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Effect of soil water deficit on flowers and plant-pollinator interactions of two blueberry cultivars

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Abstract

Pollination is a key ecosystem service currently threatened by multiple environmental pressures, including climate change. Drought increases plant physiological stress, reducing the resources available for reproduction and potentially affecting flower traits, mutualistic interactions and fruit production. In blueberry, previous studies have shown that post-harvest drought can reduce flower production in the following year, but its effects on plant-pollinator interactions and fruit set remain poorly understood. Here, we investigated how low water availability influences flower display size, volatile emissions, and nectar rewards, and how these potential changes affect pollinator behavior and fruit production in two insect-dependent blueberry cultivars ('Bluecrop' and 'Duke'). Starting at bud break and continuing throughout flowering, half of the plants of each cultivar were exposed to controlled water deficit, while the remaining plants were well-watered. Overall, our results demonstrate that northern highbush cultivars 'Bluecrop' and 'Duke' differ in several floral traits, yet no significant interaction between cultivar and water treatment was detected, indicating that the response to water deficit was not cultivar dependent. In both cultivars, water deficit reduced nectar production, which likely decreased visitation rates by floral visitors, leading to a decline in fruit set. The solitary bee Anthophora plumipes accounted for the vast majority of visits and showed a preference for control flowers. Our results show that water deficit may influence floral traits linked with pollinator attraction and fidelity and, subsequently, impact the floral visitor behavior and fitness of highbush blueberry.

Keywords Climate change · Crops · Floral scent, floral rewards · Flower traits, pollination services

Introduction

Around 88% of angiosperms and more than 75% of crop species are pollinated by animals (Klein et al. 2007; Ollerton 2021). Both wild and cultivated plants advertise their flowers to animal pollinators through signals such as flower size and scent emissions, while offering rewards like nectar and pollen that encourage visitation and promote pollinator fidelity (Parachnowitsch et al. 2019). However, floral traits such as size, morphology, nectar quantity and quality, and scent emissions respond differently to environmental drivers, which often interact in complex and non-linear ways (Kuppler and Kotowska 2021; Plos et al. 2023; Day Briggs and Anderson 2024). Moreover, the response of these traits to environmental conditions can vary not only among species but also among cultivars of the same crop (Borghi et al. 2019; Höfer et al. 2022). Yet, the links between floral trait responses and pollinator behavior remain poorly understood (Höfer et al. 2021). Understanding how environmental stresses, such as reduced water availability, affect floral traits could provide key insights into their consequences for pollination and fruit production, especially under current climate change scenarios.

Floral scent, composed of volatile organic compounds (VOCs), varies across species and cultivars, influencing pollinator behavior (Rodriguez-Saona et al. 2011; Klatt et al. 2013). For example, Klatt et al. (2013) found that three

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strawberry cultivars emitted the same compounds but in different quantities, which was associated with distinct foraging preferences of *Osmia bicornis*. Similarly, Rodriguez-Saona et al. (2011) reported that although total volatile emissions were similar among blueberry cultivars, the relative emission of specific compounds, such as esters and terpenoids, differed significantly. Importantly, higher volatile emissions were linked to increased bee visitation, highlighting the ecological relevance of cultivar-specific scent profiles.

Floral scent emissions can be strongly influenced by environmental conditions, including temperature and water availability (Burkle and Runyon 2016; Gallagher and Campbell 2017; Glenny et al. 2018; Cordeiro and Dötterl 2023a). These effects may arise from the up- or down-regulation of biochemical pathways (Borghi et al. 2019) and are often species- or cultivar-specific, resulting in variable impacts on pollinator interactions. Some studies have shown that environmental stress alters both the total VOC emissions and the composition of floral volatiles in wild and crop species, with these changes being accompanied by shifts in pollinator visitation patterns (Gallagher and Campbell 2017; Glenny et al. 2018; Rering et al. 2020). Conversely, other studies report no detectable effects of environmental conditions on scent emission (Barman et al. 2024), or they report species-specific responses (Burkle and Runyon 2016; Höfer et al. 2021). Nevertheless, floral visitors are highly sensitive to both qualitative and quantitative differences in floral scents, often responding even to subtle intraspecific variations (Schiestl and Dötterl 2012; Vega-Polanco et al. 2023). Thus, changes in scent composition and/or quantity can influence plant–pollinator interactions and ultimately affect crop production, underscoring the need to better understand these linkages (Knauer and Schiestl 2015; Höfer et al. 2021).

Nectar, pollen, and floral morphology are also key determinants of flower handling time and pollinator efficiency (Parachnowitsch et al. 2019). Environmental stresses, such as water deficit, can alter reward availability and thereby affect the behavior, preferences, and fidelity of insect pollinators (Klatt et al. 2013), indirectly influencing fruit production. However, relatively few studies have addressed how pollinators respond to changes in floral morphology and rewards caused by water stress. Existing results are mixed: some studies report no effect on pollinator visitation (Glenny et al. 2018), while others show significant decreases (Descamps et al. 2018; Rering et al. 2020; Barman et al. 2024), with responses often depending on the pollinator species involved (Burkle and Runyon 2016; Kuppler and Kotowska 2021). For floral morphology, water stress appears to consistently exert negative effects, likely reflecting resource allocation trade-offs under limited water availability (Kuppler and Kotowska 2021). By contrast, the effects of water stress on nectar production are less consistent and seem to be species-dependent, possibly reflecting adaptive responses to drought (Phillips et al. 2018). For instance, reported effects on nectar quantity and sugar content range from significant reductions to no measurable change, depending on the species studied (Descamps et al. 2018, 2020; Phillips et al. 2018; Rering et al. 2020; Barman et al. 2024; Brandes and Beyer 2025).

Highbush blueberry (*Vaccinium* spp.) is a pollinator-dependent crop of increasing economic importance (Eeraerts et al. 2023; Siopa et al. 2025). Its inflorescences are composed of multiple single flowers arranged around a central stem. Each flower bears functional female and male organs enclosed within a pendulous urceolate corolla formed by fused petals that end in a narrow aperture. The corolla morphology, namely the length, and width and throat diameter, can vary across blueberry cultivars, with implications on pollinator behavior (Courcelles et al. 2013; DeVetter et al. 2022). An earlier study comparing blueberry cultivars showed that ‘Duke’ displayed wider corollas and had more visits from honeybees, while ‘Bluecrop’, which displayed narrower corollas had fewer visits and an increased incidence of nectar robbing (Courcelles et al. 2013). The pistil is typically concealed within the corolla, with the stigma generally non-exserted, although this is variable among cultivars (Vander Kloet 1988; DeVetter et al. 2022). Stamens are generally shorter than the pistil, resulting in substantial stigma–anther separation, which may also differ among cultivars (Cromie et al. 2024). The poricidal anthers release pollen more efficiently under buzz pollination, although some passive pollen release occurs (Vander Kloet 1988). Flowers produce nectar in nectaries located at the base of the corolla. Consequently, the floral morphology and downward-facing orientation make rewards relatively difficult to access, influencing pollinator behavior and plant-pollinator interactions (Courcelles et al. 2013; Cromie et al. 2024). Additionally, emission rates of volatile compounds were shown to differ significantly among cultivars (Rodriguez-Saona et al. 2011), and volatile emissions have been shown to impact pollinator attraction in multiple species (e.g. Vega-Pollanco et al. 2023). Yet, the impact of water stress on floral traits or nectar production and the cascading effects on plant-pollinator interactions remain unclear.

