)



astrapia CC BY-NC

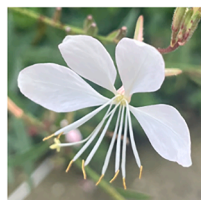
(F)
Salvia farinacea
“Epi Bleu”
(SALFAR)



gewarbler CC BY-NC

Onagraceae

(G)
Gaura lindheimeri
(GAULIN)



gracie_shoe CC BY-NC

Verbenaceae

(H)
Verbena × hybrida
“Muriel”
(VERMUR)

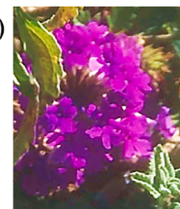


Fig. 1. Pictures illustrating morphologies of the studied plants. Sources for pictures (A), (B), (C), (E), (F): <https://www.inaturalist.org> (plant varieties are not specified on this source); (D), (H): author pictures.

were grown in a standard potting soil (Stender Export, Germany) composed of 73 % blond peat of medium structure low in fiber, 15 % brown peat and 12 % coconut fibers. Twelve individuals per species were subjected to each of two treatments for six weeks from the beginning of flowering, which ranged among species from 23 May to 13 June 2022. The control treatment consisted of watering each plant with 400 mL of water each day, except for VERMUR and AGEALO, which were watered less frequently because they were less tolerant of over-watering. The drought treatment consisted of watering each plant with 133 mL of water every other day, except from 16 to 19 June 2022, when each received 266 mL each day due to higher temperatures. Plants were organized into eight blocks: four control blocks (A to D) and four drought blocks (E to H) (Fig. 2). Each block contained three rows of plants, each containing one individual of each species. During these six weeks of experimentation, few pollinators could access the greenhouse because it was not completely closed.

Morphological traits

Measurement frequency of each functional trait varied (Table 2). Floral height was measured to the nearest mm as the stretched distance from the base of the plant (the crown) to the top of the highest floral unit (FU) using a tape measure. A FU was one or more flowers that a pollinator could access without needing to fly (Baldock et al., 2015). A FU was a single flower for all species except AGEALO, CORTIN and VERMUR, for which it was an inflorescence. Floral area was calculated as $\pi(\text{diameter}/2)^2$ when circular or length \times width when not by taking measurements to the nearest 0.01 mm with a digital caliper.

To calculate the mass of flowers and petals, one FU was collected from each individual and then dissected to separate the petals from the other parts of the FU. After placing all parts of the FU in an oven at 60 °C for 72 h, the dry mass of petals was weighed to the nearest mg and then divided by the number of petals to obtain the mean petal mass. Finally, the rest of the FU was added to the petals to obtain the entire dry mass.

Barrier traits

To measure nectar tube depth, pistil length and stamen length, one flower was collected from each individual. Barrier traits were then measured to the nearest 0.01 μm in the laboratory using MOTICAM 5+ and *MoticImages* software with a binocular microscope (MOTIC) at a magnification of 1–5 \times . Nectar tube depth equaled the distance between the nectar glands and the entrance of the flower where only the pollinator’s mouthparts can penetrate (Goulnik et al., 2020). When necessary, flowers were dissected to isolate the parts to be measured before placing them under the binocular magnifier.

Table 2

Traits measured for each plant ($n = 12$) of each of the eight species and their frequency of measurement. FU = floral unit.

	Type of trait	Trait	Measuring frequency
Floral	Morphological	Plant height	Weekly
	Morphological	Floral area	Weekly
	Morphological	Number of FUs	Weekly
	Morphological	Number of flowers/FU	Weekly
	Morphological	Dry mass of FU	Every two weeks
	Morphological	Dry mass of petals	Every two weeks
	Barrier	Nectar tube depth	Once in week 3 of treatment
	Barrier	Stamen length	Once in week 3 of treatment
	Barrier	Pistil length	Once in week 3 of treatment
	Resource	Nectar sugar concentration	Every two weeks
Resource	Total pollen volume	Once at the end of experiment	
		Once at the end of experiment	
Leaf	Aerial	Leaf area	Every two to three weeks
	Aerial	Specific leaf area	Once at the end of experiment

Resource traits

Nectar sugar concentration was measured for each individual when at least one flower was open for the two treatments. The sampling procedure took place over two days. On the first day, flowers were bagged with nets with a mesh size of 1 mm \times 1 mm, which prevented pollinators from taking the nectar. On the next day, the nectar was harvested in the same order that the flowers had been bagged. To do this, the nectar was diluted by adding 1–3 μL of distilled water to the nectar glands of the flower, except for SALCOC and SALFAR. After dilution, the nectar was taken using microcaps, in which the liquid rises by capillary action. The quantity of sugar was then measured by transferring the collected nectar to a refractometer (0–50 Brix, Eclipse, Bellingham and Stanley, Tunbridge Wells, Kent, UK). Then, we calculated sugar production by nectar per flower in 24 h (s ; μg of sugar.flower⁻¹.24 h⁻¹) using the following formula: $s = 10 \text{ dvC}$ with s the density of a sucrose solution at concentration C (g sucrose.100 g⁻¹ solution) read from refractometers, and v (μL) the volume of nectar produced by a single flower. Density d was obtained using the formula $d = 0.0037921C + 0.0000178C^2 + 0.998860$ (Baude et al., 2016).

