Plant fitness is shaped by cascading effects of aridity and drought on floral traits and pollination services

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ABSTRACT

Floral signals mediate crucial plant-pollinator interactions thus impacting plant reproductive success, yet their responses to water scarcity induced by climate change remain poorly understood. We exposed *Sinapis alba* plants from populations along an aridity gradient to controlled irrigation treatments, measuring physiological responses, floral traits, volatile organic compounds (VOCs), pollinator behavior, and reproductive outcomes. While arid-origin populations exhibited enhanced drought tolerance, immediate water availability primarily shaped floral signals across all populations. Drought reduced floral display and induced complex shifts in VOC profiles — decreasing in pollinator-attracting benzenoids and terpenoids while increasing stress-related alkanes and green leaf volatiles. Pollinators favored plants with larger displays and higher VOC emissions but avoided physiologically stressed plants. Seed production reflected both plant condition and pollination success, with germination rates highest in seeds from arid origins. These results demonstrate how water limitation significantly alters the plant-pollinator communication system, ultimately affecting plant fitness. Our findings highlight the need for integrative approaches to understand and preserve plant-pollinator interactions under climate change, with direct implications for agricultural productivity in water-limited regions.

1. Introduction

Climate change is already disrupting plant-pollinator networks worldwide, resulting in reductions in pollinator visits not only to natural plant communities, but also to agricultural crops (Kantsa et al., 2023; Potts et al., 2010). To cope with the ongoing climate crisis organisms must adopt "move, adapt, or perish" strategies. For plants, movement is achieved through shifts in distribution range along altitude and latitude, mainly driven by dispersal (e.g. Corlett and Westcott, 2013). Such shifts carry significant consequences for natural and agricultural ecosystems, especially for pollinator-dependent crops, whose reproductive success depends on the presence of effective pollinators and precise ecological

timing (e.g. Nicholson and Egan, 2020; Semeraro et al., 2023). Yet, due to their sessile nature, plants must primarily rely on acclimation and adaptation to survive the changing conditions (e.g. Bussotti and Pollastrini, 2021; Sachdev et al., 2021). Given that 90 % of angiosperms depend on animal pollinators to secure reproductive success (Ollerton et al., 2011), potential breakdown of plant-pollinator networks poses an acute and immediate threat. It is therefore essential that plant adaptive responses to climate change also encompass strategies to preserve these mutualistic interactions. Surprisingly, despite the central role of animal pollinators – especially insects – in securing reproductive success in both natural and agricultural ecosystems, plant-pollinator interactions remain strikingly underexplored in the context of climate change

(Burkle and Runyon, 2016; Jaworski et al., 2022).

Successful plant-pollinator interactions rely heavily on effective communication. From the perspective of plants, this communication is primarily shaped by floral signaling, which encompasses mainly visual cues and scent (Chittka and Thomson, 2001; Raguso, 2008; Schiestl, 2015). These floral signals are expected to be particularly sensitive to two key consequences of climate change: reduced precipitation (and the resulting increase in drought stress) and rising temperatures (Day Briggs and Anderson, 2024). Among floral visual cues, studies have shown that floral size is affected by temperature and drought stress, with plants in drier and warmer conditions producing smaller, shorter-lived flowers (e. g. Burkle and Runyon, 2016). Additionally, drought stress has been associated with reduced flower numbers (e.g. Rering et al., 2020), which directly affects the visibility of floral displays to pollinators.

Floral scent, another critical component of plant signaling, is highly effective for host recognition and thus plays a significant role in guiding pollinators toward receptive flowers (Schiestl, 2015). In addition, it facilitates communication with seed dispersers, herbivores, pathogens and neighboring plants (Raguso, 2008; Yuan et al., 2009). Effective insect-plant communication – and pollinator-plant communication in particular – is essential for sustaining this long-term mutualism (Chittka and Thomson, 2001). Because this communication relies on honest and precise signals, even subtle changes in the information emitted can have critical consequences for plants, leading to reduced pollination efficiency or increased vulnerability to herbivores and pathogens (Schiestl, 2015). Floral scent is produced through the biosynthesis of volatile organic compounds (VOCs). These compounds can be divided to three major classes – terpenoids, phenylpropanoids/benzenoids, and fatty acid derivatives, based on their biosynthetic origin (Muhlemann et al., 2014). Their composition and emission vary across species and environmental conditions and play a key role in shaping pollinator behavior (Abbas et al., 2022; Raguso, 2008). Due to their chemical nature, VOC emission is sensitive to temperature changes, which can directly influence their volatility, solubility, and diffusivity (Niinemets et al., 2004). Temperature also indirectly affects VOC emission by altering physiological processes, such as biosynthetic pathways and stomatal activity (Farré-Armengol et al., 2014). While many studies have focused on temperature's role in modifying floral scent, less is known about the effect of water stress (Campbell et al., 2019; Rering et al., 2020). Nevertheless, since plants regulate their metabolic activity in response to water availability, drought is likely to alter VOC emission as well (Ameye et al., 2018; Jogawat et al., 2021; Yuan et al., 2009). Furthermore, water stress is expected to reduce the overall release volume of volatiles because volatile emission is closely linked to stomatal activity (e.g. Lin et al., 2022; Salman et al., 2022).

These climate-induced shifts in floral signals are likely to further interact with other climate-driven changes in plant-pollinator interactions, such as altered plant and pollinator phenology (Gerard et al., 2020), and changes in pollinator distributions (Kantsa et al., 2023) and abundance (Potts et al., 2016), to reduce pollination services. Combined with evidence that flowers are a significant source of water loss (e.g. Bourbia et al., 2020), and that pollen viability decreases under drought conditions (e.g. Ejsmond et al., 2011), these changes present a substantial risk to plant reproductive success under predicted climate scenarios. Considering the urgent need to better understand the effect of climate change on pollination services and their impact on plant performance, it is surprising that studies that focus on the influence of water limitations on flower signaling in general, and floral volatile emission in particular, are still relatively rare (e.g. Campbell et al., 2019; Farré-Armengol et al., 2020; Jaworski et al., 2022; Lin et al., 2023). Moreover, there is still only limited information on pollinator responses to these climatic effects (Rering et al., 2020; e.g. Scaven and Rafferty, 2013).

The eastern Mediterranean is an ideal region for studying these potential effects, as it is already characterized by water scarcity and relatively warm temperatures. Moreover, the region is predicted to experience a decrease in precipitation of up to 30 % and a significant rise in temperatures (e.g. Lelieveld et al., 2012). It is also recognized as a global biodiversity hotspot for plants and pollinators due to its location at the crossroads of three continents (Kantsa et al., 2023; Myers et al., 2000), and serves as an important genetic reservoir, particularly for crop species (Vincent et al., 2022), making research in this region highly relevant. Specifically, we used wild populations of *Sinapis alba* (L.), Brassicaceae, a common, agricultural relevant species, and grew them at a site near the species' natural arid distribution edge. By doing so, we exposed the plants to natural yet extreme arid conditions, allowing us to assess how drier and warmer conditions affect *S. alba*'s performance and floral signaling, and whether the resulting changes influence pollination services and, consequently, the plants' reproductive success. By combining exposure of plant populations to harsh conditions with in-situ irrigation manipulations, we could compare the responses of *S. alba* to both immediate drought conditions and to the more general impact of aridity, as predicted by climate change. We asked (1) whether the exposure of *S. alba* plants originated in different climatic conditions to drier and warmer conditions affects their physiological performance. We predicted that (i) plant individuals originating from more mesic conditions would experience greater stress when exposed to arid conditions. We additionally predicted that (ii) plant individuals originating from more arid conditions would be better in utilizing water availability to compensate for the arid habitat. This is because we expected individuals from more arid conditions to be more adapted to such conditions, which included not only more tolerance and more resistance to aridity, but also a more plastic response to windows of opportunities in their local habitat (Krintza et al., 2024; e.g. Lázaro-Nogal et al., 2015). We further asked (2) whether the exposure to drier and warmer conditions affects floral signaling of *S. alba*. We predicted that (i) plants from different origins would differ in their profile of floral signals (e.g de Manincor et al., 2022). We additionally predicted that (ii) exposure to immediate drought conditions would decrease visual signals to reduce potential water loss. However, we also expected to detect an increase in floral scent emissions because plants might rely more on the immediate production of VOC to attract pollinators during a shorter flowering period. Finally, we asked (3) whether pollination services were changing in response to the change in floral signaling. We predicted that (i) pollinators would respond to the level of plant's stress and its shift in signaling and would visit the drought plants less than the irrigated plants (see also Salman et al., 2022). We additionally expected that (ii) the local pollinator community would prefer the local plants relative to the more remote (and perhaps less adapted) plants. Finally, we predicted that (iii) any change in the pollination services to the plants would be expressed in the plants' reproductive success.

