



Salinity impacts biocontrol: a tri-trophic assessment of the effects of soil salinity on plant signaling and parasitoid fitness

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Abstract

Soil salinization and insect herbivory pose significant threats to global food security. While biocontrol agents like parasitoid wasps are a key pest management strategy, their efficacy may be compromised by abiotic stressors cascading through trophic levels. This study investigates the tri-trophic interactions among tomato plants (*Solanum lycopersicum*), the caterpillar pest *Helicoverpa zea*, and its specialist endoparasitoid *Microplitis croceipes*, under salinity stress. In Y-tube olfactometer assays, *M. croceipes* were significantly more attracted to herbivore-damaged plants grown under control conditions compared to those under salinity stress. While the volatile blend emitted by plants did not differ between treatments, shifts in volatile emissions of α -copaene, 3E-hexenol, methoxy phenyl oxime, and TMTT, likely influenced parasitoid choices. To determine whether these plant-mediated changes extended to host quality, we conducted separate behavioral and developmental assays. When presented with a choice, female wasps exhibited no oviposition preference between “non-salty” and “salty” hosts. However, the impact of salinity on parasitoid performance was stage-dependent with salinity stress significantly delaying larval development but not affecting offspring sex ratios. These findings suggest that salinity induces complex trade-offs between parasitoid attraction and fitness metrics, influencing top-down control exerted by parasitoids. This highlights the critical need for integrated frameworks that account for abiotic factors when designing biological control strategies for herbivore populations in saline environments.

Keywords Salt stress · Insect herbivory · Parasitoids · Biocontrol

Introduction

Insect pests, such as the tomato fruitworm (*Helicoverpa zea*), present a major threat to global food security, causing over 40% in crop yield losses (Del Pozo-Valdivia et al. 2021). A key sustainable management strategy involves the use of biocontrol agents like endoparasitoid wasps that lay eggs inside the caterpillar, ultimately killing it as the parasitoid larva develops and emerges (Jervis 2007). The success of these wasps is intimately linked to the quality of their host, as their reproductive fitness depends on the host's nutritional content (Smilanich et al. 2011). This delicate

host-parasitoid balance can be disturbed by cascading effects of abiotic factors on plants.

The salinization of agricultural land is an important abiotic stress, commonly seen in dry, arid areas with improper irrigation (Hassani et al. 2021). Soil salinity leads to the accumulation of salts in plant tissue, negatively impacting plant growth and can even cascade up trophic levels (Pawar et al. 2025a). For instance, a previous study showed that salt-stressed tomato plants are poor-quality food for *H. zea*, leading to reduced caterpillar growth due to ionic toxicity (Pawar et al. 2025b). This alteration to plant and caterpillar quality (as a host) can subsequently affect parasitoid recruitment and performance, with some studies showing lower parasitism rates in saline environments (Moon and Moon 2010; Marroquin et al. 2023; Rahman et al. 2023). A potential mechanism for this involves changes to plant volatiles. To conserve water, salt-stressed plants often close their stomata, which can reduce the emission of volatile organic compounds (VOCs) (Munns and Tester 2008; Forieri et al.

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2016; Lin et al. 2022a). These emissions include herbivore-induced plant volatiles (HIPVs), which parasitoids use as chemical cues to locate their hosts (Paudel Timilsena et al. 2020). This raises a critical question: How does the concurrent stress of salinity and herbivory affect a plant's ability to recruit natural enemies? Moreover, how does the effect of salinity in soil cascade through trophic levels and affect the behavior and performance of a parasitoid?

Specialist solitary parasitoids lay a single egg per host, making careful host selection decisions to optimize offspring's survival and fitness (Hemerik et al. 2002; Hegazi et al. 2020). Beyond host location, they must assess host quality for oviposition, which can be influenced by factors such as host diet, size, and developmental stage (Burke and Sharanowski 2024). Higher parasitoid fitness is observed when eggs are laid in an environment conducive to larval development. Female wasps utilize a haplodiploid reproductive system, allowing them to control the sex of their offspring by either fertilizing an egg to produce a diploid female or laying an unfertilized egg to produce a haploid male (Burke and Sharanowski 2024). This decision often made at the moment of oviposition can allow for rapid adaptation to changing environmental cues and host quality (Ode and Heinz 2002). Female wasps often adjust sex allocation based on host quality, which is frequently dictated by the host's developmental stage or instar. For example, *Microplitis similis* has been shown to lay fewer fertilized eggs in small 1st instar larvae, suggesting a careful evaluation of host quality (Chen et al. 2017). The control of offspring sex ratios by parasitoid wasps influences their performance and durability in agricultural applications.