Floral buds of plants for each treatment were collected at the end of the experiment. When the floral buds opened, stamens were collected and preserved in tubes with 96 % ethanol. When the composed inflorescence had been collected (i.e., Asteraceae), flowers were dissected

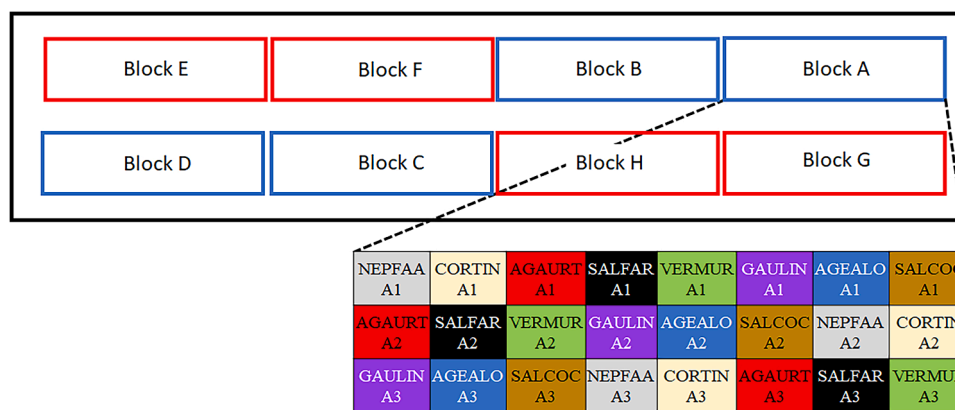


Fig. 2. Experimental design of the plants studied in the greenhouse with eight blocks. Blue contours represent the control treatment, while red contours represent the drought treatment. An example of the arrangement of pots in block A is shown. Three pots per plant species were arranged in each block. The abbreviated names of the plants are provided in Fig. 1.

beforehand. A mean of 20 stamens was necessary to obtain a visible pellet of pollen, and five replicates were performed. To extract the pollen, the stamens in their tubes were passed through an ultrasonic bath of water. Next, the liquid was taken from each tube (avoiding plant debris) and placed in another tube. Stamens were then rinsed until the second tube was filled. If pollen remained in the stamens, they were rinsed or passed through the ultrasonic bath again, depending on the number of pollen grains remaining. Next, tubes with the extracted pollen were centrifuged for 5 min at 10,000 rpm, some of the supernatant was removed, and the rest was passed through a vacuum concentrator (SpeedVac, Thermo Fisher Scientific, Waltham, Massachusetts, USA) for 45 min at 30 °C. The pellet was then placed back in suspension with 100–1000 µL of 70 % ethanol depending on the size of the pellet. After vortexing the tube, 20 µL of the solution was deposited in a counting cell. Then, the number of pollen grains was counted under a microscope at 10 × magnification, from the bottom to the top of the cell. When 200 grains had been counted, the count was stopped, and the number of tiles in the cell needed to reach 200 grains was recorded. Then we calculated the number of pollen grains in the cell and finally the number of pollen grains per FU, knowing the number of FUs collected for each sample.

To calculate the volume of one pollen grain, 200 µL of ethanol was added to the pollen solution used for counting and vortexed. Next, 10–20 µL of the preparation was placed between a slide and coverslip and then examined under a microscope at 100 × magnification. The equatorial axis (b) and polar axis (a) of the grain (µm) were measured using *MoticImages* software, and the volume of a pollen grain was calculated as $a/2 \times b/2 \times c/2 \times 4/3\pi$, where c equaled “a” for an oblate grain or “b” for a spheroid grain. We used “total pollen volume” per FU in the results which measured the quantity of pollen synthesized by the plant while considering the volume of pollen grains that vary between species. Total pollen volume was calculated by multiplying the per-grain volume by the number of pollen grains per sample.

Leaf traits

In addition to floral traits, we measured two leaf traits to determine how these leaf traits co-varied with the floral traits and whether these co-variations were similar between the control and drought treatments. Thus, we examined trade-offs between vegetative and reproductive traits. Leaf area (mm²) was measured non-destructively using a planimeter (LI-3000C, LI-COR, Lincoln, Nebraska, USA) on the two highest mature leaves per individual (Pérez-Harguindeguy et al., 2003). For each leaf, the mean of two measurements was calculated. A difference of 0.5–1.0 cm² between these two measurements was tolerated, depending on the leaf's size and shape (single or compound). The two leaves were placed in an oven at 60 °C for at least 72 h and then weighed to measure their mean dry mass (mg). Finally, specific leaf area (SLA) was calculated for each species as leaf area divided by leaf dry mass.

Plant-pollinator interactions

In addition to the greenhouse experiment, plant-pollinator interactions were observed *in situ* during six sessions from 21 July to 22 August 2022 (three sessions each in the morning and afternoon) within an experimental flower bed not subjected to the drought treatment near to Nancy's city greenhouse. These observations only concerned six of the eight species studied, because CORTIN failed to grow during this experiment, and NEPFAA did not flower. An experimental flower bed containing five individuals of each species divided into five observation squares was set up and the plants were regularly watered. Observations were made at temperatures of 21–32 °C, with a maximum wind speed of 13 km.h⁻¹, less than 40 % cloud cover, and always under sunny conditions. During the sessions, the plants were observed in pairs drawn at random for 5 min, which resulted in 705 min of observation. All FU visits were recorded, and pollinators were identified according to 12 morphotypes: honeybees, large and small wild bees, bumblebees, wasps,

other Hymenoptera, hoverflies, greater bee flies, other Diptera, butterflies, Coleoptera, and other. Visits were counted at the FU scale (i.e., a new interaction was considered only when the pollinator changed FU).