In this study, we aimed to assess whether soil water deficit influences insect visitor diversity, behavior, and visitation rates through changes in floral morphology, scent emission, and nectar production. We hypothesized that these traits may respond differently to environmental stress in different cultivars, potentially leading to distinct plant-pollinator interaction patterns. To test this, we used two highbush blueberry cultivars to evaluate potential cultivar-specific responses to water deficit. Specifically, we examined: (1) the effects of soil water deficit on floral morphology, nectar production, and scent emission; (2) how these changes influence the behavior and visitation patterns of insect pollinators; and (3) the subsequent impacts on fruit production.

Methods

Experimental design

Two commonly planted cultivars of northern highbush blueberry (*Vaccinium corymbosum* L., Ericaceae; Eeraerts et al. 2024) with overlapping flowering times, 'Duke' and 'Bluecrop'(Supplementary Fig. 1), were acquired at a blueberry plant nursery (Mirtilusa; Sever do Vouga, Portugal) in 2021. The two-years old plants were transferred to 6 L pots filled with commercial blueberry substrate (pine bark mulch and peat moss, pH 4.5–5.0, > 70% organic matter, enriched with NPK 17-9-11; Siro, Mira, Portugal), about a year prior to the beginning of the experiment, and randomly placed outdoors at the Botanical Garden of the University of Coimbra (Supplementary Fig. 2). During this time the plants were watered twice a week and the mean temperature averaged 18 °C ranging from 8.5 °C in winter and 37 °C in summer (values from Coimbra meteorologic station of the Instituto Português do Mar e da Atmosfera).

A total of 48 three-year-old plants (24 per cultivar) were used for the experiment. From floral bud break through the flowering period (23 February to 5 May 2022), half of the plants of each cultivar were subjected to moderate water deficit (33% of field capacity), while the remaining plants were kept well-watered (≥80% of field capacity). Soil water content was monitored by weighing the pots twice a week, using a scale, and rewetting them to maintain the target levels (see Supplementary material for more detailed description). Weeds were cleaned regularly to avoid effects of weeds on water availability and no pruning, or pest management was required. Mean daily temperatures during the experimental period ranged from 13 °C to 18 °C (values from Coimbra meteorologic station of the Instituto Português do Mar e da Atmosfera). To prevent rainfall from confounding the drought treatment, stressed plants were sheltered under a hollow iron structure covered with transparent plastic whenever precipitation was forecast (plants were caged only on rainy days; see Supplementary material for more detail; Supplementary Fig. 3). While the temperatures inside the cage were not recorded, whenever possible during these rainy days, care was taken to open the cage on the sides to allow air circulation and avoid subjecting the plants to increases in temperature.

At peak flowering, one leaf per individual plant was hand-collected in the morning to determine relative water content (RWC) as an indicator of plant water status. RWC (%) was calculated as: RWC (%) = (fresh weight – dry weight) / (turgid weight – dry weight) ×100 (Brito et al. 2018). Fresh weight was recorded immediately after leaf collection. Leaves were then placed in 15 mL tubes (Delta Lab) filled with water and kept overnight at 4 °C in the dark to obtain turgid weight, which was measured after removing the excess water from the leaf surface with a paper towel. Finally, dry weight was determined after oven-drying leaves at 40 °C for seven days (Brito et al. 2018). Weight (mg), at all stages, was taken using a microscale (Kern, 0.1–100 g).

Flower morphology and rewards

For all 48 plants, the second open flower from the tip was collected from one to two inflorescences per plant for morphological measurements, following the methodology described by (Courcelles et al. 2013). As blueberry flowers are urn-shaped, we measured variables capturing shape variation which include corolla length, corolla diameter at the widest point, and corolla throat diameter (from now on corolla opening). All measurements were taken immediately after collection, using a digital caliper (Toolland, 150 mm, resolution 0.01 mm).

Nectar volume was quantified in the morning (between 9:00 and 12:00 CET + 1) to minimize daily variation, which is known to occur in highbush blueberries due to evapotranspiration (Brewer and Dobson, 1969). Inflorescences were bagged with white mesh tulle bags the evening before sampling to allow nectar accumulation overnight and prevent nectar removal by early morning floral visitors. Nectar was extracted from one to four fully open flowers per plant using 2 µL microcapillaries, following Dafni et al. (2005). Briefly, young flowers were selected, and nectar was extracted by inserting a microcapillary tube into the corolla until extraction was complete; in some flowers, more than one microcapillary was needed to collect the full volume. To minimize the effect of time or day, individuals from each cultivar and water treatment were sampled alternated, so that all treatments and cultivars were represented throughout the nectar collection period. Sugar content (°Brix, in %) was measured with a handheld refractometer (Eclipse 0–50 °Brix). Nectar could not be collected from all plants and the sample size for nectar volume was $N = 32$. Some of the sampled flowers contained no nectar and the sample size for sugar content was $N = 25$.

Flower volatiles collection and analysis

Floral volatiles were collected from one inflorescence per plant. Collection was not possible for all plants hence, 8 plants per treatment and cultivar were sampled, excep for 'Bluecrop' controls (7 plants, totaling 31 samples) between

9:30 and 16:30 (CET + 1) from 4 to 6 April and on 19–20 April 2022 using the dynamic headspace method (Barman et al. 2024; Dötterl et al., 2006). Samples were collected alternating between different cultivars and treatments to minimize impacts of hour and date. To ensure that the flowers used for floral volatiles' collection were not visited by insects prior to collection, which could influence volatile emissions (Rodriguez-Saona et al. 2011), inflorescences were bagged with white mesh tulle bags prior to flower opening. Each inflorescence, attached to the plant and consisting of 2–6 flowers, was enclosed in a polyethylene oven bag after having removed the tulle bags (Toppits®, Minden, Germany; 15.5 × 7.5 cm). A small slit was made at one upper corner of the bag to insert an adsorbent tube (25 mm quartz glass cylinder, 2 mm diameter) packed with 3 mg of a 1:1 mixture of Tenax-TA (60–80 mesh, Supelco, Merck KGaA, Darmstadt, Germany) and Carbotrap B (20–40 mesh, Supelco). A rotary vane membrane pump (G12/01 EB; Rietschle Thomas Inc., Puchheim, Germany) maintained a constant flow rate of 200 mL·min^{-1} for 30 min to trap volatiles. Using the same headspace method, VOCs from ambient air and nearby leaves were collected, serving as negative controls to account for contamination and non-floral emissions ($N = 5$).

Volatiles were analysed using automated thermal desorption (TD) (TD-20, Shimadzu, Japan) coupled to GC–MS (QP2010 Ultra EI, Shimadzu, Japan) equipped with a ZB-5 fused silica column (5% phenyl polysiloxane; 60 m length, 0.25 mm inner diameter, 0.25 µm film thickness). Compounds were identified by comparing retention indices and mass spectra against reference libraries (NIST 11, Wiley 9, Essential Oils, FFNSC 2, Adams 2007) and confirmed, where possible, using authentic synthetic standards available at the Plant Ecology Lab, University of Salzburg.

A custom in-house spectral library of blueberry floral scents was constructed to enable semi-automated peak detection and integration based on selected representative chromatograms in the LabSolutions GCMS Postrun Analysis software (version 4.50; Shimadzu Corporation, Kyoto, Japan). Given that scent samples were collected from inflorescences comprising 2–6 flowers, the chromatographic peak areas were divided by the number of flowers per inflorescence to derive a per-flower peak area. An estimation of total floral scent emission per flower (ng) was obtained by summing the peak areas of all identified compounds and converting the resulting total ion count (TIC) into nanograms using the mean TIC (total ion current) of standard compounds (benzaldehyde, (Z)-3-hexenyl acetate, linalool) added in known amounts (100 ng each) to adsorbent traps following Barman et al. (2024).