2. Methods

2.1. Plant species and experimental design

Our work took place in the Eastern Mediterranean region, which is characterized by a steep rainfall gradient and a strong water limitation. This region's aridity gradient serves as a model system, representative of Mediterranean-type ecosystems that are particularly vulnerable to climate change worldwide. Our model species was *S. alba*, an annual of the Brassicaceae family. The Brassicaceae family includes economically important crop species such as vegetables, industrial oilseed, and fodder plants (Warwick, 2011). Among the species of this family, *S. alba* is commonly cultivated for seeds, oil, fodder, and catch crops (Akter and Klečka, 2022). Because *S. alba*, like several related species, produces glucosinolates, it has natural pesticidal properties that help suppress soil-borne pests and weeds (e.g. Borek and Morra, 2005). In addition, *S. alba* often serves as a common model species, as it is considered a valuable resource for genetic improvement of agricultural crops (Castillo-Lorenzo et al., 2024). Moreover, *S. alba* was a convenient model plant for this study because it grows rapidly, has a short

vegetation period and shows population differentiation in relation to pollinators (Gibson-Forty et al., 2022). In the Eastern Mediterranean region, *S. alba* has a flowering period that typically spans 3–4 weeks during early spring (March-April), making timing of observations critical for capturing peak pollination activity (Danin and Fragman-Sapir, 2016).

We collected seeds from six populations of *S. alba* that grew under different annual precipitation and temperature along this gradient (supplementary material Table S1.1). The aridity gradient was defined primarily by differences in mean annual precipitation and temperature across the populations' native sites (see Table S1.1), with southern populations experiencing drier and warmer conditions. Seeds from these populations were sown in a common garden at Sde-Boqer campus of Ben-Gurion University of the Negev (for general description of the garden experiment, see Fig. 1). Using a common garden approach, we were able to control environmental variability and isolate the effects of plant origin and water availability on phenotypic traits and pollination while maintaining exposure to natural abiotic (e.g. sunlight, temperature) and biotic (e.g. local pollinator community) conditions (Schwinning et al., 2022). The garden was located in the southernmost region of the species distribution not far from the location of the most arid population used in this study (Dimona population, supplementary material Table S1.1). Thus, the natural yet controlled conditions to which the plants were exposed simulated potential arid conditions under climate change, where the species might still survive. The experiment consisted of 36 0.5 m² plots. The plot size was chosen to represent the natural size of an *S. alba* patch in the region. Each of the six populations was randomly assigned to six plots. We germinated the seeds under natural field conditions, until 27 seedlings were established (i.e. produced four real leaves) in each plot. All other germinating plants were manually removed from the plot to maintain the density. After the seedling establishment, three plots per population were randomly assigned to high or low irrigation treatment. Irrigation treatments were chosen to simulate natural conditions at the more arid (equal to 250 mm) vs. more mesic (equal to 540 mm) end of the geographic range. Over the course of the experiment, the high irrigation treatment averaged ~36 mm/week and the low irrigation treatment ~17 mm/week, applied per 0.5 m² plot. Irrigation was applied through a drip irrigation system that allowed us to control for the amount of water each plot received and ensure that all other characteristics of the irrigation treatments, such as water distribution and regime, were the same.

2.2. Physiological measurements

We used a LICOR 6400 portable photosynthesis system (LICOR, Lincoln, NE, USA) to measure physiological parameters of the plants. Specifically, we haphazardly selected two leaves from each plot and measured 16 physiological traits (see supplementary material Table S2.1 for details). Light intensity was monitored prior to each measurement and kept constant at 1200 μmol photons m^{-2} s^{-1} (10 % blue light). Airflow rate was kept constant at 500 μmol s^{-1}, and the reference CO_2 concentration was 400 ppm.

2.3. Floral resources and flower size

The floral season of *S. alba* in the region does not exceed one month. During this period, we counted the total number of flowers per plot once, at the peak of flowering. *Sinapis alba* flowers typically remain open for 1–2 days without closing during that period. In accordance, for flower size, we selected ten random fully anthetic flowers from each plot. Based on the protocol provided by Nikolov (2019), each flower was photographed with the corolla parallel to the surface, and images were analyzed with ImageJ (http:// rsb.info.nih.gov/ij/). Following calibration, flower size was determined by measuring the length of the corolla.

2.4. Primary metabolites

To assess the metabolic profile of the flowers, we collected large number of flowers from each plot and freeze-dried at - 80°C. To extract the metabolites, we grinded 20 mg of each sample using a pre-chilled RETCH-mill with two grinding beads for 4 min at 15 Hz. The extraction process, adapted from Fiehn et al. (2000), involved adding 100 μl of pre-chilled 100 % methanol and 1 ml of extraction mixture (methanol: chloroform: water; 2.5:1:1 v/v/v) to the frozen powder, followed by incubation for 10 min at 4°C on an orbital shaker and for another 10 min in an ultrasonication bath at room temperature. After centrifugation to separate the metabolites from cell debris, we separated the polar metabolites from non-polar metabolites by adding 300 μl of UPLC grade
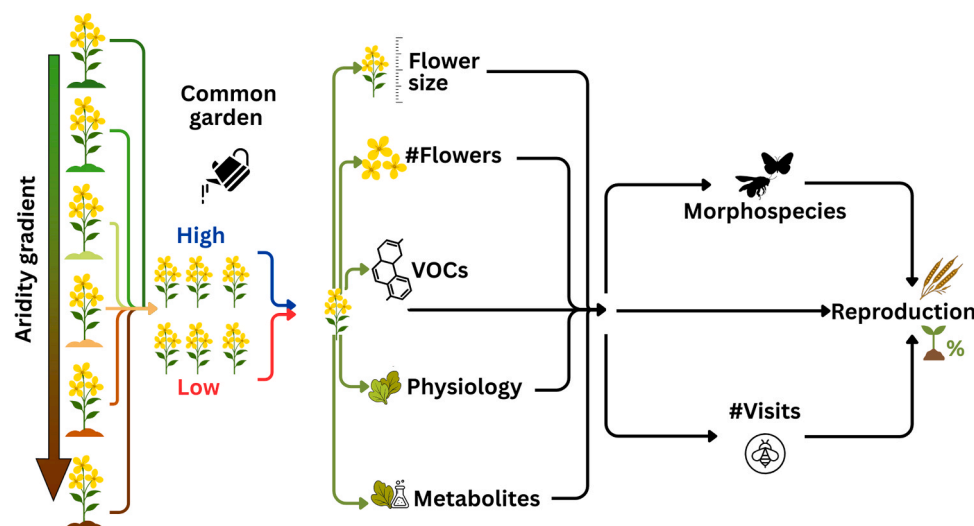
Fig. 1. Graphical illustration of the experimental design. Sinapis alba individuals from six populations were exposed to two irrigation levels in a garden experiment. The garden was located near the arid edge of the species' distribution, simulating conditions expected under future climate change. The seed source populations represented a range of aridity levels across the species' natural distribution. This full-factorial design enabled us to test the combined effects of plant origin ('aridity') and water availability (high and low irrigation) on plant performance (physiological and metabolic) and floral signals (flower size, number of flowers, and volatile organic compounds). We also monitored insect pollination visitation, classifying the visitors into broad taxonomic groups ('morphospecies') and quantifying the number of visits per plot. Finally, plant fitness was estimated by measuring the number of seeds per plant and germination rate.