Our study focuses on the specialist braconid endoparasitoid - *Microplitis croceipes*, a promising biocontrol agent for *Helicoverpa* caterpillars (Tomberlin et al. 2005). We predicted that (1) salt stress reduces HIPV emissions and parasitoid attraction, (2) parasitoids would prefer "non-salty" hosts, and (3) parasitoid development would be negatively affected in "salty" hosts. Along with investigating parasitoid recruitment to plants, this study aims to understand how *M. croceipes* assesses "non-salty" versus "salty" *H. zea* larvae, investigating its ovipositional choices and performance. Having a thorough understanding of intricate parasitoid–host pair interactions is essential for optimizing biocontrol strategies in increasingly saline agricultural ecosystems.

Materials and methods

Plants

We grew tomato plants (*Solanum lycopersicum* cv. Better Boy, Harris Seeds, Rochester, NY, USA) in a greenhouse (25 ± 2 °C, 60–70% RH, 16:8 L:D photoperiod) at the

Pennsylvania State University. We watered plants that reached the four-leaf stage with 200 ml of salt solutions (0 mM NaCl and 200 mM NaCl) for three days, following which they were used in all experiments (Pawar et al. 2025b).

Insects

We purchased tomato fruitworm (*H. zea*) eggs from Benzon Research (Carlisle, PA, USA) and reared caterpillars in the laboratory as previously described (Peiffer and Felton 2005). We placed freshly hatched *H. zea* neonates on a control artificial diet (875 mg/kg of Na⁺) and a salt-supplemented artificial diet (4560 mg/kg Na⁺) and reared them till the 2nd instar for all parasitoid experiments (Chen et al. 2017; Pawar et al. 2025a, 2025b). Larvae reared on control diet are referred to as "non-salty" larvae and larvae reared on NaCl-supplemented artificial diet are referred to as "salty" larvae. Although we did not measure specific hemolymph or tissue Na⁺ concentrations, previous work showed that salinity increased total larval Na⁺ concentrations ~4fold, leading to a reduction in growth rate and an increase in mortality (Pawar et al. 2025a). Artificial diet was used to mirror prior plant-based work; it reduced logistical challenges and eliminated interference from secondary plant compounds, allowing for a clearer isolation of Na⁺ effects.

We maintained parasitoid wasp colonies (*M. croceipes*) as described in Tan et al. (2020). Female wasps were allowed to parasitize 2nd instar *H. zea* larvae, following which parasitized larvae were placed in insect rearing cups with artificial insect diet (Tan et al. 2020). Successful parasitization of *H. zea* larvae was characterized by the parasitoid bending its abdomen to expose its ovipositor, leaping onto the host, and pressing the ovipositor against the larval cuticle—presumably to deposit an egg within the host's body. Wasp pupae emerging from *H. zea* larvae were kept in cages and adults were provided 10% honey solution and water for feeding. As *M. croceipes* is haplodiploid, we used 1-day-old mated females in all experiments to allow production of both male and female offspring (Makatiani et al. 2013).

Y-tube olfactometer choice assay

Y-tube olfactometer studies are routinely used to depict insect choice and investigate natural enemy recruitment to plants (Jones 2020; Lin et al. 2022b; Zhan et al. 2023). We subjected *M. croceipes* females to a Y-tube olfactometer choice assay (12 cm stem, 7.5 cm arms, 2 cm diameter), conducted in a growth chamber (25 ± 2 °C, $50\% \pm 10\%$ R.H.) (Pawar et al. 2025a). Plants were kept in a glass chamber (35 cm x 15 cm) and charcoal filtered, purified air was pushed into the chamber at a flow rate of 1.5 L/min via Teflon tubes. An outlet Teflon tube from the glass

chambers was connected to each Y-tube arm, showing a flow rate of 0.5 L/min. We released individual female parasitoid wasps at the base of the Y-tube olfactometer. Wasp choice was recorded as the arm it entered; assays lasting more than five minutes without a choice were excluded. Glass chambers containing plant treatments were isolated from the Y-tubes to remove the influence of visual cues. Teflon tube connections were randomized, Y-tubes were rotated 180 degrees after each trial, cleaned with acetone and hexane to remove residual olfactory cues, and plant material was refreshed every 12 trials to minimize positional biases (Park et al. 2019). Each pairwise comparison included 30–90 replicates. Plants as part of the herbivore-damaged treatments were used once the larvae (5th instar *H. zea*) had fed freely on the plants for three hours (giving enough time for plants to emit VOCs and HIPVs as part of short-term as well as long-term responses to recruit natural enemies of insect herbivores) (War et al. 2011). Choice tests included: no-salt-treated vs salt-treated (undamaged plants), no-salt-treated vs salt-treated (herbivore-damaged plants), and control combinations (empty arm vs empty arm, empty arm vs no salt (damaged, undamaged), empty arm vs salt (damaged, undamaged), salt (undamaged) vs salt (damaged) and no salt (undamaged) vs no salt (damaged)).