Statistical analyses

Statistical analyses were performed using R software, version 4.1.1 (R Core Team, 2021), via RStudio. For analyses we calculated the mean values of individual traits except for height and number of FUs where the maximum value was used. Principal component analysis (PCA) was performed using the “factoextra” and “FactoMineR” packages of R. The first PCA aimed to highlight floral and leaf traits that were likely to covary. A second PCA was performed to visualize which floral traits measured in the control treatment were attractive to pollinator morphotypes observed *in-situ* flower bed. None of the trait data followed a normal distribution even after transformation; so, means were compared using the Kruskal-Wallis test to assess the effect of drought on the floral traits by species. Pairwise comparisons were performed using non-parametric Wilcoxon tests with Bonferroni correction to highlight interspecific differences in floral traits.

Results

Covariation in floral and vegetative traits

For the control treatment, the first two axes of the PCA explained 56 % of the variance (Fig. 3A). Axis 1 explained 37 % of the total inertia and was correlated with SLA ($r = -0.81$), pistil and stamen lengths ($r = 0.76$ and 0.75 , respectively), petal mass ($r = 0.76$) and total pollen volume ($r = 0.78$). Axis 2 explained 19 % of the total inertia and was correlated with nectar sugar concentration ($r = 0.79$) and flower mass ($r = 0.80$). Floral area was negatively correlated with the number of FUs, while plant height and stamen length covaried. SLA was negatively correlated with total pollen volume and plant height. GAULIN had a large nectar sugar concentration. VERMUR, SALCOC and SALFAR had heavy petals and deep nectar tubes. NEPFAA and AGAURT had a large number of FUs. AGEALO and CORTIN had high SLA.

For the drought treatment, the first two axes of the PCA explained 58.5 % of the variance (Fig. 3B). Axis 1 explained 38 % of the total inertia and was correlated with SLA ($r = -0.73$), pistil and stamen length ($r = 0.80$ and 0.74 , respectively) and floral area ($r = 0.78$). Axis 2 explained 20 % of the total inertia and was correlated with nectar tube depth ($r = -0.68$). The number of FUs and leaf area were negatively correlated with flower mass and nectar tube depth, unlike for the control treatment, for which the number of FUs and leaf area were negatively correlated with floral area and nectar sugar concentration. Nectar sugar concentration and petal mass were negatively correlated with SLA, like for the control treatment. Plant height, total pollen volume and stamen length covaried, as did nectar sugar concentration and petal mass. GAULIN had a large nectar sugar concentration, while VERMUR had a deep nectar tube. SALCOC had a tall height, a large total pollen volume and a long stamen. AGAURT had many flowers. CORTIN and NEPFAA had high SLA. Only SALFAR differed between treatments, with a larger leaf area, taller height, higher pollen concentration and longer stamen under drought conditions.

Differences in floral traits among species

Morphological traits

GAULIN, SALFAR and AGAURT were the tallest species (99.9 ± 19.3 (mean \pm SD), 87.8 ± 18.6 and 85.1 ± 18.6 cm, respectively), while AGEALO was the shortest (19.3 ± 5.3 cm) (Fig. 4A). The floral area differed among all species ($p < 0.05$). VERMUR and GAULIN had the largest FU (1291 ± 408 and 929 ± 263 mm², respectively), while NEPFAA and AGAURT had the smallest (87 ± 141 and 30 ± 13 mm², respectively) (Fig. 4B). The number of FUs differed greatly among



Fig. 3. Biplot of the principal component analysis of floral and leaf trait variables of the eight plant species in the (A) control treatment and (B) drought treatment superimposed on the species. The abbreviated names of the plants are provided in Fig. 1.

species, with AGAURT, AGEALO and SALCOC having the most (231 ± 168 , 211 ± 148 and 167 ± 82 , respectively) and GAULIN and VERMUR having the fewest (24 ± 15 and 9 ± 5 , respectively) (Fig. 4C).

Barrier traits

The species with the deepest nectar tube was VERMUR ($42,904 \pm 26,605 \mu\text{m}$), followed by SALCOC ($16,136 \pm 3134 \mu\text{m}$), NEPFÁA ($9510 \pm 1045 \mu\text{m}$), SALFAR ($7246 \pm 1070 \mu\text{m}$) and AGAURT ($6609 \pm 987 \mu\text{m}$) (Fig. 5A). CORTIN had the shallowest nectar tube ($2534 \pm 375 \mu\text{m}$). SALCOC and GAULIN had the longest stamens ($16,641 \pm 3407$ and $16,800 \pm 11,302 \mu\text{m}$, respectively) (Fig. 5B). AGEALO had the shortest stamens ($394 \pm 363 \mu\text{m}$). SALCOC had the longest pistil ($31,165 \pm 6722 \mu\text{m}$), while CORTIN had the shortest pistil ($3383 \pm 607 \mu\text{m}$).

Resource traits

GAULIN had the highest nectar sugar concentration ($897 \pm 543 \mu\text{L FU}^{-1} 24 \text{ h}^{-1}$), while CORTIN, AGEALO, AGAURT, NEPFÁA and VERMUR had the lowest (136 ± 122 , 140 ± 132 , 105 ± 123 , 96 ± 91 and $118 \pm 152 \mu\text{L FU}^{-1} 24 \text{ h}^{-1}$, respectively) (Fig. 6A). SALCOC, GAULIN and SALFAR had the largest total pollen volume (1057 ± 868 , 170 ± 99 and $439 \pm 165 \mu\text{m}^3 \text{FU}^{-1}$, respectively) while AGEALO had the smallest ($3 \pm 8 \mu\text{m}^3 \text{FU}^{-1}$) (Fig. 6B).