Pollinator's observation

Pollinator activity was monitored during flowering under sunny conditions with mean temperatures of 15 °C, ranging from 10 to 21 °C, following standard protocols (Dafni et al. 2005). Briefly, floral visits were recorded in 10-minute sessions conducted at different times of day (09:00–17:00 CET + 1), across multiple days (7 days between 1 and 20 April 2022), totaling 11 h 20 min of net observation (68 monitoring moments).

Plants were randomly arranged into four groups of 12 plants, each with three individuals from each cultivar and treatment. Plants were spaced approximately 30 cm apart, with around 50 cm between groups. Pots were rotated twice per day to avoid bias in insect visitors. During each 10-minutes session, the observer monitored one group at a time, sequentially rotating among the four groups. A visit was counted whenever an insect inserted its proboscis, head or both into the corolla. For each monitoring moment, we recorded: (i) the identity of the visitors (species level whenever possible), (ii) treatment and cultivar visited, and (iii) number of flowers visited per plant per visitor species. The number of open flowers per plant was also recorded for each treatment and cultivar. Visitors were photographed and their identification confirmed by an entomologist. Visitation rates (%) were calculated as: Visitation rates (%) = (total number of flowers visited per plant per monitoring moment/number of flowers open per plant per monitoring moment) ×100.

We calculated a floral preference index for the main pollinator species [*Anthophora plumipes* (Fabricius, 1781)], excluding visits involving fewer than three visited flowers to avoid noise and data biases due to low frequency interactions (Dafni et al. 2005; De Aguiar et al. 2019; Castro et al. 2020). To test the preference for plants under control conditions over plants under water deficit conditions, the index was calculated as the ratio between the number of visits to plants under control conditions (overall or within each cultivar; $N = 63$) and the total number of visits. Values near 0 indicate preference for stressed plants and values near 1 indicate preference for control plants. To test the preference for plants of cultivar 'Duke' over 'Bluecrop', the index was calculated as the ratio between the number of visits to plants of cultivar 'Duke' and the total number of visits ($N = 63$). Values near 0 indicate preference 'Bluecrop', and values near 1 indicate preference for 'Duke'. In all cases values of 0.5 indicate no preference.

Fruit set

Fruit set was calculated as the ratio between the number of fruits produced per inflorescence, following open pollination, and the initial number of flowers. Three inflorescences per plant were randomly selected on different sides of the plant and marked with color threads. The number of flowers per inflorescence was recorded during flowering, and the number of developed fruits was counted four weeks after corolla drop (Retamales and Hancock 2018). Fruit set (%) was calculated as: Fruit set (%) = (Number of fruits per inflorescence/Number of flowers per inflorescence) × 100.

Data analysis

All analyses were conducted in R version 3.3.2 (Core Development Team 2016). To test the effect of treatment (control and water deficit), cultivar ('Bluecrop' and 'Duke') and their interaction on RWC, flower morphological traits (corolla length, corolla width and corolla opening), nectar volume and sugar content, total volatile emissions, and fruit set, we used general linear models (GLMs). For that, RWC, corolla length, corolla width, corolla opening, nectar volume, nectar sugar content, total volatile emissions, or fruit set was defined as dependent variable and treatment (control and water deficit), cultivar ('Bluecrop' and 'Duke') and their interaction as fixed factors. Visitation rates were analyzed using a beta regression model with logit link (package *betareg* in R), as variance heterogeneity could not be resolved through data transformation, with visitation rates as dependent variable and treatment (control and water deficit), cultivar ('Bluecrop' and 'Duke') and their interaction as fixed factors. We assessed model fit using the diagnostic plots of the DHARMa package (Hartig 2016). When appropriate, pos-hoc comparisons were done using emmeans package (Lenth 2016). Plots were done using ggplot2 (Wickham et al. 2024). Differences in floral scent composition were assessed using PERMANOVA (10,000 permutations) based on Bray–Curtis similarities of square-root transformed relative scent data (PRIMER 7; Clarke and Gorley 2015). Canonical analysis of principal coordinates (CAP) was used to visualise clustering patterns by treatment. As PERMANOVA detected significant differences only between cultivars, SIMPER analyses were performed to identify the compounds contributing most to dissimilarities between 'Duke' and 'Bluecrop'. The relative amounts of the top compounds (together explaining ~ 50% of the variance: 2-nonanone, (*Z*)-3-hexenyl acetate, (*Z*)-3-hexen-1-ol, (*E*)-2-hexenyl acetate, (*E*)-cinnamaldehyde, (*E*)-cinnamyl alcohol, 2-aminobenzaldehyde) were further tested for significant cultivar effects using GLMs. The floral preference index was analysed as the deviation from the expected random value of 0.5 using one-sample t-tests. Statistical significance was set at $P < 0.05$.

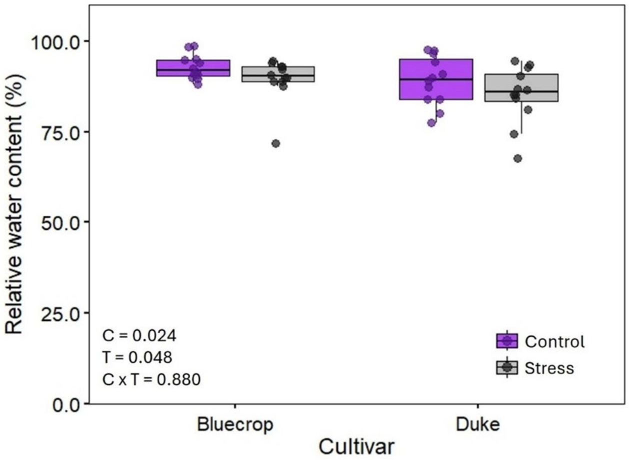


Fig. 1 Box plot of relative water content (RWC; %) of leaves from the blueberry cultivars 'Bluecrop' and 'Duke' under control and water stress conditions. P-values from GLM analyses are shown for the effects of cultivar (C), treatment (T) and their interaction (C × T)

Table 1 Results from general linear models (GLMs) testing the effects of cultivar (C), treatment (T), and their interaction (C × T) on floral morphological traits, nectar volume, sugar content, floral scent emission, visitation rates, and fruit set

RWC	*N*	Cultivar (C)	Treatment (T)	C x T
	48	X_1= 5.11, **p=0.024**	X_1= 3.91, **p=0.048**	X_1= 0.04, p=0.880
Corolla length	48	X_1= 7.24, **p=0.007**	X_1= 3.48, p=0.062	X_1= 0.01, p=0.929
Corolla width	48	X_1= 19.28, **p<0.001**	X_1= 3.51, p=0.061	X_1= 0.15, p=0.699
Corolla opening	48	X_1= 20.23, **p<0.001**	X_1= 1.70, p=0.193	X_1= 0.13, p=0.720
Nectar volume	32	X_1= 5.14, **p=0.023**	X_1= 5.63, **p=0.018**	X_1= 3.04, p=0.081
Nectar sugar content	25	X_1= 0.01, p=0.916	X_1= 2.28, p=0.131	X_1= 3.22, p=0.073
Total VOCs	31	X_1= 2.36, p=0.125	X_1= 0.21, p=0.651	X_1= 0.02, p=0.888
Visitation rates	68	X_1= 0.01, p=0.926	X_1= 8.76, **p=0.003**	X_1= 1.46, p=0.227
Fruit set	48	X_1= 0.61, p=0.452	X_1= 5.90, **p=0.015**	X_1= 1.61, p=0.204

Significant P-values ($P < 0.05$) are highlighted in bold, and the sample size (N) is indicated

Results

Relative water content (RWC)

In both 'Bluecrop' and 'Duke' cultivars, RWC was lower in plants subjected to water deficit compared to control plants (X_1= 3.91, p=0.048), with overall RWC being slightly lower in 'Duke' than in 'Bluecrop' (X_1= 5.11, p=0.024; Fig. 1; Table 1).