Volatile collection and analysis

We collected headspace volatiles from no-salt-treated, herbivore-damaged plants and salt-treated, herbivore-damaged plants ($n=9$ per group) 3 h after introduction of *H. zea* larvae, corresponding to the time point used in Y-tube choice assays. The volatile collection setup utilized 9-L glass chambers, Teflon tube connections, and a charcoal-air-filtered pump system. Volatiles were collected for 3 h using a push–pull system at a push flow rate of 1 L/min and a pull flow rate of 0.8 L/min. Volatiles were captured using adsorbent filters containing 45 mg Haye-Sep-Q (Hutchinson Hayes Separation Inc., USA). Following collection, the traps were eluted with 150 μ l dichloromethane into 2 ml glass vials equipped with a 250- μ l glass insert. We added 5 μ l of nonyl acetate as an internal standard (40 ng/ μ l) to normalize compound abundances and estimate nanogram-level quantities per sample. Samples were analyzed by GC–MS using an Agilent-7890A gas chromatograph equipped with an Agilent HP-5MS UI (30 m $\times$ 0.25 mm $\times$ 0.25 μ m) column coupled to an Agilent-5975C mass spectrometer with standard EI tune settings. We performed splitless injections (1 μ l) at an inlet temperature of 250 °C using helium as a carrier gas and a constant flow rate of 0.7 ml/min. The oven program started at 40 °C, increased by 10 °C per minute, and was held at 300 °C for 4 min (Pawar et al. 2025b). To remove non-biogenic or laboratory-derived artifacts, we filtered known contaminant compounds from the

chromatogram. Compounds were tentatively identified using library matches from ADAMS, NIST17, and CHEMECOL libraries and confirmed by comparing their retention indices from published databases, including the Pherobase (Helms et al. 2017; Lin et al. 2021). We further retained only those compounds detected in at least three independent samples within a treatment group to ensure that all analyzed volatiles represented consistently expressed, biologically meaningful signals rather than sporadic or single-sample occurrences. See the statistical analysis section for stats methods and Supplementary Table S1 for volatile emissions from plants (in ng).

Parasitoid stinging experiment

To assess whether *M. croceipes* wasps preferentially sting potentially healthy (“non-salty”) or unhealthy (“salty”) hosts, we placed one *H. zea* larva from each treatment (of similar weights) at opposite ends of a Petri dish (90 mm $\times$ 15 mm, Sigma-Aldrich, St. Louis, MO, USA, Cat. No. Z717223). We then introduced a single naïve female *M. croceipes* wasp and recorded parasitoid choice as the first larva to be stung ($n=80$). The Petri dish setup was kept in the laboratory at 27 ± 2 °C, $30\% \pm 10\%$ R.H.

Parasitoid egg-laying choice experiment

We first exposed naïve female *M. croceipes* to ten “non-salty” and ten “salty” *H. zea* larvae. We then used these “experienced” wasps in our experiment, where they were allowed to sting *H. zea* larvae in a random alternating sequence of “non-salty” and “salty” hosts. Each female wasp stung a total of five “non-salty” and five “salty” hosts. This design enabled wasps to allocate eggs of potentially different quality to each host type. We then reared parasitized larvae from both treatments on a “non-salty” artificial diet to standardize post-parasitism conditions, ensuring that developmental differences were attributable to the quality of eggs laid or the initial host environment, rather than diet during parasitoid development. Parasitism events were intentionally randomized across multiple female wasps, preventing clustering of hosts by maternal identity. Each parasitized caterpillar was treated as an independent observational unit in the analyses. Because female identity was not tracked across all experiments, we could not account for potential non-independence among hosts parasitized by the same female. For each parasitized caterpillar ($n=90$ per treatment), parameters recorded included *H. zea* caterpillar weight at parasitoid emergence, cocoon formation success and timing, cocoon weight (as a proxy for adult size and reproductive fitness), time to adult emergence, adult emergence success, and sex ratio of emerged wasps (Charnov 1982; Godfray 1994; Harvey et al. 2009). Insects

were kept in a growth chamber at 27 ± 2 °C, $30\% \pm 10\%$ R.H., with a 16-h photoperiod.

Parasitoid development experiment

In contrast to the previous assay, this experiment evaluated parasitoid development in *H. zea* caterpillars reared under “no salt” and “salt” diet conditions. We allowed naïve female *M. croceipes* wasps to sting untreated *H. zea* larvae, after which the parasitized hosts were assigned to either a no-salt artificial diet or a salt-supplemented artificial diet for the remainder of their development. Parasitism was distributed across many female wasps in a randomized manner, with each female wasp stinging on average ten *H. zea* larvae. Each parasitized caterpillar was treated as an independent observational unit in the analyses. Because female identity was not tracked across all experiments, we could not account for potential non-independence among hosts parasitized by the same female. The same developmental parameters as described above were recorded for each parasitized caterpillar ($n = 90$). Insects were kept in a growth chamber at 27 ± 2 °C, $30\% \pm 10\%$ R.H., with a 16-h photoperiod.