Differences in floral traits among species between treatments

Morphological traits

Overall, morphological traits were impacted the most by the drought treatment. For all species except GAULIN, plant height decreased significantly with drought ($p < 0.05$) (from -24% for VERMUR to -40% for SALCOC) (Fig. 4A). Floral area decreased with drought for all species except VERMUR. The impact of drought floral height differed among species (from -16% for GAULIN to -63% for NEPFÁA) (Fig. 4B). The number of FUs decreased greatly with drought for all species, except VERMUR (from -74% for NEPFÁA to -55% for SALCOC) (Fig. 4C).

Barrier traits

Barrier traits were impacted the least by the drought treatment. GAULIN had no nectar tube, and NEPFÁA yielded only one data point for the drought treatment, which prevented comparing these species to the others. For the other six species, nectar tube depth did not differ significantly between treatments (Fig. 5A). Only SALCOC and AGAURT had significantly shorter stamens with drought (-24% and -19% , respectively) (Fig. 5B). Drought significantly decreased the pistil length of SALFAR, AGEALO and SALCOC (-13% , -23% and -28% , respectively) but increased that of VERMUR ($+100\%$) (Fig. 5C).

Resource traits

Drought influenced resource traits less than morphological traits.

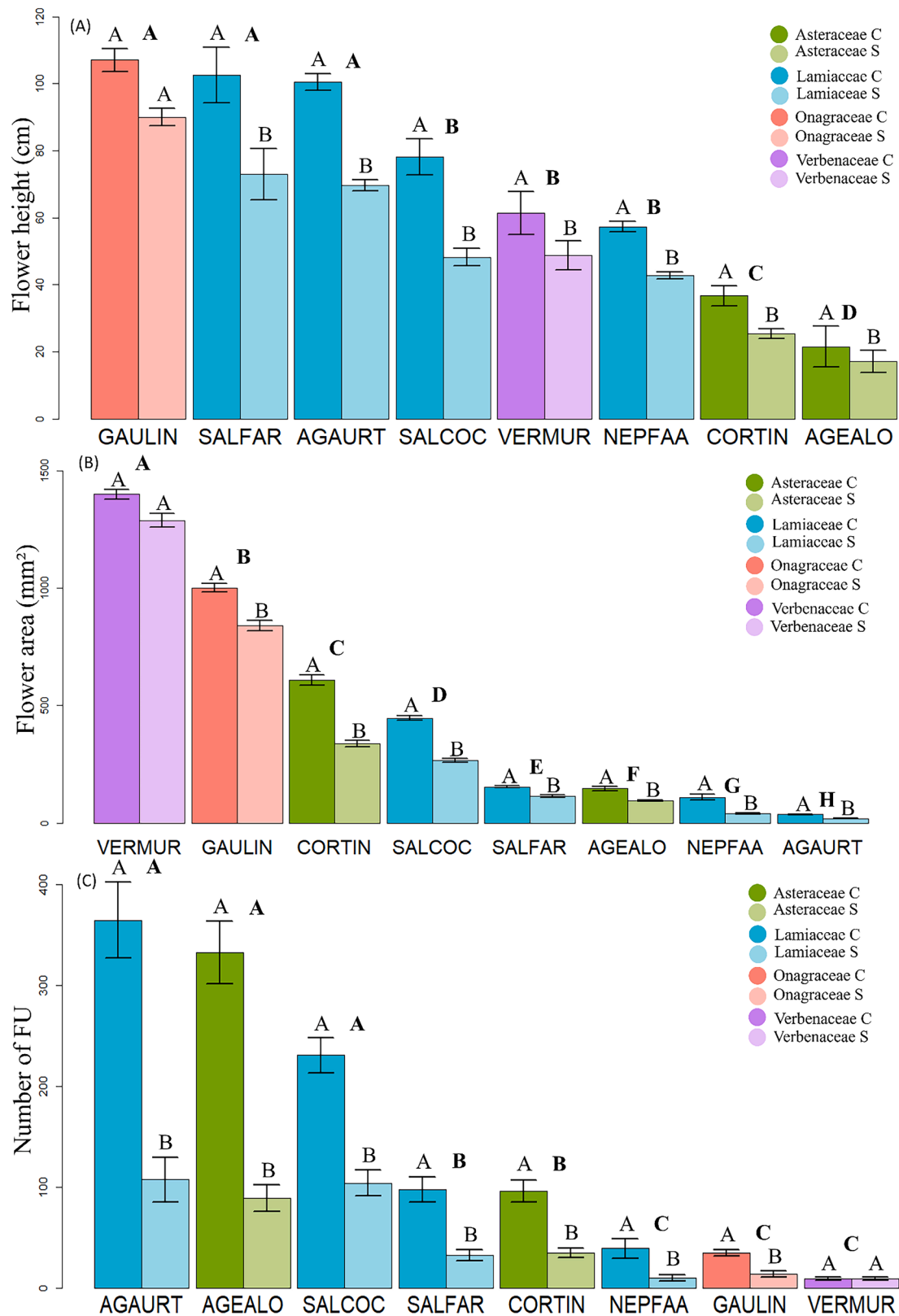


Fig. 4. Barplot of mean floral traits: (A) maximum plant height, (B) floral area of plant, and (C) number of floral units per plant for each species studied ($n = 8$). The four colors corresponded to plant families. Dark colors represent the control treatment, while light colors represent the drought treatment. Different lower-case letters represent significant intraspecific differences between treatments ($p < 0.05$). Different capital letters represent significant differences among species for all treatments combined ($p < 0.05$). Error bars represent ± 1 standard deviation. C: control treatment. S: drought treatment. The abbreviated names of the plants are provided in Fig. 1.