Floral morphological traits

Corolla length (X_1= 3.48, $p=0.062$; Fig. 2A), corolla width (X_1= 3.51, $p=0.061$; Fig. 2B), and corolla opening (X_1= 1.70, $p=0.193$; Fig. 2C) did not differ significantly between plants under control and water deficit conditions (Table 1). However, these traits varied significantly between cultivars, with no significant treatment × cultivar interaction (Fig. 2; Table 1). Compared to 'Duke' (mean ± SE: 8.92 ± 0.16 mm), 'Bluecrop' flowers (9.42 ± 0.12 mm) had longer corollas (X_1= 7.24, $p=0.007$), but narrower corollas (6.70 ± 0.15 mm vs. 7.66 ± 0.15 mm; X_1= 19.28, $p<0.001$) and a smaller corolla opening (3.29 ± 0.13 mm vs. 4.07 ± 0.11 mm; X_1= 20.23, $p<0.001$).

Nectar production

Nectar volume ranged from 0.00 to 2.73 µL in plants under water deficit treatment and from 0.39 to 5.32 µL in control plants. Flowers from plants under water deficit conditions (1.10 ± 0.21 µL) produced significantly less nectar (X_1= 5.63, $p=0.018$; Fig. 3A; Table 1) compared to plants under control conditions (1.90 ± 0.34 µL). Independently of the water treatment, 'Bluecrop' flowers produced more nectar than 'Duke' (2.07 ± 0.28 µL vs. 1.18 ± 0.21 µL; X_1= 5.14, $p=0.023$; Fig. 3A). Sugar content ranged from 9.0 to 36.0% in control plants and from 22.5 to 43.0% in plants under water deficit treatment. There were neither differences in sugar content between treatments (X_1= 2.28, $p=0.131$) nor between cultivars (X_1= 0.01, $p=0.916$; Fig. 3B; Table 1).

Floral scent

We identified a total of 31 volatile organic compounds (VOCs), 28 of which were shared by both cultivars (Table 2). The floral scent profile was dominated by fatty acid derivatives (15 compounds), followed by phenylpropanoids/benzenoids (11), terpenoids (4), and a single nitrogen-containing compound. The total floral scent emission per flower was similar between cultivars (X_1= 2.36, $p=0.125$) and was

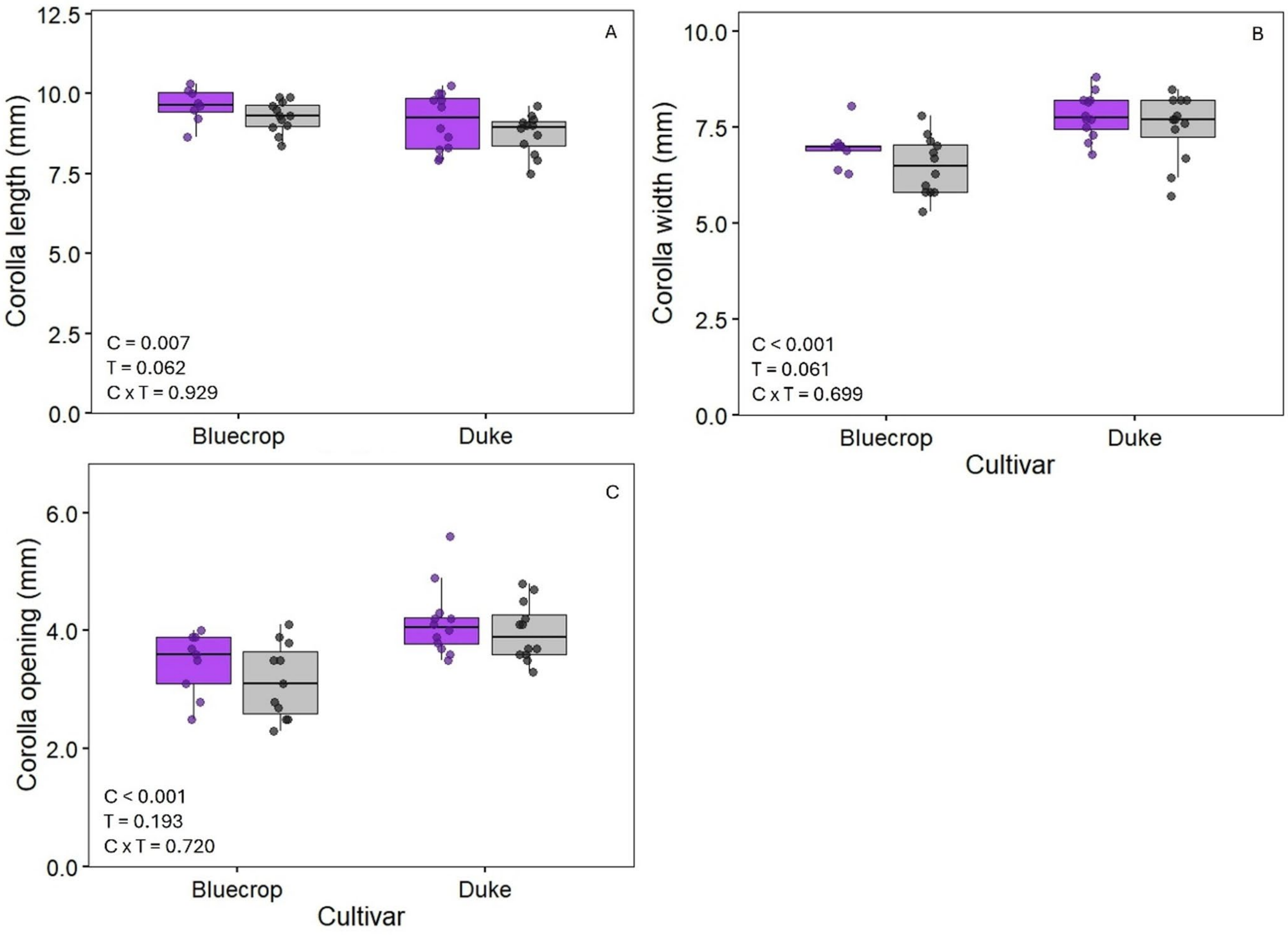


Fig. 2 Box plot of corolla length (mm; **A**), corolla width (mm; **B**), and corolla opening (mm; **C**) of blueberry flowers from 'Bluecrop' and 'Duke' under control and water stress conditions. P-values from GLM analyses are shown for the effects of cultivar (C), treatment (T) and their interaction (C × T)