Statistical analysis

All statistical analyses were performed using R (R Core Team 2025). To evaluate differences in volatile profiles, we calculated Bray–Curtis dissimilarities and ran permutational multivariate analysis of variance (PERMANOVA) using the *adonis2()* function from the *vegan* package (Oksanen 2015). We assessed group dispersion using *betadisper()* and visualized sample separation using non-metric multidimensional scaling (NMDS). To test the effect of salinity on individual compound emissions, we used models appropriate for continuous, zero-inflated VOC data. When one treatment had zero detections, we used Fisher exact tests on presence–absence data and reported their *P* value. For compounds with low zero inflation, we fitted gamma GLMs with a log link to abundances after replacing zeros with a small constant. For compounds with moderate zero inflation and sufficient nonzero observations in both treatments, we fitted Tweedie GLMs. When nonzero observations were limited in at least one treatment, we used a two-part hurdle approach (binomial model for presence–absence and Gamma model for positive values).

The effects of salt treatment on various biological parameters were analyzed separately for the egg-laying choice experiment and the development experiment using linear models (LM) or generalized linear models (GLM), depending on the nature of the response variable. Statistical significance was assessed using type II ANOVA (*Anova* function, *car* package) (Fox et al. 2007). For larval weight at pupation, LM was used to examine the effect of salt

treatment. For % cocoon formation and % wasp emergence, a binary response variable (yes/no) was analyzed using a binomial GLM with a logit link function, followed by Type II ANOVA for inference. Similarly, LMs were applied to assess the effect of salt treatment on cocoon weight, days to cocoon formation, and days from cocoon formation to wasp emergence, with statistical significance determined using Type II ANOVA. For sex ratio, only adult parasitoids that successfully emerged and had recorded sex were included in the sex ratio analysis. Sex was modeled as a binary response variable (1 = female, 0 = male), with a GLM fitted with the *glmmTMB* package (Brooks et al. 2017) with binomial error distribution and salt treatment as a fixed effect. A limitation of our study is that female identity was not tracked across all experiments and thus multiple hosts have been parasitized by the same female, leading to potential non-independence among hosts.

Results

Y-tube olfactometer choice assay

In the absence of insect herbivory, parasitoids were not significantly attracted to either no-salt-treated or salt-treated plants (Fig. 1a; $\chi^2 = 0.095$, $df = 1$, $P = 0.758$). However, herbivore damage made no-salt-treated plants more attractive (Fig. 1b; $\chi^2 = 12.84$, $df = 1$, $P = 0.00026$), indicating that salt treatment reduces volatile-mediated parasitoid attraction. Control combinations validated parasitoid attraction to plant-derived volatile cues over clean air (empty arms) (Supplementary Fig. S1a; empty arm vs no-salt-treated, undamaged: $\chi^2 = 8.96$, $df = 1$, $P = 0.0027$, Supplementary Fig. S1b; empty arm vs salt-treated, undamaged: $\chi^2 = 16.29$, $df = 1$, $P < 0.0001$, Supplementary Fig. S1c; empty arm vs no-salt-treated, herbivore-damaged: $\chi^2 = 17.69$, $df = 1$, $P < 0.0001$, and Supplementary Fig. S1d; empty arm vs salt-treated, herbivore-damaged: $\chi^2 = 9.045$, $df = 1$, $P < 0.0001$) and herbivore-damaged plants over undamaged plants (Supplementary Fig. S1f; no salt: $\chi^2 = 7.046$, $df = 1$, $P = 0.007$, Supplementary Fig. S1e; salt: $\chi^2 = 17.046$, $df = 1$, $P < 0.0001$).

Parasitoid stinging experiment

“Non-salty” and “salty” caterpillars were equally attractive to naïve female *M. croceipes* wasps in a Petri dish assay (Fig. 1c; $\chi^2 = 1.250$, $df = 1$, $P = 0.2636$).