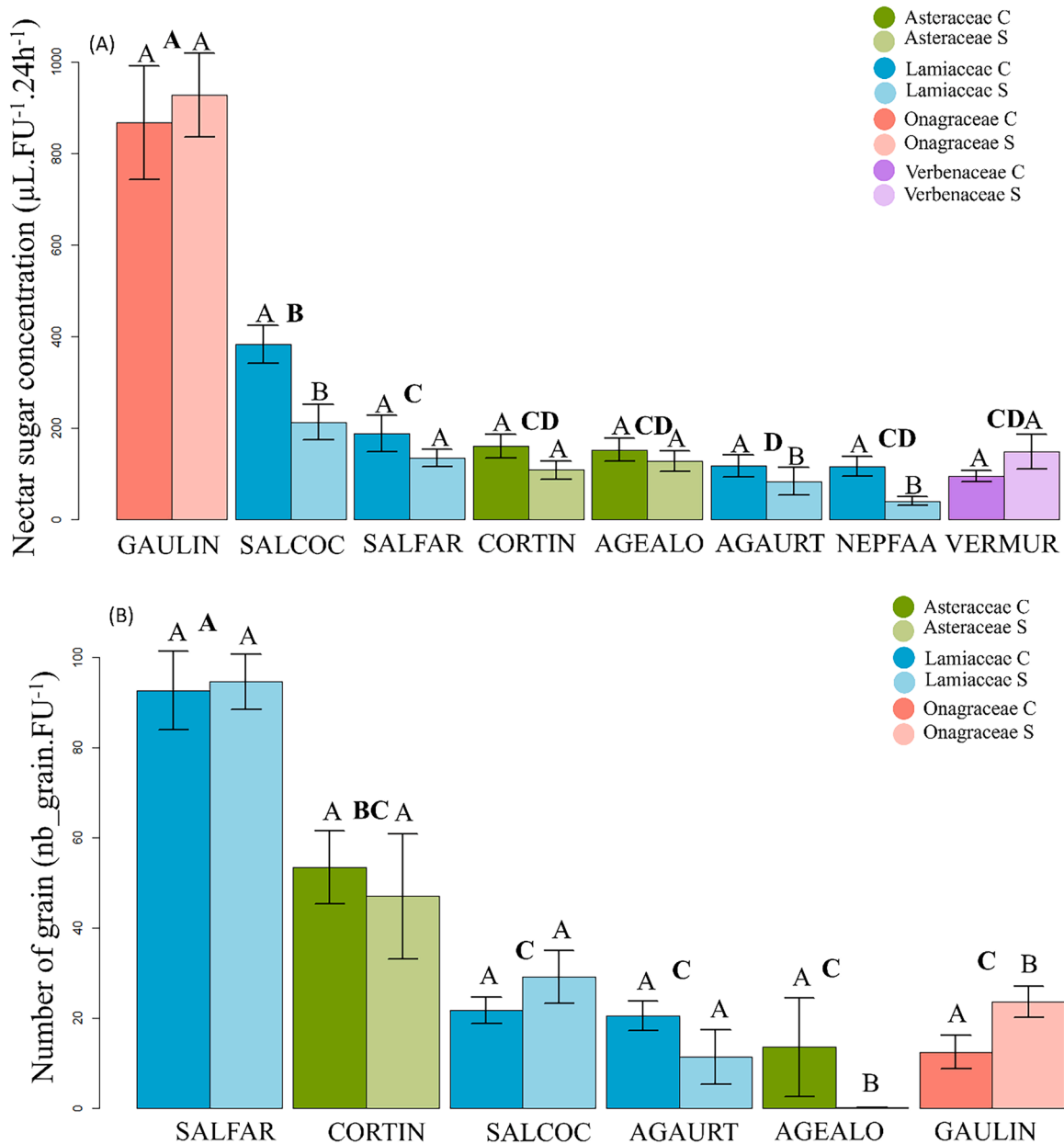


Fig. 5. Barplot of mean resource traits: (A) mean nectar sugar concentration and (B) mean total pollen volume per FU. The four colors corresponded to plant families. Dark colors represent the control treatment, while light colors represent the drought treatment. Different lower-case letters represent significant intraspecific differences between treatments ($p < 0.05$). Different capital letters represent significant differences among species for all treatments combined. Error bars represent ± 1 standard deviation. C: control treatment. S: drought treatment. The abbreviated names of the plants are provided in Fig. 1.

AGAURT, SALCOC and NEPFAR had significantly lower nectar sugar concentration with drought (-29 %, -44 % and -65 %, respectively) (Fig. 6A). Of the five species studied for total pollen volume, drought significantly influenced only that of GAULIN (+103 %) and AGEALO (-99 %), and in different directions (Fig. 6B). This difference was due to significant changes in number of pollen grains per FU ($p < 0.05$) for these two species under drought. There was not significant difference in pollen volume per grain between control and drought treatment for all species (data not shown).