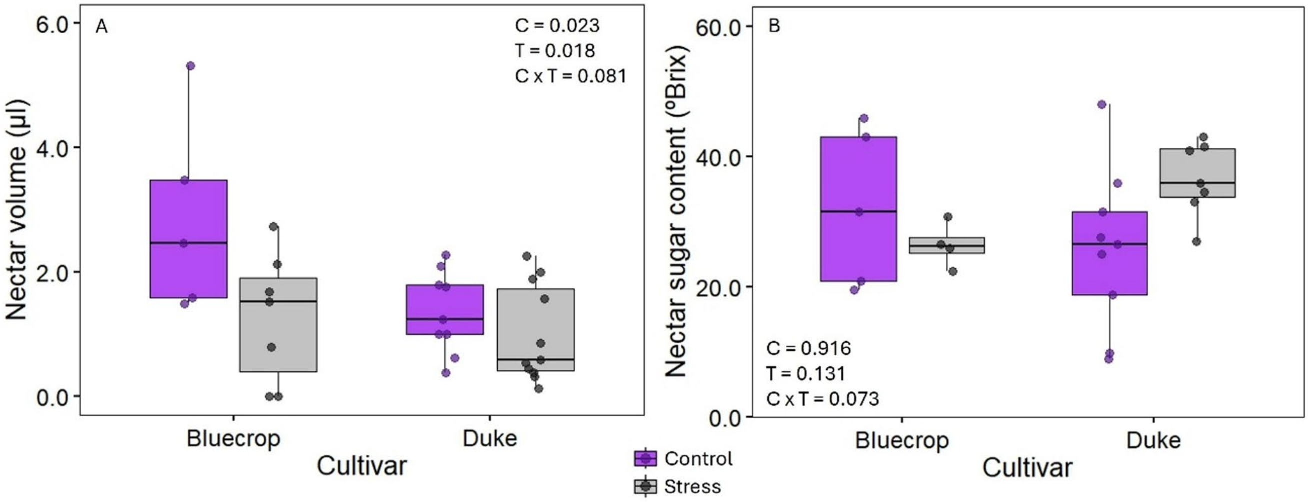


Fig. 3 Box plot of nectar volume (µl; **A**) and sugar content (°Brix; **B**) of blueberry flowers from 'Bluecrop' and 'Duke' under control and water stress conditions. P-values from GLM analyses are shown for the effects of cultivar (C), treatment (T) and their interaction (C × T)

not affected by water treatment (X_1= 0.21, p=0.651; Fig. 4; Table 1). However, relative scent composition differed significantly between cultivars (pseudo-$F_{1,27}$ = 3.87, p=0.01) but did not differ between treatments (pseudo-$F_{1,27}$ = 0.64, p=0.64), with no significant interaction effect (pseudo-$F_{1,27}$ = 0.37, p=0.87; Fig. 5).

The compounds contributing most to scent dissimilarity between cultivars were: 2-nonanone, emitted in higher amounts in 'Duke' (X^2 = 72.23, p<0.001), and (*E*)-2-hexenyl acetate (X^2 = 6.28, p=0.012) as well as 2-aminobenzaldehyde (X^2 = 14.55, p<0.001) emitted in higher amounts in 'Bluecrop'.

Plant-pollinator interactions

A total of six insect species were observed visiting blueberry flowers, with *Anthophora plumipes* accounting for 97.83% of visits. Other visitors included *Bombus terrestris* (Linnaeus, 1758; 0.99%), *Andrena* sp. (0.74%), *Melanostoma* sp. (0.22%), *Lasioglossum malachurum* (Kirby, 1802; 0.15%), and *Lasioglussum* sp. (0.07%). Visitation rates were similar between cultivars (X_1= 0.01, p=0.926) but significantly higher in control than in plants under the stress treatment (X_1= 8.76, p=0.003; Fig. 6; Table 1). Analysis of the floral preference index revealed that *A. plumipes* showed an overall preference for control flowers (mean ± SE: 0.59 ± 0.04; t=2.153, p=0.035). Within 'Bluecrop', a significant preference was recorded for control plants (mean ± SE: 0.65 ± 0.05; t=3.139, p=0.003), whereas no preference for any of the treatments was recorded for 'Duke' (mean ± SE: 0.55 ± 0.05; t=1.112, p=0.271). *A. plumipes* did not exhibit a significant preference for either cultivar (mean ± SE: 0.48 ± 0.03; t=0.851, p=0.398).

Fruit set

Fruit set was significantly higher in control plants than in plants under water stress conditions (X_1= 5.90, p=0.015), regardless of cultivar (Fig. 7; Table 1), and did not differ between cultivars (X_1= 0.61, p=0.452).

Discussion

Our results show that water deficit may influence floral traits linked with pollinator attraction and fidelity and, subsequently, impact the fitness of highbush blueberry. The results revealed distinct effects of cultivar and water treatment, depending on the parameter measured, with higher nectar production, visitation rates and fruit set in control plants than in plants under water deficit. Additionally, differences among cultivars were detected for floral traits. Yet, no significant interaction between cultivar and water treatment was detected, indicating that, under the conditions tested, the response to water deficit was not cultivar dependent. The results are discussed below in detail.

Cultivar effect

Floral morphological traits of highbush blueberry are known to vary among cultivars (Stockmann et al. 2013; Arrington and DeVetter 2018; Castro et al. 2023), likely as an indirect consequence of cultivar selection (DeVetter et al. 2022). These differences can affect the accessibility of floral rewards to pollinators and potentially impact visitation rates (Courcelles et al. 2013). Consistent with previous findings, we detected significant cultivar effects on floral

Table 2 Classification of floral volatile compounds identified in the blueberry cultivars 'Bluecrop' and 'Duke' and their mean relative abundance (±SE) per flower

Chemical class/compounds	'Bluecrop'		'Duke'	
Fatty acid derivatives	Control	Stress	Control	Stress
(*E*)-2-Hexen-1-ol*	0.00±0.00	0.81±0.43	0.00±0.00	0.31±0.21
(*E*)-2-Hexenyl acetate	4.67±1.31	7.71±1.68	2.55±0.77	3.47±0.98
(*E*)-2-Hexenyl butyrate*	1.52±0.52	1.66±0.48	0.41±0.21	0.44±0.15
(*E,E*)-2,4-Hexadienal*	0.03±0.02	0.38±0.19	0.04±0.04	0.10±0.10
(*E*)-2-Hexenal*	1.37±0.38	1.99±0.51	0.76±0.19	1.48±0.48
(*Z*)-3-Hexen-1-ol*	3.01±1.29	2.54±1.31	3.29±1.27	3.27±1.70
(*Z*)-3-hexenyl 2-methylbutanoate*	0.47±0.13	0.17±0.07	0.33±0.13	0.38±0.11
(*Z*)-3-Hexenyl acetate*	27.04±4.43	25.49±4.56	27.84±5.20	27.18±5.46
(*Z*)-3-Hexenyl butyrate*	2.70±0.90	2.16±0.82	2.69±1.05	2.05±0.54
1-Hexanol	2.12±0.63	2.74±0.49	2.41±0.67	4.50±1.13
2-Nonanone*	1.31±0.38	0.89±0.20	6.36±0.85	6.98±0.91
2,3-Butanediol_Isomer1*	0.00±0.00	0.09±0.07	0.00±0.00	0.00±0.00
2,3-Butanediol_Isomer2*	0.00±0.00	0.19±0.14	0.00±0.00	0.00±0.00
Hexyl acetate*	2.19±0.69	2.36±0.28	2.59±0.75	3.48±0.88
Hexyl butyrate*	0.17±0.14	0.01±0.01	0.08±0.06	0.16±0.07
Phenylpropanoids/Benzenenoids				
(*E*)-Cinnamaldehyde*	20.97±5.71	17.63±2.59	21.78±3.62	16.40±2.97
(*E*)-Cinnamyl acetate*	2.42±0.73	2.20±0.77	0.73±0.24	1.08±0.28
(*E*)-Cinnamyl alcohol*	2.52±0.95	3.20±0.74	7.31±2.83	4.04±1.30
(*E*)-Cinnamyl formate	0.09±0.05	0.09±0.05	0.17±0.08	0.03±0.02
(*Z*)-Cinnamaldehyde*	2.14±0.62	1.77±0.24	1.95±0.35	2.13±0.47
(*Z*)-Cinnamyl acetate*	2.59±0.75	2.54±0.70	1.20±0.26	2.27±0.43
(*Z*)-Cinnamyl alcohol*	3.97±1.19	4.62±1.00	5.58±2.02	5.43±1.63
3-Phenylpropanol*	2.08±0.82	1.47±0.27	2.91±0.58	4.17±0.89
3-Phenylpropyl acetate*	0.60±0.15	0.58±0.17	1.18±0.25	1.53±0.27
Benzyl acetate*	1.62±0.34	3.47±1.07	0.73±0.20	1.56±0.23
Benzyl alcohol*	1.46±0.27	3.26±0.97	1.23±0.13	1.61±0.30
Terpenoids				
(*E*)-4,8-dimethyl-1,3,7-nonatriene*	0.31±0.29	0.28±0.13	0.06±0.06	0.00±0.00
4-Oxoisophorone*	0.00±0.00	0.05±0.05	0.00±0.00	0.00±0.00
α-Pinene*	0.79±0.13	2.11±0.79	1.90±0.92	2.72±1.11
Camphene*	0.17±0.11	1.02±0.60	1.41±0.72	0.25±0.25
N-containing compounds				
2-Aminobenzaldehyde*	1.94±0.46	3.12±1.37	0.37±0.09	0.44±0.14