Volatile organic compound (VOC) analysis

Whole plant volatile blends (in ng) between herbivore-damaged, no-salt-treated and herbivore-damaged, salt-treated tomato plants showed no significant differences (Fig. 2a;

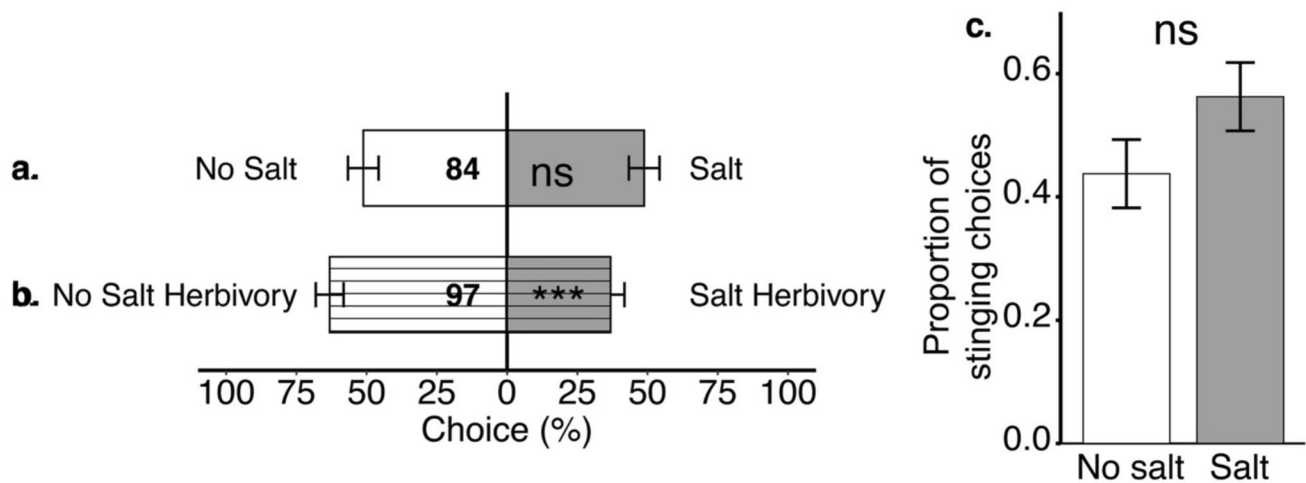


Fig. 1 Behavioral responses of *M. croceipes* females to plant and host treatments. Panels **a** and **b** show the percentage of wasp choices in a Y-tube olfactometer assay. In the solid bars (undamaged treatments), wasps chose between volatile cues from no-salt and salt-treated plants ($n=84$). In the patterned bars, wasps chose between herbivore-damaged plants (no salt and salt, $n=97$). **c** shows the proportion of sting-

ing choices by naïve female wasps presented with caterpillars reared on no salt or salt-supplemented diet in a Petri dish-based assay. Bars represent mean ($\pm$ SEM). White bars indicate no salt while gray bars indicate salt treatment. Asterisks indicate significant differences ($***P<0.001$), and “ns” denotes no significant difference ($P>0.05$)

PERMANOVA: $F_{(1, 41)}=2.078$, $R^2=0.048$, $P=0.073$). Several individual compounds differed between treatments (Fig. 2b–f; Supplementary Table S1). Decanal was higher under salt herbivory (Fig. 2b; $t=-59.8275$, $P<0.0001$), whereas α -copaene and TMTT were higher under no-salt herbivory (Fig. 2c; Fisher exact test, $P<0.0001$; Fig. 2d; $t=-5.0216$, $P<0.0001$). Emission of 3E-hexenol was higher under salt herbivory (Fig. 2e; $\chi^2=22.3081$, $P<0.0001$). Methoxy phenyl oxime was higher under no-salt herbivory (Fig. 2f; Fisher exact test, $P=0.0161$). All other compounds did not differ significantly between treatments (Supplementary Table S1).