Attractiveness of ornamental plants to pollinators

We observed 2729 interactions between ornamental plants and pollinators in the experimental flower bed. The mean interaction frequency on ornamental plant species was relatively high with 232 insects/h. Hymenoptera contributed 95 % of plant visits: 46 % honeybees,

27 % bumblebees and 22 % large wild bees. The first two axes of the PCA of floral traits and pollinator abundance explained 58 % of the variance (Fig. 7). Axis 1 explained 32 % of the total inertia of the PCA and was correlated with nectar sugar concentration ($r = 0.89$), the abundance of wasps ($r = 0.82$) and the abundance of small solitary bees ($r = 0.92$). Axis 2 explained 26 % of the total inertia of the PCA and was correlated with floral area ($r = -0.72$), nectar tube depth ($r = -0.73$), number of FUs ($r = 0.62$), abundance of honeybees ($r = 0.81$), abundance of bumblebees ($r = 0.75$) and abundance of butterflies ($r = -0.80$). Honeybees and bumblebees visited mainly AGAURT, which had a large number of FUs. Large solitary bees performed 86 % of their visits to SALFAR, which had average floral trait values. Wasps and small solitary bees were attracted to tall plants with a large nectar sugar concentration and large stamens (i.e., GAULIN and SALCOC). VERMUR, with its deep nectar tube, attracted 88 % of butterflies visits.

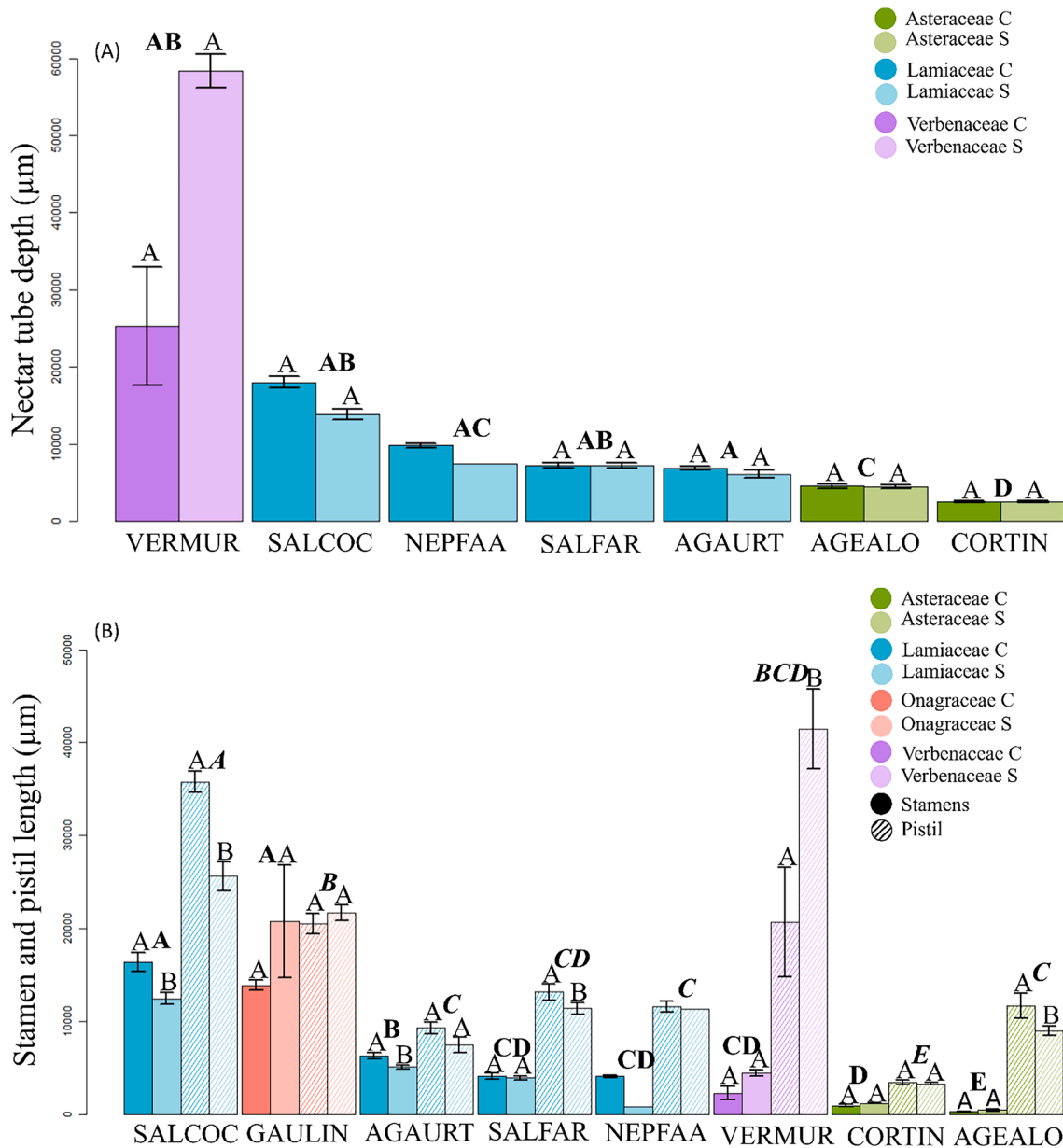


Fig. 6. Barplot of mean barrier traits: (A) nectar tube depth and (B) stamen and pistil length ($n = 8$). The four colors corresponded to plant families. Solid bars represent stamen length, while hatched bars represent pistil length. Dark colors represent the control treatment, while light colors represent the drought treatment. Different lower-case letters represent significant intraspecific differences between drought and control treatment ($p < 0.05$). Different capital letters represent significant differences among species for all treatments combined. Error bars represent ± 1 standard deviation. C: control treatment. S: drought treatment. The abbreviated names of the plants are provided in Fig. 1.