Compounds are grouped by chemical class. Compounds contributing most to scent dissimilarity between cultivars are highlighted in bold. Compounds marked with an asterisk were identified based on synthetic standards

morphology: 'Bluecrop' flowers had longer and narrower corollas, whereas 'Duke' flowers were shorter but wider, with a larger corolla opening. Courcelles et al. (2013) similarly reported wider corolla openings in 'Duke' compared to 'Bluecrop', which in their study correlated with higher visitation by honeybees. In our study, however, differences in corolla morphology likely did not influence visitation rates or preference indices. This lack of effect is likely explained by the identity of the main pollinator observed, *Anthophora plumipes*, which possesses a relatively long proboscis [9 mm (Cappellari et al. 2022); 12–15 mm (Stone et al. 1995); 14 mm (Deschepper et al. 2018)] and can, therefore, easily access nectar in both cultivars, regardless of the corolla tube length.

Nectar volume also varied significantly between cultivars, with 'Bluecrop' producing more nectar than 'Duke', whereas sugar content remained similar. Between cultivar differences in nectar volume have been shown to vary within northern highbush cultivars (Jablonski et al. 1985) and within southern highbush cultivars (Cromie et al. 2024), as well as among cultivars of other crops such as strawberry (Symington and Glover 2024). Although increased nectar availability has been associated with higher visitation rates in some studies (Cromie et al. 2024; Jablonski et al. 1985), this pattern was not observed in our study, since the effect of cultivar on visitation rates was non-significant.

Regarding floral scent, most compounds were shared between cultivars, in line with Rodriguez-Saona et al. (2011), who also reported similar numbers of compounds for 'Bluecrop' and 'Duke'. However, the overlap between studies was surprisingly low: only 8 compounds were common, with 23 compounds detected exclusively in our study and 19 only in Rodriguez-Saona et al. (2011). Differences in dominant compounds were also observed. In Rodriguez-Saona

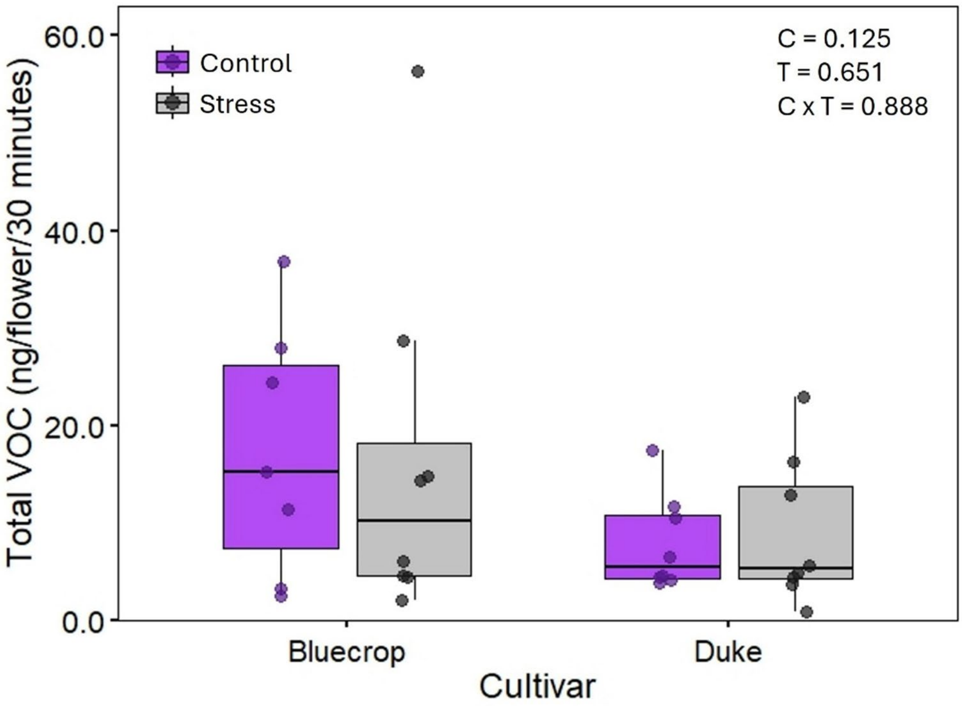


Fig. 4 Box plot of total emission volatile organic compounds (VOC; ng/flower/30minutes) of blueberry flowers from 'Bluecrop' and 'Duke' under control and water stress conditions. P-values from GLM analyses are shown for the effects of cultivar (C), treatment (T) and their interaction (C × T)

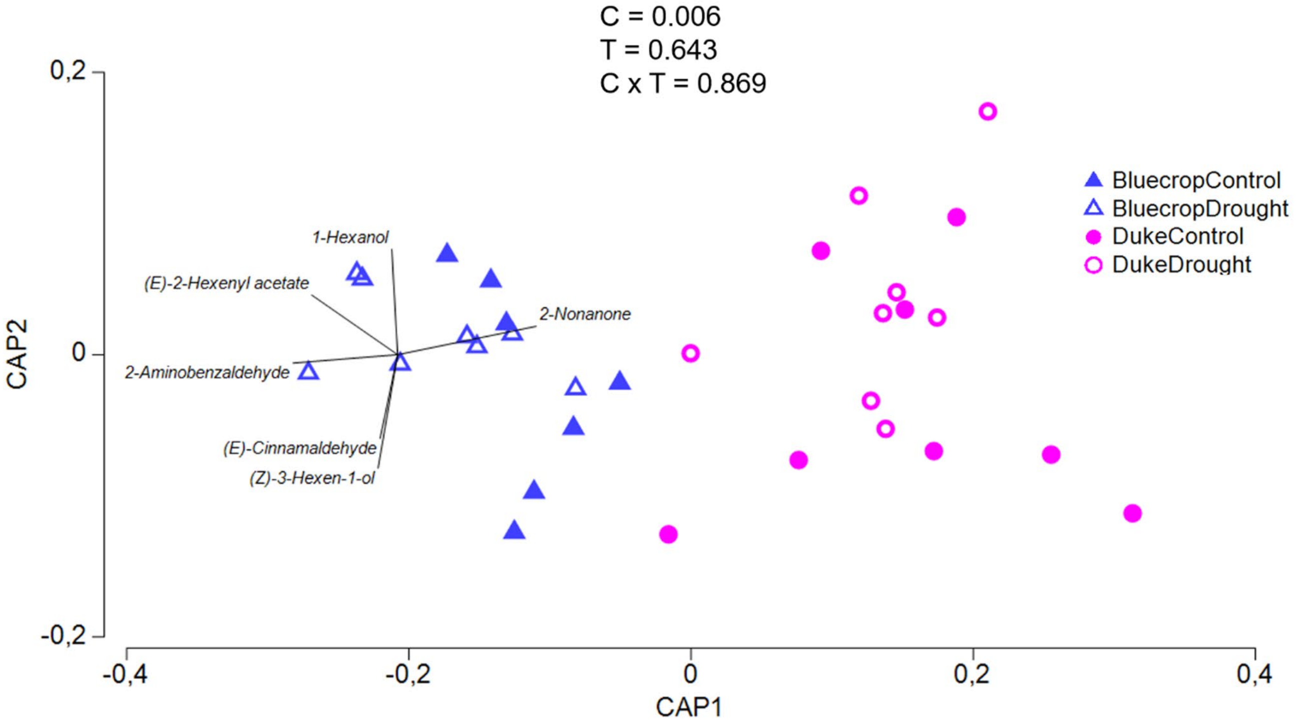


Fig. 5 Canonical analysis of principal coordinates (CAP) based on Bray–Curtis dissimilarity indices of square-root transformed relative scent data for 'Bluecrop' and 'Duke' under control and water stress conditions. Compounds most correlated with the ordination axes are indicated