Parasitoid egg-laying choice experiment

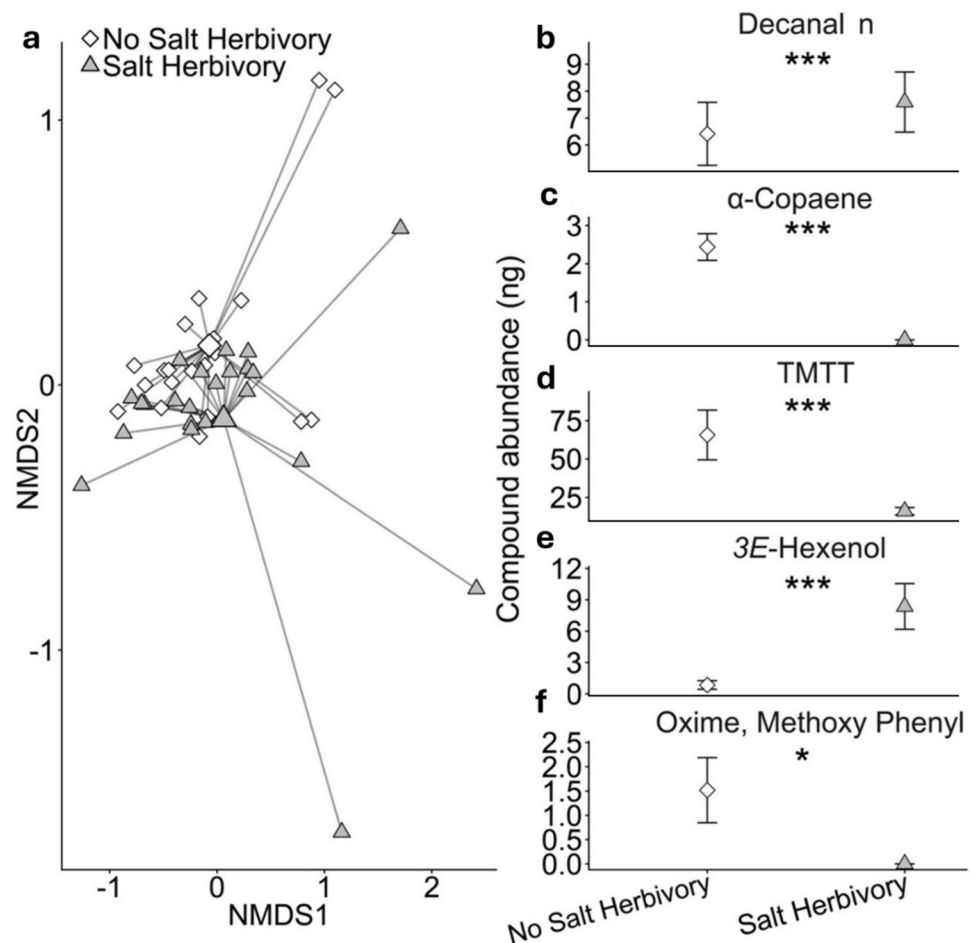
On average, parasitoids took a significantly shorter time to form a cocoon in “non-salty” caterpillars compared to “salty” caterpillars (Fig. 3a; $F_{(1,114)}=8.072$, $P=0.0053$). While salt treatment did not have a significant effect on % cocoon formation ($\chi^2=1.1416$, $df=1$, $P=0.2853$), average cocoon biomass (mg) of parasitoids grown from “non-salty” caterpillars was significantly higher than those grown from “salty” caterpillars (Fig. 3b; $F_{(1,89)}=5.459$, $P=0.0217$). While % wasp emergence was not significantly different between treatments ($\chi^2=0.51$, $df=1$, $P=0.474$), parasitoids took a significantly shorter time to emerge as wasps from cocoons in “non-salty” caterpillars compared to “salty” caterpillars (Fig. 3c; $F_{(1,77)}=4.074$, $P=0.047$). “Non-salty” and “salty” caterpillars gave rise to equal proportions of male and female parasitoid wasps (Fig. 3d; $\chi^2=0.0002$, $df=1$, $P=0.988$). Lastly, salt treatment had a negative

effect on *H. zea* caterpillar weight at parasitoid emergence: ($F_{(1,106)}=29.29$, $P<0.0001$).

Parasitoid development experiment

On average, parasitoids took a significantly shorter time to form a cocoon in caterpillars on “non-salty” diets compared to “salty” caterpillars (Fig. 3e; $F_{(1,86)}=30.40$, $P<0.0001$). While salt treatment did not have a significant effect on % cocoon formation ($\chi^2=0.7068$, $df=1$, $P=0.4005$), average cocoon biomass (mg) of parasitoids grown from “non-salty” caterpillars was significantly lower than “salty” caterpillars (Fig. 3f; $F_{(1,56)}=13.06$, $P=0.0006$). Although percentage wasp emergence was not significantly higher from “salty” cocoons ($60.61 \pm 5\%$) than “non-salty” cocoons ($45.35 \pm 5\%$) ($\chi^2=4.32$, $df=1$, $P=0.377$), parasitoids took significantly longer to emerge as wasps from “salty” cocoons than “non-salty” cocoons (Fig. 3g; $F_{(1,37)}=5.82$, $P=0.0209$). “Non-salty” and “salty” caterpillars gave rise to equal proportions of male and female parasitoid wasps (Fig. 3h; $\chi^2=0.64$, $df=1$, $P=0.4237$). Salt treatment had a negative effect on *H. zea* caterpillar weight at parasitoid emergence ($F_{(1,93)}=10.67$, $P=0.0015$).

Fig. 2 Effects of salt and insect herbivory on plant volatile compound profiles. **a** Non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis dissimilarities of volatile compound abundance profiles across two treatments: No-salt herbivory (white diamonds) and salt herbivory (gray triangles). Each point represents a sample, and lines connect each point to its group centroid ($n=9$). **b–f** Mean abundance ($\pm$ SEM) of individual compounds that showed significant differences between treatments. Shapes and colors match those in the NMDS plot. Asterisks indicate significance levels (* $P < 0.05$, *** $P < 0.001$)



Discussion

Our findings demonstrate that soil salinity interferes with tri-trophic interactions between plants, herbivores, and parasitoids by altering HIPVs and compromising host quality.