Discussion

Covariation in floral traits

Regarding morphological traits, the number of FUs and floral area revealed a trade-off well identified in older studies (e.g., Worley & Barrett, 2000 for *Eichhornia paniculata*; Sargent et al., 2007 for 251 species) and more recently (e.g., Genty et al., 2023 for Mediterranean weeds; Lanuza et al., 2023 for 1236 species). This result can be explained by the limitation of carbon assimilation caused by drought, which prevents plants from allocating carbon to the production of many FUs and large flowers. Some ornamental plants such as SALCOC, GAULIN and VERMUR had large FU areas, which generally attract more pollinators. Indeed, Lanuza et al. (2023) found that all pollinator guilds

interacted more frequently with species that had large floral displays and little ability to self-pollinate, in agreement with previous studies (Hegland & Totland, 2005; Kaiser-Bunbury et al., 2014; Lázaro et al., 2013). Other species such as NEPFAA, or AGAURT could have a more ruderal strategy (Grime, 1974), with high SLA and less costly floral traits (e.g. short floral height, many small flowers). This relation between ruderal strategies and floral traits was recently highlighted by Genty et al. (2023) for Mediterranean weeds.

Floral resources were positioned along the axis of the number of FUs/ floral area, with total pollen volume related to petal mass and stamen length in both treatments and to pistil length in the control treatment, which may be related to the strategies of insect-pollinated plants. Surprisingly, nectar sugar concentration did not lie on the same axis as pollen under control conditions, which differed from results of Lanuza

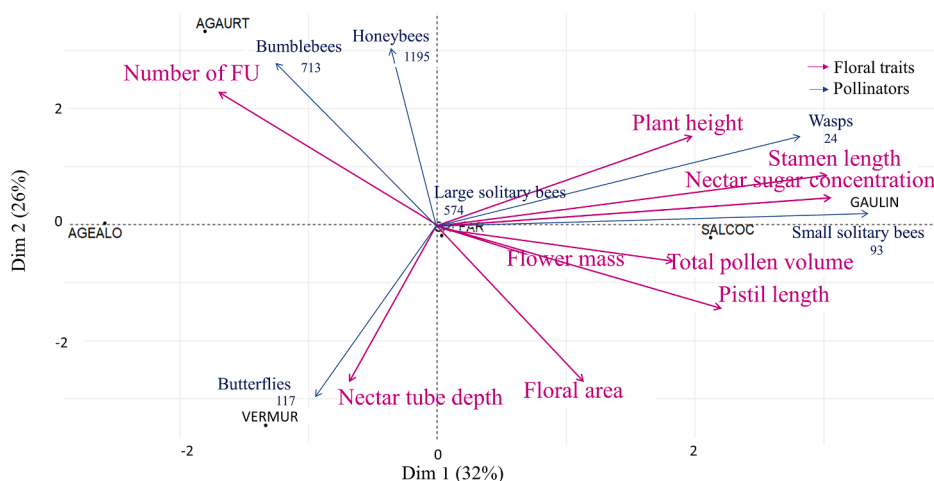


Fig. 7. Biplot of principal component analysis of mean floral traits (purple) for eight plant species and number of pollinator visits by morphotype as variables (blue) superimposed on the species. The abbreviated names of the plants are provided in Fig. 1.

et al. (2023) and Genty et al. (2023). However, nectar sugar concentration and pollen seemed to covary under drought conditions, which highlights a change in trait covariation with drought. Drought decreased the nectar sugar concentration of SALCOC, AGAURT and NEPFAA, with no change in total pollen volume, but considerably increased the total pollen volume of GAULIN. The limitation of carbon assimilation caused by drought could lead to different strategies among species for allocating carbon between nectar sugar production and pollen production. Moreover, pollen-resource traits are generally more phylogenetically conserved than those of nectar (Lanuza et al., 2023), and nectar sugar concentration is sensitive to environmental conditions (Corbet, 2003).

Drought influences floral traits

Although some ornamental plants provide resources for pollinators at the end of summer (Salisbury et al., 2017; Zaninotto et al. 2023), drought significantly changed floral traits in the present study. Drought had more effect on morphological traits such as height, floral area and number of FUs than on barrier or resource traits, as Kuppler and Kotowska (2021) observed in a meta-analysis of 45 herbaceous angiosperm species. Regarding morphological traits, floral height decreased more with drought (−24 % to −40 %) than it did in the review of Descamps et al. (2021) (−10 % to −20 %), which considered 55 insect-pollinated herbaceous species. Only the floral height of GAULIN was not influenced by drought, suggesting that this species resists drought better than the other species. Except for VERMUR, results of the present study revealed a mean decrease of 39 % in floral area, which lies in the range (−5 % to −60 %) reviewed by Descamps et al. (2021). Producing a large floral area requires a large supply of carbon from the plant. Reducing the floral area limits carbon use (Roddy et al., 2021) and decreases water loss by decreasing the exchange surface during evapotranspiration (Descamps et al., 2021). Indeed, larger flowers require more water to maintain turgor because their tissues have lower cell wall densities; thus, having smaller flowers requires less water (Galen et al., 1999). The number of FUs of ornamental plants seemed to be impacted more by drought (from −55 % to −74 %) than that of other species (−30 % to −50 % in the review of Descamps et al. (2021)). This decrease is likely due to stomata closing during drought, which limits the quantity of carbon allocated to plant reproduction and thus decreases the number of FUs produced.