water and 300 μl of chloroform to the samples. We then used 30 μl of the upper phase for gas chromatography–mass spectrometry (GC-MS) analysis, following a derivatization protocol (Hochberg et al., 2013). We quantified several sugars (sucrose, maltose, trehalose, and raffinose) and amino acids (e.g. glycine) that are highly relevant for flower metabolism and are known to vary with environmental conditions (Penna et al., 2006; Sharma et al., 2023), using a calibration curve of standards (Sigma-Aldrich, MO, USA).

2.5. Flower volatiles extraction

To collect flower volatiles, 1 g of flowers was sampled per plot and freeze-dried at −80°C. The samples were analyzed using headspace solid phase microextraction (HS-SPME) coupled with GC-MS (Weinblum et al., 2021). Tissue samples were frozen in liquid nitrogen and in 20 ml glass vials with 1 g of NaCl and 7 ml of a 20 % (w/v) NaCl solution, and Isobutylbenzene (10 mg/L, Sigma-Aldrich, Israel) was added as an internal standard (Tholl et al., 2006; Zvi et al., 2008). Before analysis, the glass vials were heated to 60°C for 15 min with a PAL COMBI-xt (CTC Analytics AG Switzerland) to release free volatiles into the headspace. A 10 mm long SPME fiber, assembly 50/30 μm, divinylbenzene/carboxen/polydimethylsiloxane (Supelco, Bellefonte, PA, USA), was introduced into the headspace for 15 min at 60°C. The fiber was then desorbed for 10 min at 250°C in splitless mode within the inlet of a 7890 A GC (Agilent, Santa Clara, CA, USA) equipped with an VF-5MS 10 m EZ guard capillary column (30 m × 0.25 mm inner diameter, 0.25 μm film thickness; Agilent CP9013, USA), coupled to a 5977B MS detector (Agilent). Helium was used as carrier gas at a constant pressure mode rate of 1 ml·min^{-1}. The GC temperature was programmed to increase from 40°C (1 min) to 250°C at 6°C·min^{-1}. Ionization energy was 70 eV with a mass acquisition range of 40–400 m/z, and a scanning rate of 6.34 spectra/s. The retention index (RI) was calculated by running C8–C20 n-alkanes, and compounds were identified using the Wiley 10 with NIST 2014 mass spectral library data with the Mass Hunter software package (version B.08.00, Agilent, USA). Further identification of major compounds was based on a comparison of mass spectra and retention index. Compounds with authentic standards (Sigma-Aldrich, Israel) were analyzed under similar conditions. Compound quantification was performed semi-quantitatively by comparing peak areas of target VOCs to the internal standard, allowing normalization across samples.

2.6. Pollinator observations

To assess pollination services to the plants, we conducted a series of observations in each plot. Each plot was observed separately for 5 min from a fixed position, three times per observation day (8:00–10:00, 11:00–13:00, 14:00–16:00, total of 15-minute observation per plot per observation day), to account for potential variation in pollinator community throughout the day. All observations took place on sunny days, with air temperature above 20°C, no precipitation, and minimal wind speed.

Trained observers conducted all sessions using a standardized identification protocol. Before data collection began, observers calibrated their methods to ensure consistency in identifying pollinator groups and recording visits across sessions. Given the relatively small plot size, we minimized directional visitation bias by randomizing the order in which plots were monitored and by avoiding simultaneous monitoring of neighboring plots. Although repeated visits by individual insects cannot be entirely ruled out, we expected such events to occur randomly and be evenly distributed across plots, thus not introducing systematic bias to the results. The chosen plot size also enabled manageable observation units and close monitoring of flower visitation. Therefore, while small plots may not capture the full complexity of pollinator dynamics in larger plant communities, they allowed for high-resolution quantification of treatment-level differences.

In total, we conducted 108 plot-observation sessions over a ten-day period during the plant's peak flowering phase in the garden. It is important to note that at the arid edge of the species' distribution, the flowering period does not exceed one month. This allowed us to avoid environmental and phenological shifts in the local pollinator community and to focus on the potential pollination services provided to *S. alba* during its primary pollination window in the study region.

All pollinator visits, defined as insect landing on a flower, were recorded. Due to the nature of the observations, complete identification of insect visitors was not always possible. Following established protocols (e.g. Seifan et al., 2014), insects were identified to broader taxonomic groups that included: *Andrena* sp., *Eucera* sp., *Osmia* sp., *Bombyllius* sp., *Halictid* sp. and 'other' (including Asilidae and Drosophiidae flies, Bruchinae and Curculionoidea weevils and Chrysomelidae beetles). All the recorded groups are known as serves as pollinators of Brassicaceae species in the region (e.g. Gibson-Forty et al., 2022). Interestingly, we observed very few individuals of *Bombus* sp. and no visits from *Apis* sp. during our monitoring period. Unidentified insects were caught and sent to the Steinhardt Museum of Natural History, Tel Aviv, for identification; voucher specimens were archived there. Based on the resulting visitor lists, we calculated pollinator visitation rate per plot and for dominant pollinator groups, expressed as the total number of visits per total number of flowers in the plot per 15-minutes observation session (Seifan et al., 2014).

2.7. Fruit production and seed set

To estimate fruit production, we haphazardly selected two plants per plot and covered two of their inflorescences with mesh bags on the same day until seed formation. Once the fruit ripened, we collected the bagged inflorescences. We counted the number of fruits and developed seeds produced per inflorescence. Using this data we calculated 1. the mean number of seeds per pod. 2. total seed production per plant, calculated by multiplying the meant number of seeds per pod by the total number of flowers on the plant. Finally, to assess seed viability, we tested germination rate by germinating ten seeds from each inflorescence.

2.8. Statistical analysis

Our data analysis comprised of three parts. In the **first part** we analyzed each group of measurements (physiology, primary metabolites, volatile compounds) separately. Specifically, because each of measurement group generated a large about of data, resulting in high autocorrelation among traits, we chose to first apply a dimensional reduction method (Principal Component Analyses, PCA) to avoid violating the multicollinearity assumptions of linear models. Following each PCA we identified the axes that contribute the most to the variance, based on their eigenvalues (Šmilauer and Lepš, 2014). These axes were then used as a representative of the group of measurement in the next analyses sections. Analyses were conducted using Jamovi (Version 2.6).

The **second part** of the analysis was focused on the effects of habitat conditions on *S. alba* physiology and floral signals. Habitat conditions were divided into two components: the irrigation received by the plants in the garden, and the aridity at the native sites from which each population was originally collected. These native sites, representing different climatic conditions along the species' natural distribution range, are referred to as the 'site of origin'.