Natural enemy attraction and VOC analysis

When undamaged plants were subjected to salt stress, *Microplitis croceipes* wasps did not orient toward either no-salt-treated or salt-treated plants. However, they were significantly attracted to no-salt-treated, herbivore-damaged plants over salt-treated, herbivore-damaged plants. A previous study showed that salt treatment significantly changes plant volatile blends (Pawar et al. 2025b), but we see that they become more similar post insect herbivory. The increased preference for no-salt-treated, herbivore-damaged plants thus likely stems from quantitative changes to individual compounds in the volatile blend. We observed significant reductions in key attractive compounds, specifically α -copaene, methoxy phenyl oxime, and TMTT. TMTT is a well-documented, reliable cue for various parasitic wasps (Wei et al. 2007), and its suppression suggests

that salinity stress may antagonize the jasmonic acid (JA) signaling pathway required for its synthesis, a phenomenon often attributed to crosstalk with the abscisic acid (ABA) pathway upregulated during osmotic stress (Ament et al. 2006; Alonso et al. 2024). Interestingly, while we detected higher emissions of 3E-hexenol in salt-treated plants, a compound typically attractive to *M. croceipes*, it failed to restore attraction (Burrows 2016). This supports the hypothesis that parasitoids rely on specific ratios within a blend rather than individual compounds and the elevated background noise of stress volatiles may mask specific volatiles, influencing host detection (Morawo and Fadamiro 2016). While *M. croceipes* is attracted to insect frass-derived volatiles such as 13-methylhentriacontane, we did not detect it in our volatile sampling, and it seems unlikely that insect-derived compounds would influence parasitoid choices under the strong background of plant volatiles (Lewis and Jones 1971; Lewis and Tumlinson 1988). Additionally, since late instar *H. zea* were used for Y-tube assays and volatile collection to standardize plant damage, this might influence HIPV-mediated attraction of *M. croceipes* as it does not represent the correct host stage for parasitization. Changes in the chemical composition of HIPVs due to salinity stress may affect the ability