et al. (2011), cinnamyl alcohol dominated both cultivars' scent profiles, whereas in our study it was present but not dominant. Instead, (*E*)-cinnamaldehyde and (*Z*)-3-hexenyl acetate were among the most abundant compounds in our samples but were absent or detected only in trace amounts by Rodriguez-Saona et al. (2011). These strong differences in scent among the studies are very likely driven by differences in the chemical ecological methods applied (e.g., ex

Fig. 6 Box plot of visitation rates (per 10 min period; %) to blueberry flowers from 'Bluecrop' and 'Duke' under control and water stress conditions. P-values from beta regression models are shown for the effects of cultivar (C), treatment (T) and their interaction (C × T)

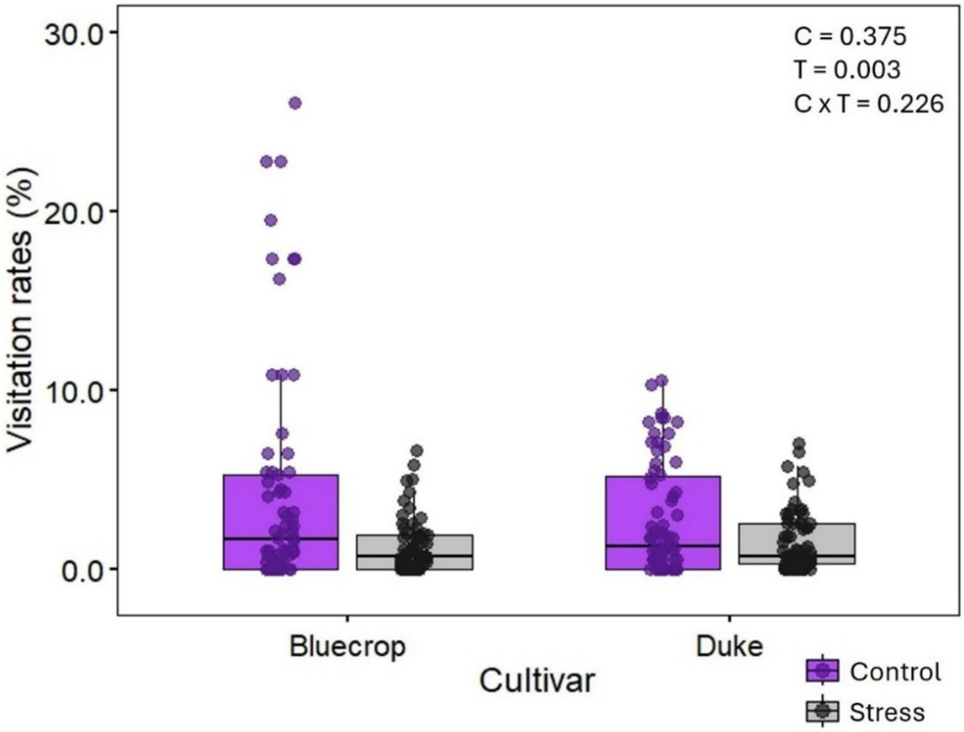
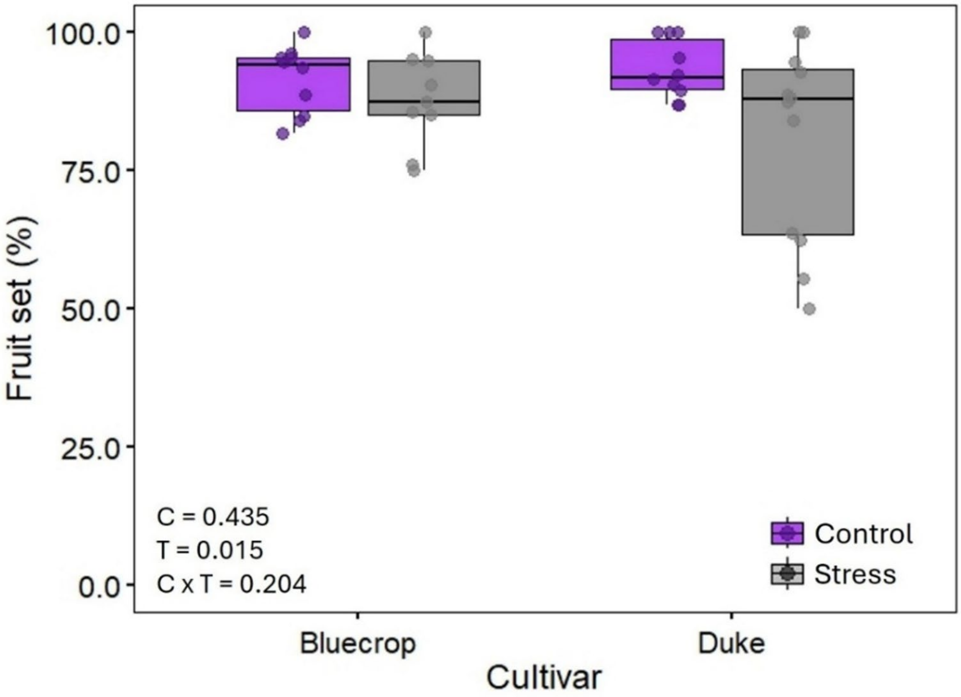


Fig. 7 Box plot of fruit set (%) in blueberry cultivars 'Bluecrop' and 'Duke' under control and water stress conditions. P-values from GLM analyses are shown for the effects of cultivar (C), treatment (T) and their interaction (C × T)



situ vs. in situ sampling of volatiles; adsorbents: Super-Q vs. Tenax/Carbotrap; sampling durations: 3 h vs. 30 min; solvent extraction of volatiles from adsorbent tubes vs. thermal desorption; Alborn 2018; Ramírez et al. 2010; Marcillo et al. 2020), but might also be mainly due to differences in the cultivation and the environmental conditions (e.g. temperature) during cultivation that might have been different between the two studies. Indeed, temperature, which likely differed between the study sites (23 °C vs. 18 °C), is known to influence floral scent emissions (e.g.Barman and Mitra 2021; Cordeiro and Dötterl 2023a, b).

Despite cultivar-specific differences in floral morphology, nectar volume, and scent composition, the pollinator visitation rates, preference indices, and fruit set were unaffected. This suggests that under our experimental conditions, cultivar identity did not significantly influence pollination success. It is possible that, while statistically detectable, these differences were too small to influence pollinator behavior or that pollinators failed to detect them (Essenberg 2021). Additionally, individuals with lower attractiveness may have benefited from the proximity of more attractive individuals, as, the distribution of the plants was close enough and the area small enough to be perceived by pollinators as a single patch (Klinkhamer et al. 2001; Essenberg 2021).