In the present study, drought impacted barrier traits the least, as Kuppler and Kotowska (2021) observed for 45 species. However, slight decreases in nectar tube depth and corolla length with drought have been observed for *Sinapis arvensis* (−12 %, Kuppler et al. (2021)) and *Lobelia siphilitica* (Caruso, 2006). Descamps et al. (2020) also found that

drought lead to a decrease in flower corolla length by 50 %. Barrier traits influence pollinators' access to floral resources and have co-evolved with pollinators, which makes them less plastic in response to changes in the environment. In fact, studies have observed that the length of insect mouthparts was positively correlated with flower corolla length of the flowers they pollinate (Anderson & Johnson, 2008).

Like Descamps et al. (2021) and Kuppler and Kotowska (2021) observed for other species, resource traits (i.e., nectar sugar concentration and total pollen volume), the number of FUs and floral area revealed a trade-off well identified in the literature. However, nectar was more sensitive to drought, which can be explained by its sensitivity to evaporation. Nectar is costly for plants to synthesize during drought, since its stock has to be resynthesized every 24 h (Corbet, 2003). Based on these results, some floral traits of ornamental plants seemed to be impacted more by drought than those of other herbaceous species. However, these results should be confirmed by *in situ* experiments with no limitations on growth. Some species, such as GAULIN, SALFAR and SALCOC, appeared relatively drought-resistant and could remain sufficiently nourishing for insects during drought. The response of perennial species (GAULIN and NEPFAA) was contrasted by a large decrease in floral trait values for NEPFAA, whereas no such decrease was observed for GAULIN. Although only the nectar sugar concentration of VERMUR was studied, this species could be interesting for flowering urban green spaces because drought impacted only its floral height.

Attractiveness of ornamental plants to pollinators

The ornamental species studied were relatively attractive to pollinators. Hymenoptera were the main pollinators, with 95 % of total plant visits (46 % honeybees, 27 % bumblebees and 22 % large wild bees), which agrees with general observations of pollinator visits to ornamental plants (Erickson et al., 2020; Rahimi et al., 2022; Silva et al., 2023). The experimental site has several beehives in close proximity, which can lead to competition between honey bees and wild pollinators (Iwasaki & Hogendoorn, 2022). Another study that inventoried pollinators in 12 urban green spaces in the Nancy metropolitan area in 2021 (unpublished data) found mainly Hymenoptera as visitors of ornamental plants (70 %) (53 % honeybees and 17 % bumblebees) and also observed visits by Diptera (23 %), which was not observed in the present study, perhaps due to the few plant species and sites observed, which limited pollinator diversity. Interestingly, the same 2021 inventory observed a mean frequency of 44 visits/h to ornamental plants, which was similar to the 39 visits/h to wild plant species of urban grasslands and occurred mainly at the end of the season (August and September). Thus, ornamental plants seemed to attract more generalist Hymenoptera than

other morphotypes of pollinators, with an interaction frequency relatively similar to that of other urban habitats, especially at the end of the season.

Overall, the scores that managers had attributed to the ornamental plants coincided with our observations: AGAURT and SALFAR were the most attractive to pollinators. However, their assessments of nectar and pollen production differed from the study's results, in particular for GAULIN, which received a score of 0/3 for nectar production but had the highest nectar sugar concentration in the study, and AGAURT, which received a score of 3/3 for nectar production but had a small nectar sugar concentration in the study. This difference highlights the need to make quantitative measurements of floral traits to improve management of flower resources in urban areas.

In this study, an increase in floral trait diversity increased the number of pollinator morphotypes that visited. For example, we observed visits of butterflies to VERMUR, which had deep nectar tubes, and small solitary bees and wasps to GAULIN and SALCOC, which had large nectar sugar concentrations and large stamens. This result highlights the need to increase the functional diversity of floral traits of urban ornamental plants with complementary ecological niches in order to maintain biodiversity (Carmona et al., 2021; Goulunik et al., 2020; Mason et al., 2005). This diversity could include host species for specialist pollinators, which are usually rare in urban areas (Deguines et al., 2016).

Conclusion

We observed variability in floral traits among the eight ornamental species and a change in covariation between total pollen volume and nectar sugar concentration with drought. Comparing our results with those of previous studies, drought seemed influence morphological traits of ornamental plants more than those of other herbaceous species. However, drought seemed to impact more morphological traits of AGAURT and SALFAR and less GAULIN and VERMUR. A community with different ornamental species could attract different pollinator morphotypes to help conserve them and could be used at the end of the season to supplement floral resources in cities. However, it is essential to verify whether these plants are nutritious for pollinators by measuring nectar and pollen compositions. It is also necessary to evaluate the competition for pollinators between exotic and native species, in various urban green space plant communities. Moreover, managing these species requires several waterings per week, and some are used as annual plants despite their perennial nature. This raises questions about sustainability if management practices are not adapted in response to climate change.

CRediT authorship contribution statement

Margaux Quinanzoni: Data curation, Formal analysis, Methodology, Validation, Visualization, Writing – original draft. **David Marcelet:** Methodology, Data curation. **Alice Michelot-Antalik:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the research reported in this article.

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