To test for the combined effects of these two factors, we used a set of generalized liner models (GLM; Bolker, 2007) with aridity at the site of origin, irrigation treatment (high or low) and their interaction as explanatory fixed variables. The first and second PCA axes for physiological measurements, first and second axes for primary metabolites, flower number, floral size, and overall VOC concentration served as dependent variables. We used models with normal distribution and identity link for all dependent variables except for number of flowers,

where we used Poisson distribution with log link. Before running the statistical models, we tested the relevant assumptions for each dataset and distribution selected.

For more thorough understanding of the effects of the habitat conditions on VOC, we further grouped the compounds according to their chemical structure (Knudsen and Gershenzon, 2020). We then tested the effects of aridity at site of origin and irrigation on the concentration of the various VOCs in each group using a set of GLMs, with aridity, irrigation, compound identity, and all the two-way interactions among them as fixed factors (normal distribution and identity link). Analyses were conducted using jamovi's GamLj package (Version 3).

Finally, in the **third part**, we grouped all the relevant information from the previous two parts to analyze how changes in habitat conditions (site of origin and irrigation) affected plant performance and consequently plant-pollinator communication and its outcome as plant fitness. To answer this, we used structural equation modeling (SEM; Grace, 2006) to model the hierarchical relationships between habitat conditions, plant traits (physiology, metabolism and floral signals), pollinator services, and reproductive success (seed production and germination success). The a-priori model structure and a more thorough explanation of the method are detailed in supplementary material S6. All path coefficients (β) were standardized from −1–1 to enable comparison across paths. We chose SEM because it allowed us to simultaneously test multiple interconnected hypotheses about the causal pathways linking environmental conditions to plant performance and reproductive success. Unlike traditional statistical approaches that examine relationships in isolation, SEM enabled us to model the complex web of direct and indirect effects between physiological responses, floral traits, pollinator behavior, and fitness outcomes within a single analytical framework.

Model fit was evaluated using the χ^2 test, standardized root mean square residual (SRMR), and root mean square error of approximation (RMSEA). As the initial model provided a poor fit, we iteratively added biologically plausible paths based on modification indices (MI > 4) until no further paths with MI > 4 remained. Each additional path was tested for its impact on model fit using the χ^2 difference test.

The final model was selected based on these fit criteria and biological plausibility. Direct, indirect, and total effects were calculated using the standardized path coefficients (β), with bootstrapped standard errors and p-values used to assess the significance of each effect.

We ran a second SEM to test the hierarchical relationship between habitat conditions, flower signaling and attraction of specific pollinator groups to the plants. Full information and results for this model can be found in supplementary material S7. SEM analyses were conducted in R (Version 4.4) using the lavaan package.

3. Results

3.1. Physiological measurements

We measured 16 physiological traits in total (see supplementary material Table S2.1 for the full list). The PCA analysis, that provided a low dimensional representation of these traits, showed that the first two axes explained 78.20 % of the variance in total. The first axis that explained 54.48 % of the total variance was positively correlated to saturation vapor pressure, leaf temperature and vapor pressures and to intercellular CO_2, and negatively correlated to relative humidity, boundary layer conductance and assimilation (full results in supplementary material Table S2.2). The second axis that explained 23.77 % of the total variance was positively correlated with sensible heat flux, net thermal, transpiration, stomatal conductance, assimilation and the sum of energy balance components and negatively correlated with ambient CO_2 (full results in supplementary material Table S2.2 and Fig. S2.1).

Effects of site of origin and irrigation levels on physiological measurements: Neither aridity at the site of origin, irrigation, nor their interaction had a significant effect on the first physiology PCA axis (Table 1; Fig. 2A). Conversely, both aridity at the site of origin and irrigation had a negative significant effect on the second PCA axis (Table 1; Fig. 2B). Furthermore, their interaction was also significant, with the negative response along the aridity gradient being stronger in high irrigation relative to low irrigation treatments.

3.2. Primary metabolites

We measured the concentrations of five primary metabolites, including trehalose, maltose, sucrose, raffinose, and glycine. The PCA analysis showed that the first two axes explain 82.30 % of the variance in total. The first axis that explained 49.93 % of the variance was positively correlated with trehalose, maltose and glycine (full results in supplementary material Table S3.1). The second axis that explained 32.39 % of the variance was positively correlated with raffinose and sucrose (full results in supplementary material Table S3.1 and Fig. S3.1).

Effects of site of origin and irrigation levels on primary metabolites: both irrigation and aridity at the site of origin had significant positive effects on the first PCA axis (Table 1; Fig. 2C). None of the factors nor their interaction term had a significant effect on the second PCA axis (Table 1; Fig. 2D).
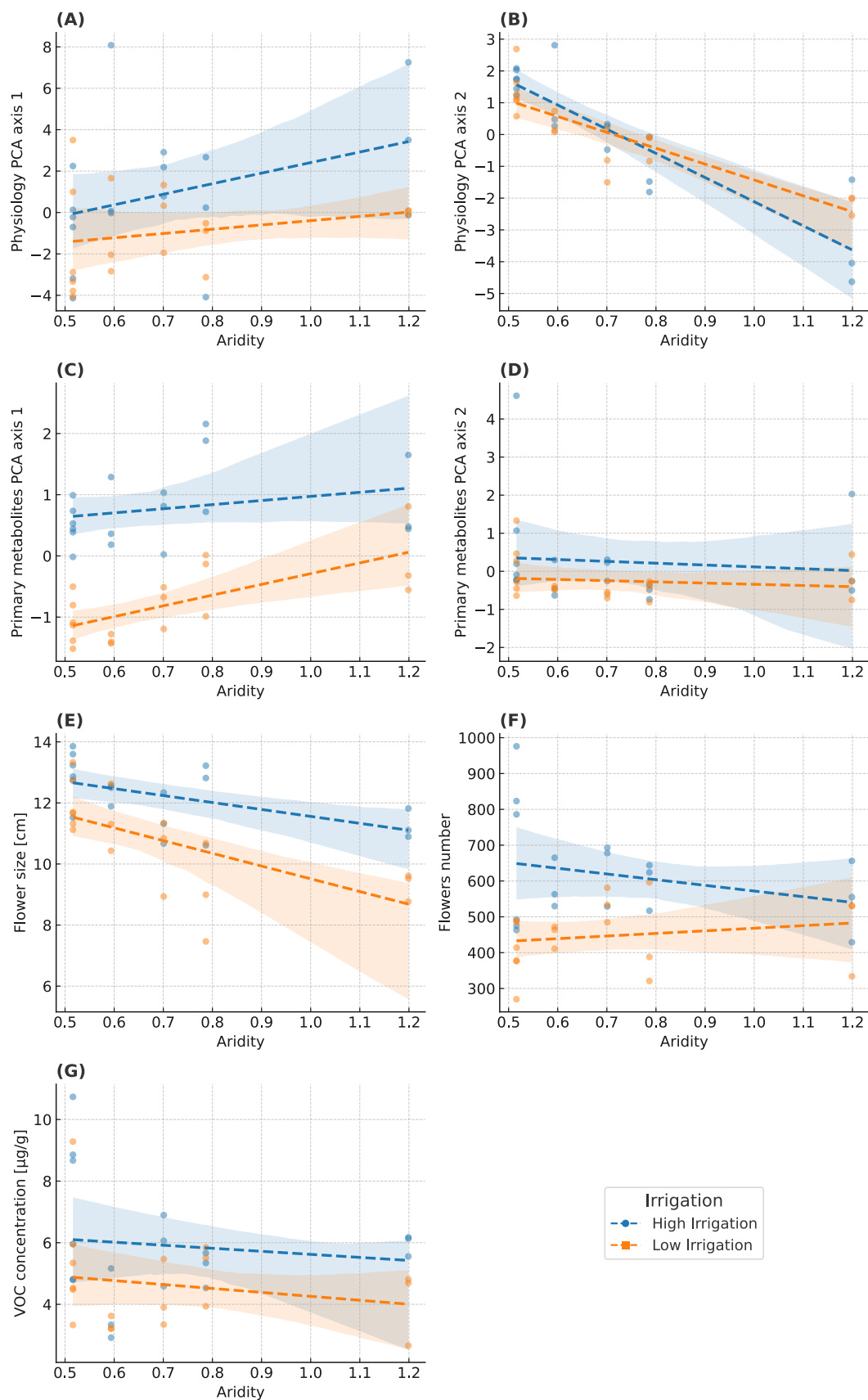
4. Floral signals