Water treatment effect

Water deficits are known to induce physiological stress in plants, potentially reducing resource allocation to reproductive structures such as flowers and fruits (Eziz et al. 2017). Leaf relative water content (RWC) is a reliable indicator of plant water status, as it reflects the balance between water supply and transpiration (Jones 2007). The results for RWC confirm that the imposed water deficit induced physiological stress, yet the effect was relatively mild, as RWC remained above 80%. This suggests that plants were able to maintain leaf turgor through stomatal regulation and/or osmotic adjustment (Mingeau et al. 2001; Ru et al. 2024). The phenology of the cultivars likely contributed to this resilience. These cultivars are deciduous, shedding their leaves in autumn and entering a period of dormancy. Growth resumes in spring with the development of both floral and vegetative buds (Retamales and Hancock, 2018). In our study, floral bud development began in late February, and flowering occurred in April under mild temperatures and relatively high atmospheric humidity, conditions that reduce plant water demand. At this stage, flower development relies largely on stored reserves rather than on current photosynthesis. Consequently, the effects of water deficit on relative water content (RWC) were less pronounced than at later stages, such as fruit development or ripening, when water demand is greater (Bryla and Strik 2007).

Nevertheless, we detected significant effects of water deficit on nectar production, visitation rates, and fruit set, whereas the remaining floral traits did not differ between treatments. Plants subjected to water deficit experienced markedly reduced visitation, with *A. plumipes* exhibiting a clear preference for flowers of control plants. Given that water deficit did not significantly alter floral morphology or scent composition, the most plausible explanation lies in the reduction in nectar volume under water deficit conditions. Associations between nectar depletion and reduced visitation have been reported for several other species (Waser and Price 2016; Descamps et al. 2018; Höfer et al. 2021). Nectar function as a reward may encourage bee individuals to revisit flowers that offer higher amounts of nectar (Barman et al. 2024) and discourage further visits to flowers from plants under water deficit which offer lower amounts of nectar. Nevertheless, considering that we found differences in nectar volume among cultivars and that this did not affect visitation rates or preference, we need to consider additional factors may be at play in influencing visitation rates and *A. plumipes* preferences. Variations in floral CO_2, floral humidity or floral temperature can influence insect attraction (Thom et al. 2004; Dyer et al. 2006; Harrap et al. 2024; Dahake et al. 2025). For example, floral temperature can be used as a cue to higher sucrose rewards, with lower temperature cuing higher sucrose content (Dyer et al. 2006; Whitney et al. 2008; Harrap et al. 2024). Reduced floral humidity was associated with fewer visits in squash (*Cucurbita* spp; Dahake et al. 2025). Additionally, while we did not detect significant shift in other floral traits, subtle changes in sugar content and volatile emission or that of particular compounds could add up to shifts in nectar volume leading to a change in the global information given to pollinators by floral signals (Essenberg 2021).

Interestingly, floral scent emission remained stable under water deficit, suggesting that both cultivars can maintain a consistent volatile bouquet despite reduced water availability. These results are consistent with findings for other crops such as *Sinapis arvensis* (Höfer et al. 2022), buckwheat (*Fagopyrum esculentum*; Rering et al. 2020), and *Cucurbita pepo* (Barman et al. 2024), where floral emissions were also unaffected by water deficit, but contrast with increased emissions for *Campanula rotundifolia*, *Phacelia hastata* and *Potentilla recta* (Glenny et al. 2018), and *Brassica napus* and *Sinapis alba*, although here there was an interaction with nitrogen fertilization (Höfer et al. 2022). This variation in the effect of water deficit on scent emission among plant species may be possible as every volatile compound is produced via a distinct biosynthetic pathway, and these pathways may respond differently to stress conditions (Farré-Armengol et al. 2020; Reinecke et al. 2024). Also, water treatments and deficits differed among study systems, which also might contribute to the differences. In our study, the water deficit might have been too low to effect floral scent emissions (see also Farré-Armengol et al. 2020), whereas the stability of floral scent emission under water deficit conditions might (also) be the outcome of pollinator-mediated selection for consistent signaling.

Similarly, floral morphology remained unaffected by water deficit, likely because flower growth depends on stored resources accumulated before flowering. Our findings align with Lyrene (1994), who reported minimal environmental effects on flower morphology across blueberry cultivars, and with other studies showing that floral display is maintained under water deficit in *Campanula rotundifolia* and *Heterotheca villosa* (Glenny et al. 2018). However, they contrast with studies that have documented water deficit changes in floral morphology in other plant species, like reduction of flower size in *Sinapis arvensis* (Kuppler et al. 2021), *Cucurbita pepo* L. subsp. *pepo* (Barman et al. 2024), and *Potentilla recta* (Glenny et al. 2018), and that correlated with reduced visitation of pollinators. It is important to consider that, in our study, the stress imposed on the plants by the water stress treatment was mild, as indicated by the RWC around 80%. At relatively high levels of RWC plants are generally able to maintain cellular turgor and metabolic activity thereby sustaining normal physiological function (Parkash and Singh 2020). Additionally, while the sensitivity to water stress varies with cultivar, blueberries are considered to have some degree of water stress tolerance (Mingeau et al. 2001; Retamales and Hancock 2018; Balboa et al. 2020). Therefore, the effects of the water stress treatment may not have been enough to induce a detectable effect on floral morphology. Furthermore, the lack of a significant effect of water treatment on flower morphology may be due to the limited sample size, which may not have captured variation in responses. Future studies should include more plants or sample multiple flowers per plant, and consider different approaches, e.g. applying water stress at the shot elongation stage, which has been shown to affect the number of flowers produced in the following season (Mingeau et al. 2001) and/or consider more severe water deficits.

An additional factor to our experiment was the need to shelter plants under the water deficit from rainfall events during the experiment, which could cause heat to become an additional stress factor. Considering that mean daily air temperatures outdoors during the experimental period ranged from 13 °C to 18 °C, and that we allowed air circulation, we do not expect temperature increases inside the cages to surpass the optimum growth temperatures for northern highbush blueberry (14–25 °C; Retamales and Hancock 2018; Walters et al. 2025), and therefore it is unlikely that heat stress has been imposed on the plants. Blueberry floral morphology showed minimal environmental effects when comparing plants kept in greenhouse (temperature range: 5–27 °C) with plants under field conditions (Lyrene 1994). Nectar secretion and floral volatile emissions have shown substantial changes only at warmer temperatures (>25º-30 °C, although this may vary with speciesCordeiro and Dötterl 2023b; Alquichire-Rojas et al. 2024).We do not expect that this potential increase in temperature will have a significant effect on the parameters measured, however the data collected in our study does not allow us to exclude this a possible effect of temperature increase.

Conclusions

Overall, our results demonstrate that northern highbush cultivars ‘Bluecrop’ and ‘Duke’ differ in floral morphology, scent emission and nectar production, yet these differences do not affect pollinator behavior or fruit set. Overall, water deficit conditions did not impact the floral traits, except for nectar production. Reduced nectar production under water deficit conditions, likely in combination with other factors, decreased visitation rates by reducing the continuous visits by individuals of *A. plumipes*, leading to a measurable decline in fruit set.

Future research should investigate the impacts of different intensities and timings of drought stress on floral traits, pollinator behavior, and the consequent fruit production, adding knowledge to the traditional drought studies that mostly consider direct effects on fruit production and physiological response, ignoring the plant-pollinator component. Such insights are crucial for developing management strategies to sustain pollination services and ensure crop productivity under increasing climate variability.

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Author contributions HC designed the study, collected and analyzed data, and produced the first draft of the manuscript. SD and MB were responsible for experimental design of VOCs collection, for VOCs analyses, VOCs data analyses and manuscript preparation. MCD contributed to water deficit implementation, data collection and manuscript preparation. JL and SC contributed to the discussion of study design and manuscript preparation.

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Data availability Data will be made available upon request to the corresponding author.

Declarations

Conflict of interest The authors declare no conflict of interest.

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