4.1. Visual signals

Effects of site of origin and irrigation levels: the two monitored visual signals – flower size and flower numbers – responded differently to habitat conditions. Both aridity at the site of origin and irrigation had

Table 1

GLM results for the effect of aridity at the site of origin and irrigation level on the plant performance (Physiology and primary metabolites) and floral signals (visual signals and total VOC concentrations) in *S. alba* plants. The analysis for physiological performance and primary metabolites was conducted on the first and second axes of PCA (see test for further information). **Bold** = P < 0.001; ** 0.001 <P < 0.01; * 0.01 <P < 0.05.

		Aridity		Irrigation		Aridity × Irrigation		$R^2_{(adj)}$
		$F_{(1, 32)}$	β±SE	$F_{(1, 32)}$	β±SE	$F_{(1, 32)}$	β±SE	
Physiology	PC1	3.55	3.59 ± 1.90	4.75*	−1.95 ± 0.90	0.64	−3.03 ± 3.80	0.15
	PC2	**114.25**	−6.30 ± 0.59	0.033	−0.05 ± 0.28	4.91*	2.61 ± 1.18	0.77
Primary metabolites	PC1	10.03**	1.21 ± 0.38	**75.31**	−1.57 ± 0.18	1.99	1.08 ± 0.77	0.71
	PC2	0.32	−0.40 ± 0.71	2.26	−0.50 ± 0.34	0.01	0.17 ± 1.42	0.08
Visual signals	Flower size	**18.57**	−3.22 ± 0.75	**18.35**	−1.51 ± 0.35	1.61	−1.90 ± 1.50	0.50
	Flowers #[&]	0.12	−0.05 ± 0.14	**22**	−0.32 ± 0.07	2.2	0.43 ± 0.29	0.40
Chemical signals	VOC concentration	0.81	−1.13 ± 1.26	14.77*	−1.28 ± 2.51	0.01	−0.29 ± 2.51	0.07

[&] Note that statistical estimator for number of flowers was χ^2, with 1 df.

Fig. 2. the effect of aridity at the site of origin and irrigation level on S. alba performance and floral signals. A. 1st physiological PCA axis; B. 2nd physiological PCA; C. 1st metabolic PCA axis; D. 2nd metabolic PCA; E. floral size; F. number of flowers per plant; F. Total VOC concentration. Dots represent the original values; lines and shaded areas represent the estimated trend of change and confidence intervals in relation to low and high irrigation respectively, based on the statistical models.

significant effects on flower size. Plants from more arid origins and those under low irrigation produced significantly smaller flowers (Table 1, Fig. 2E). In contrast, only irrigation affected flower numbers significantly, with plants under high irrigation producing more flowers (Table 1, Fig. 2F).

4.1.1. VOC

We identified 28 volatile organic compounds in the flowers of *S. alba* that can be classified into four chemical groups: benzenoids, terpenoids, alkanes, and green leaf volatiles (GLV). The full information can be found in supplementary material S4. The PCA analysis of these traits showed that the first two axes explained 50.80 % of the total variance. The first axis that explained 26.81 % of the variance was positively correlated to 15 volatiles, with strong positive correlation ($r > 0.75$) to Phenylacetaldehyde, m-Cresol, 2-Ethyl-1-hexanol, Methyl hexanoate, and negative correlation to Tridecane, Nonanal, and Hexadecane (full results in supplementary material S4). The second axis that explained 23.97 % of the total variance was positively correlated with 14 volatiles and had no significant negative correlations to any of the volatiles.

Effects of site of origin and irrigation levels on total VOC concentration: VOC composition varied substantially between populations and treatments as indicated by the PCA results. Nevertheless, the total VOC concentration was not significantly affected by aridity at the site of origin, irrigation, or their interaction (Table 1, Fig. 2 G).

Alkane compounds: We identified five alkane compounds: Hexadecane, Dodecane, Tetradecane, Tridecane, and Undecane. The total concentration of alkane compounds was higher under low irrigation, but individual compounds responded differently (Table 2, Supplementary table S5.1).

Specifically, Undecane increased in concentration under low irrigation, while Hexadecane and Tridecane decreased (Table 2, Supplementary table S5.5; Fig. 3 A,B). Additionally, significant interaction between compounds and aridity at the site of origin was also observed, driven by a significant increase in undecane concentration with increasing aridity (Fig. 3 A,B).

Benzenoid compounds: We identified six benzenoid compounds: Benzaldehyde, Ethylbenzene, Phenylacetaldehyde, Ethyl benzoate, Methyl benzoate, and m-Cresol. The total concentration of the compounds was higher under high irrigation, but individual compounds responded differently (Table 2, Supplementary Table S5.2).

Specifically, m-Cresol, Phenylacetaldehyde, and Ethyl benzoate showed a stronger increase in concentration with irrigation than Benzaldehyde and Methyl benzoate. No significant effect of aridity at the site of origin was detected for any of the compounds (Table 2, Supplementary table S5.5; Fig. 3C-D).

Terpenoid compounds: We identified nine terpenoid compounds: α-pinene, Caryophyllene, Citral., Geranylacetone, 1,6-Dimethylnaphthalene, α-Phellandrene, α-Humulene, β-Cyclocitral and Myrcene. The total concentration was higher under high irrigation, but individual compounds responded differently (Table 2, Supplementary Table S5.3).

Specifically, α-Humulene, α-Pinene and Myrcene increased in concentrations under high irrigation while the others compounds showed insignificant effects. As in the case of benzenoids, aridity at the site of origin did not show a significant effect on either of the compounds (Table 2, Supplementary table S5.5; Fig. 3E-F).

GLV compounds: We identified 8 GLV compounds: 2-Ethyl-1-hexanol, Decyl acetate, Dodecyl acetate, Methyl decanoate, Hexanal, Methyl hexanoate, Nonanal, and Pentanal. Similar to the alkanes, the total concentration of the compounds was higher under lower irrigation, but the individual compounds responded differently (Table 2, supplementary Table S5.4).

Specifically, Nonanal showed higher concentration under low irrigation while 2-Ethyl-1-hexanol and Methyl hexanoate showed lower concentrations (Table 2, Supplementary table S5.5;). Additionally, significant interaction between compounds and aridity at the site of origin was also observed, driven by decreased concentration of acetic acid decyl ester, acetic acid dodecyl ester and hexanoic acid methyl ester and an increased concentration of nonanal and decanoic acid methyl ester with increasing aridity (Fig. 3 G,H).

4.1.2. SEM

The initial model included 36 plausible paths, representing a complex array of direct and indirect effects of habitat conditions on plant performance and the pollination services they receive, and their consequences on plant reproductive success. The final model had a good fit to the data ($\chi^2_{32} = 31.14$, P = 0.51; SRMR = 0.09; RMSEA < 0.001; supplementary material S6), explaining 67 % of the variation in pollination services, 66 % of the variation measured in seed production and 28 % of the variation in germination successes. The model revealed three main pathways of effects: (1) direct environmental effects on plant traits, (2) trait-mediated effects on pollinator behavior, and (3) cascading effects on reproductive success.

As expected from our earlier analyses, environmental effects on plant performance of both aridity and irrigation directly influenced plant physiological and floral traits. Furthermore, plant trait effects on pollinator attraction were revealed by the model, demonstrating how strongly pollinators respond to multiple plant characteristics. The direct effects between aridity at the site of origin and irrigation on plant performance and floral signals reflected the results of the specific analyses presented above (Fig. 4; for full information see supplementary material S6). The model also revealed direct negative effects of the second physiological PCA axis ($\beta = -0.41$), the metabolic PCA axis ($\beta = -0.72$) and the second volatile PCA axis ($\beta = -0.41$) on pollinator visits to the plants. Number of flowers per plant ($\beta = 0.31$) and total VOC concentration ($\beta = 0.48$) had positive effects on pollinator visits. In addition, we found a negative direct effect ($\beta = -0.59$) of water scarcity on pollinator visits. Finally, the model revealed direct negative effects of the first physiological PCA axis ($\beta = -0.36$, number of flowers ($\beta = -0.44$) and the first volatile PCA axis ($\beta = -0.49$), and positive effects of pollinator visits ($\beta = 0.68$) on seed production. Seed germination success was directly negatively affected by the first physiological PCA axis ($\beta = -0.50$) and positively affected by the second physiological PCA axis ($\beta = 0.72$) and flower size ($\beta = 0.43$). Interestingly, the model also revealed a direct positive effect ($\beta = 0.86$) of the aridity at the site of origin on

Table 2

GLM results for the effect of aridity at the site of origin and irrigation level on compound concentrations in one of the four major groups of volatiles (alkanes, benzenoids, terpenoids, GLVs) in *S. alba* plants. **Bold** = P < 0.001; ** 0.001 <P < 0.01; * 0.01 <P < 0.05.

	Alkanes	Benzenoids	Terpenoids	GLVs
Aridity	$F_{(1,32)} = 2.02$	$F_{(1,32)} = 0.05$	$F_{(1,32)} = 3.02$	$F_{(1,32)} = 0.16$
Irrigation	$F_{(1,32)} = \mathbf{8.32}$	$F_{(1,32)} = 11.29**$	$F_{(1,32)} = 4.54**$	$F_{(1,32)} = 4.44**$
Compound	$F_{(4,132)} = 4.03**$	$F_{(5,165)} = 4.01**$	$F_{(8,261)} = \mathbf{4.79}$	$F_{(7,231)} = 2.85**$
Aridity × Irrigation	$F_{(1,32)} = 0.06$	$F_{(1,32)} = 0.04$	$F_{(1,32)} = 0.11$	$F_{(1,32)} = 0.36$
Aridity × Compound	$F_{(4,132)} = 3.65**$	$F_{(5,165)} = 1.40$	$F_{(8,261)} = 0.65$	$F_{(7,231)} = 2.84**$
Irrigation × Compound	$F_{(4,132)} = \mathbf{29.48}$	$F_{(5,165)} = 3.87**$	$F_{(8,261)} = \mathbf{5.88}$	$F_{(7,231)} = \mathbf{12.08}$
R^2(conditional)	0.60	0.46	0.35	0.41

* Satterthwaite method for degrees of freedom
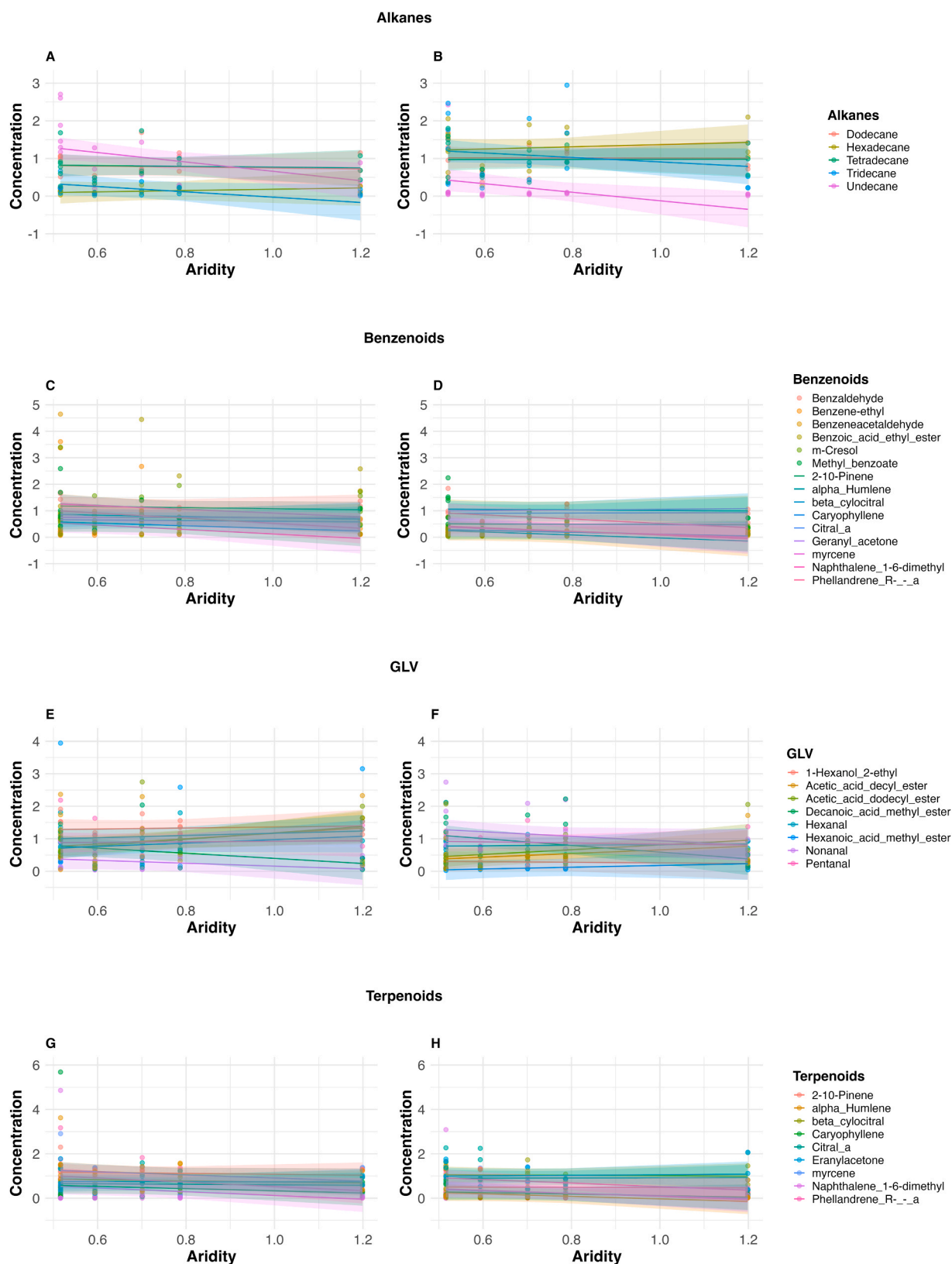
Fig. 3. the effect of aridity at the site of origin and irrigation level on VOC concentration of S. alba plants. A. alkane compounds under low irrigation treatment; B. alkane compounds under high irrigation treatment; C. benzenoid compounds under low irrigation treatment; B. benzenoid compounds under high irrigation treatment; E. terpenoid compounds under low irrigation treatment; F. terpenoid compounds under high irrigation treatment; G. GLV compounds under low irrigation treatment; H. GLV compounds under high irrigation treatment; dots represent the original values; colored lines and shaded area represent the estimated trend of change and confidence intervals in relation to each of the compounds in the group, based on the statistical models.
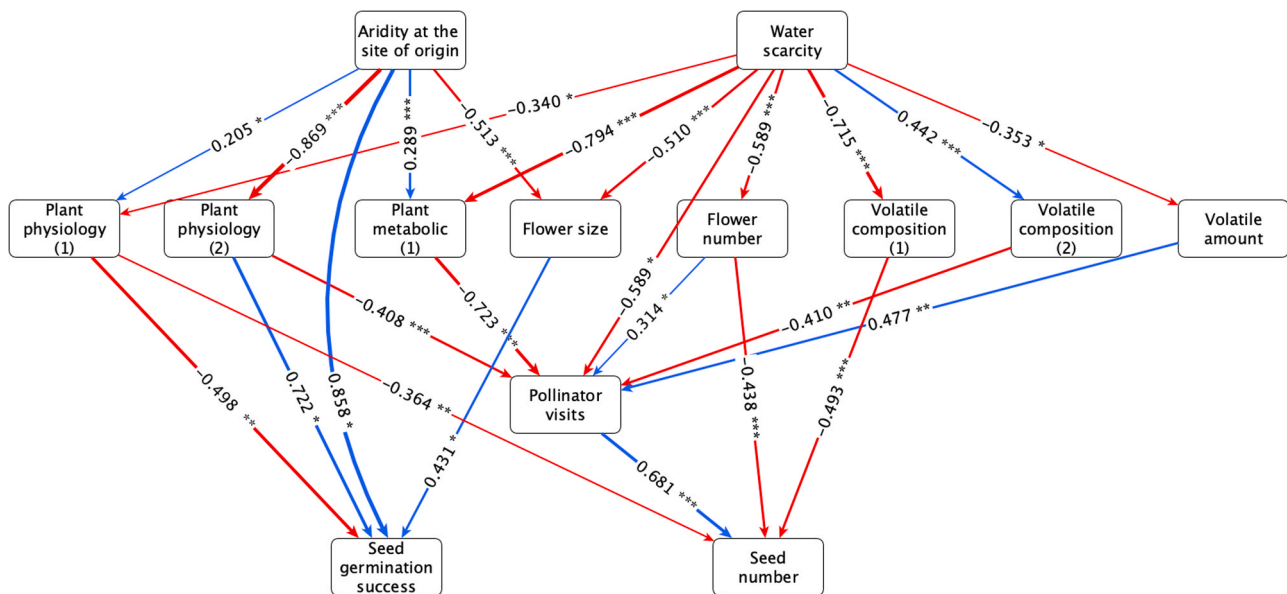
Fig. 4. a graphical representation of the direct statistically significant paths retained in the final SEM model. Standardized path coefficients and their level of significance are shown next to the arrows. Blue and red lines represent positive and negative effects respectively. Line widths are scaled based on the significant effect of the path. A full list of the coefficient values, including non-significant, indirect- and total- paths that were retained in the final model, is presented in supplementary material S6.1.

germination success.

In addition to the direct effects on seed production, the model detected three negative indirect effects: of the second physiological PCA axis ($\beta = -0.28$), the metabolic PCA axis ($\beta = -0.497$) and the second volatile PCA axis ($\beta = -0.28$), and two positive indirect effects: of number of flowers ($\beta = 0.21$) and volatile amount ($\beta = 0.31$). Seed germination success was indirectly affected only by the aridity at the site of origin ($\beta = -0.81$). For full information, see supplementary material S6.

5. Discussion

Most of the climate change scenarios indicate a significant alteration of rainfall patterns and increased frequency and severity of drought (IPCC, 2023). Such changes in water availability can affect plants and pollinators both directly and indirectly. While the changes can be subtle, plant intraspecific alternations may strongly affect pollinator preferences and change interactions patterns. In agricultural systems that rely on insect pollination, such changes could influence pollinator attraction and potentially affect crop productivity. Recognizing how environmental stress alters floral traits may help guide the selection of crop varieties that maintain pollinator visits under drier conditions, contributing to more stable yields as climate conditions become less predictable. Specifically, in our study we could show that 67 % of the variation in pollination services received by *S. alba* plants could be attributed to the combination of the effects of population adaptation to aridity and current water availability on the plants' floral signals. Moreover, these effects, together with the direct effects of water scarcity on the plant physiological responses, could explain 66 % of the variance in the plants' fitness, as manifested in their seed production.

The multivariate analysis that summarized population differences and direct effects of water availability indicated key differences in plant physiology and primary metabolites, depending on aridity at the site of origin and immediate water availability. Specifically, the first PCA axis can be linked with increased transpiration demands and decrease photosynthetic efficiency, which may be associated with increase water stress (Lavergne et al., 2020; e.g. Li et al., 2019). In contrast, the second axis can be linked with temperature regulation and photosynthetic activity, which may be associated with *S. alba* ability to continue

physiological activity in harsh conditions (e.g. Seleiman et al., 2021). Additionally, all three components that were positively linked with the first metabolic PCA axis were related to metabolic adjustments and osmoregulation during water stress (Lozano-Elena et al., 2022; e.g. Lunn et al., 2014; Seleiman et al., 2021).

Using the values derived from the multivariate analyses, we examined the direct effects of water availability on the performance of *S. alba* in relation to aridity at the site of origin as an indicator to its potential adaptation to drought conditions and water stress. However, it is important to note that terms such as 'water stress' and 'drought' are imprecise, referring to a broad range of ecological conditions where water availability is significantly below average (Slette et al., 2019). The specific impacts of these conditions vary depending on species' characteristics and the interplay of water availability with the local environment conditions (Verslues et al., 2006). In our experiment the results confirmed the prediction that immediate water scarcity negatively affected plant performance, with some evidence suggesting that populations from more arid sites responded more efficiently to water availability. These results support the general hypothesis that plants in arid and semi-arid regions are well-adapted to these conditions, enabling them to tolerate and flexibly respond to fluctuation in water availability (e.g. Krintza et al., 2024; Lázaro-Nogal et al., 2015).

Our results further demonstrated a significant effect of environmental conditions, particularly water availability, on the floral signals of *S. Alba*. As expected, aridity at the site of origin affected flower size, suggesting that the species are locally adapted (e.g. Rering et al., 2020). Additionally, immediate water limitation significantly affected all tested floral signals, supporting previous studies on the topic (e.g. Burkle and Runyon, 2016; Descamps et al., 2021; Höfer et al., 2023).

Interestingly, while visual signals diminished under water stress, the effects on floral scent were more complex. Specifically, our results showed that the concentration of benzenoids and terpenes decreased under water stress. These findings, particularly regarding the benzenoid group, are expected as many of these compounds – such as benzene acetaldehyde – are primarily produced for communication, especially with pollinators (Dötterl and Gershenzon, 2023). It is therefore not surprising that under stress the plant limits the production of these compounds, redirecting energy toward compounds that are either directly involved in the plant's response to dry conditions, or indirectly

produced during these processes (Jogawat et al., 2021).

A clear response of volatiles to water availability was also observed for alkanes and GLVs. These two groups showed an overall increase in their concentrations under immediate water limitation, aligned with previous studies that often reported increased emissions of these compound groups as part of the plant's response to both biotic and abiotic stress (Abbas et al., 2022; Engelberth, 2024). Specifically, under limited water availability, alkanes have been shown to be associated with increased oxidative stress induced by the dry and warmer conditions (Abbas et al., 2022; Rinnan et al., 2014). Notably, the dominant alkane compound detected in our study was undecane, a compound that is well known for its role in insect herbivory (Hajdu et al., 2024; Najar-Rodriguez et al., 2015) where it appears to be used by insects as an indicator of the plant's water status (Pagadala Damodaram et al., 2021).

GLVs have been shown to serve both as priming mechanisms and as direct contributors to a wide range of protective activities, including antioxidant functions, photosynthesis, and water storage (Engelberth, 2024). Interestingly, the dominant GLV compound that increased under dry conditions in our study was nonanal. This contrasts with previous findings that reported higher concentration of nonanal under conditions of increased water availability (e.g. de Manincor et al., 2022; Vallat et al., 2005).

The divergence between our findings and previous studies extends to the terpene group. Previous works have suggested that the volatile emissions of this group are generally more resilient to dry conditions, with many compounds even being enhanced under stress (Jogawat et al., 2021; Rinnan et al., 2014). However, our observations primarily showed a reduction in compound emissions under dry conditions. The differences may be linked to the remarkable diversity of terpenes as secondary metabolites in plants (Abbas et al., 2022). Interestingly, despite this diversity, our study identified some compounds that are widely shared across plant species such as myrcene (Dötterl and Gershenzon, 2023). However, even among these common compounds divergent patterns were detected. For example, α pinene exhibited an opposite trend in previous studies compared to our findings (Campbell et al., 2019). Furthermore, even when comparing our work to Höffer et al. (2022), who studied the same species but in a domesticated strain, we identified differences in the scent profile in relation to water availability. The divergence in quantitative and qualitative measurements between our study and previous ones highlights the limited understanding we currently have on volatile compounds, and on the mechanisms governing their biosynthesis, emphasizing how far we are from drawing general conclusions on the subject (Dötterl and Gershenzon, 2023).

As expected, pollination services in our study were significantly affected by the plants' physiological status and their floral signals (e.g. Burkle and Runyon, 2016; Rose-Person et al., 2024; Salman et al., 2022). Specifically, we observed that the number of flowers and total VOC concentration positively affected the number of visiting pollinators, a relationship well documented in the literature (e.g. Dötterl and Gershenzon, 2023; Seifan et al., 2014). In addition, changes in volatile composition between populations and irrigation treatments altered the preferences of the dominant pollinator groups (see supplementary material S7).

Interestingly, these findings contradict earlier studies suggesting that plants exposed to limited water availability during their growing phase, particularly before flowering (as in our study), can adjust their physiological responses and maintain scent emission (see Höfer et al., 2022, 2021; Kuppler and Kotowska, 2021). Moreover, contrary to our initial prediction, we found no evidence that populations originating from more arid sites were more attractive to local pollinators in the south. Similarly, our results did not support the general expectation that self-incompatible species, such as *S. alba*, that depend solely on external pollination services, would exhibit greater resilience to environmental changes and maintain consistent floral signals (Höfer et al., 2022). Instead, pollinators in our experiment predominantly preferred better

irrigated plants regardless of their origin. This preference likely arose from two interacting factors: the direct negative effect of low irrigation on floral signals and physiological condition, and a stronger attraction of pollinators to plots with higher irrigation, possibly due to the milder microclimate in them.

The strong effects of water availability on plant physiology and its subsequent impact on pollinator services was clearly reflected in the plant fitness, as indicated by seed production. This relationship was driven by the positive effects of both flower numbers and total VOC concentration on seed numbers. As expected, the germination probability of the produced seeds was mainly affected by the physiological condition of the plants (e.g. Höfer et al., 2023). Interestingly, we observed clear evidence of inter-population differences in germination success, with seeds from plants originating in more arid sites showing higher germination rates. However, this advantage was offset by a significant negative indirect effect of aridity at the site of origin, which negatively influenced overall plant performance and, consequently, seeds quality. The mechanisms identified here are likely to apply to other water-limited agricultural systems, particularly in regions where changing precipitation patterns threaten both wild and crop plant reproductive success.

In conclusion, cultivating diverse and productive crop species is essential for human well-being. Crop productivity, and particularly fruit set, has been consistently shown to correlate positively with insect flower visitations (Garibaldi et al., 2014). Moreover, several studies have demonstrated that the contribution of wild insects is essential for effective pollination services to crops, and that managed pollinators, such as honeybees, are insufficient to meet this need (Garibaldi et al., 2014; Woodcock et al., 2019). Given that agroecosystems (e.g. Semeraro et al., 2023) and pollinator communities (e.g. Gérard et al., 2020) are both highly sensitive to climate change, it is crucial to understand the outcome of such changes and the mechanisms driving species' responses to secure global food provision. This is particularly important considering the consistent evidence indicating negative pollinator responses to drought (Nicholson and Egan, 2020), one of the major consequences of climate change (Grünzweig et al., 2022).

Brassicaceae species are among the dominant crops worldwide (Castillo-Lorenzo et al., 2024). Crops of this family are particularly dependent on effective pollination services, showing increased seed yield and seed number when insect-pollinated (Badenes-Pérez, 2022). *Sinapis alba* is a common crop within this family, with broad agronomic usage (Akter and Klečka, 2022; Castillo-Lorenzo et al., 2024). Its well-documented resistance to pathogens, bioactive glucosinolate content and capacity for biofumigation contribute to pest suppression and soil health in agroecosystems (Borek and Morra, 2005). These traits, combined with the species' demonstrated tolerance to drought, position *S. alba* as a valuable component of sustainable agriculture. This study was designed to examine population-level responses of *S. alba* to water availability under controlled conditions, and the common garden setup was essential to minimize environmental variation and allow meaningful comparisons across populations. While we recognize that such designs cannot capture the full complexity of natural environments, they are widely used and recommended for assessing environmental responses in plants (Schwinning et al., 2022). Our goal was not to replicate natural ecosystems, but to understand how aridity at the site of origin and current water availability interact to influence floral traits and pollination services and eventually shape plant productivity. In accordance, our findings on the potential effects of even subtle variations in water availability – whether in the present (irrigation level) or even in the past (as reflected, by aridity at the site of origin) – on changes in floral traits and pollination success add a new layer to this understanding. Taken together, the findings suggest that *S. alba* is a relatively resilient species in the face of the expected climatic changes.

However, the results also reveal significant gaps in our understanding of how water availability and other climate-related stressors affect plant-pollinator systems. The complexity and discrepancies between our

findings and those of previous studies highlight that floral signals, especially volatile emission, are highly context-dependent, modulated by the specific environmental conditions and community interactions. These findings have direct implications for agroecosystems, where climate-induced disruption of plant-pollinator interactions could compromise crop yield and quality in water-limited environments. Addressing these challenges requires further research to unravel the nuanced interplay between environmental factors and biological responses, advancing toward a comprehensive framework to mitigate the potential impacts of climate change on plant-pollinator systems.

CRediT authorship contribution statement

Vered Tzin: Resources, Conceptualization, Writing – review & editing, Methodology. **Efrat Dener:** Visualization, Writing – review & editing, Formal analysis. **Merav Seifan:** Writing – original draft, Resources, Methodology, Conceptualization, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Ibrahim N.A. Salman:** Writing – original draft, Investigation, Methodology, Data curation.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT 4o for initial English editing. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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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 work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109855.

Data availability

Data will be made available on request.

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