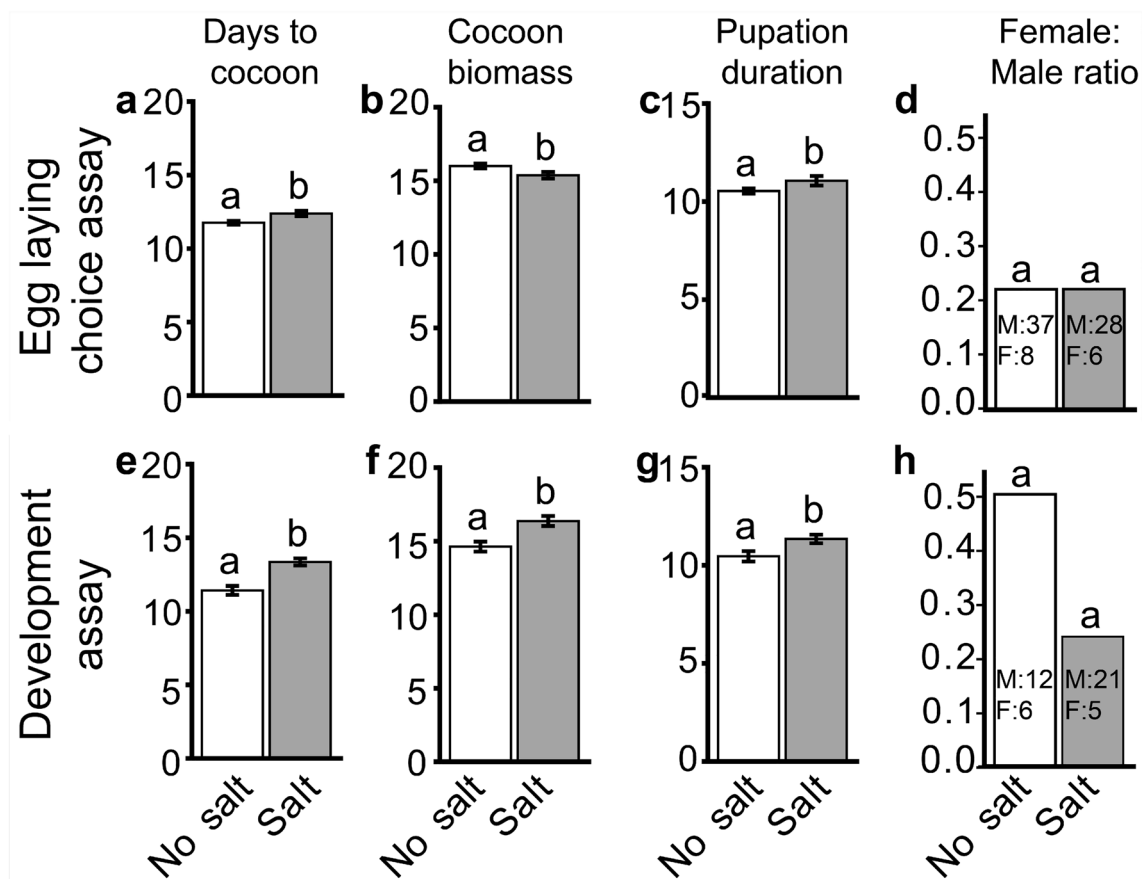


Fig. 3 Effects of salt treatment on parasitoid development parameters in *H. zea* caterpillars parasitized by *M. croceipes* across two experimental assays. Top panels **a–d**: Egg-laying choice experiment, where *M. croceipes* wasps were given sequential access to “non-salty” and “salty” *H. zea* larvae, allowing allocation of eggs based on prior host experience. Bottom panels **e–h**: Development experiment, where larvae were parasitized naïvely and then reared on either “no-salt” or “salt” diets throughout parasitoid development. Parameters assessed include days to cocoon formation (**a**, **e**), cocoon biomass (**b**, **f**), pupa-

tion duration (**c**, **g**), and sex ratio (**d**, **h**). Sex-ratio values represent the female:male ratio among adults that successfully emerged, based on the number of emerged females and males in each treatment (counts shown within bars). Sample sizes therefore differ between treatments depending on emergence success. White bars indicate no-salt treatment, while gray bars indicate salt treatment (mean $\pm$ SEM). Different letters indicate significant differences ($P < 0.05$) based on post hoc tests

of parasitoids to locate suitable hosts, leading to decreased parasitism rates and impacting host-parasitoid population dynamics (Uefune et al. 2013). Overall, our results indicate that parasitoids would visit both undamaged “non-salty” and “salty” plants during early phases of insect herbivore establishment; however, insect herbivore damage would change parasitoid attraction, making patches with lower salinity pressures more attractive.

Parasitoid host choice, egg-laying behavior and development

The differential attraction of parasitoid wasps to plants under salinity stress made us investigate parasitoid preferences and performance on “non-salty” and “salty” hosts. Specialist parasitoids exhibit complex host selection

behaviors considering various factors such as chemical cues, host age, size, and quality in order to ensure a suitable environment for their offspring and improve parasitoid fitness (Chu et al. 2014; Lewis and Tumlinson 1988; Li et al. 2015; Qiu et al. 2013). For example, a larger, more nutritious host might offer more resources for developing offspring, and have better defense against parasitoid attacks (Hoffmann and Frodsham 1993), while younger hosts might provide ample time for parasitoid development (Godfray 1994; Holmes 2020). According to the “mother-knows-best” principle, female oviposition preference should correlate with offspring performance (Henry et al. 2005; Kruitwagen et al. 2022), so we hypothesized that parasitoid preference and performance would be negatively affected in “salty” caterpillars (Rahman et al. 2023). Our stinging assays revealed a decoupling of this relationship.

Microplitis wasps stung both “non-salty” and “salty” hosts equally, yet the development experiments indicated differences in host quality. This suggests that while volatile cues (long-range) are disrupted by salt, contact cues (short-range) remain conserved or indistinguishable to the wasp. This indiscriminate stinging behavior leads to parasitoids expending energy and eggs on hosts that potentially reduce their fitness.

Parasitoid development within a caterpillar host is governed by host nutritional quality, the parasitoid’s life history and developmental needs, and the ecological context of the host-parasitoid interaction (Vinson 1990). Parasitism rates (% cocoon formation) did not differ between treatments across both the egg-laying choice experiment and development experiment. However, we observed consistently delayed cocoon formation and emergence in parasitoids developing in “salty” hosts across both experiments. These performance outcomes were timing-dependent and complex. In the development experiment where larvae fed on salt-supplemented diets continuously, parasitoids emerged heavier despite developmental delays. This suggests that parasitoids may exploit the extended development time of the slow-growing host to accumulate more resources before pupation. The nonsignificantly higher emergence rate from “salty” hosts could be attributed to this extended development time. Conversely, in the egg-laying choice experiment, cocoon weights were lower from “salty” hosts. This indicates that the initial physiological shock during the critical egg establishment phase incurred metabolic costs that could not be recovered even if the host diet quality improved post-parasitism. Future experiments should utilize an integrated design to determine if the fitness gains in cocoon mass are offset by potential costs in adult longevity or fecundity. Finally, the observed reduction in host weight at parasitoid emergence across both experiments confirmed that salinity, whether via initial exposure or continuous ingestion significantly impaired host development and thus parasitoid development.

The haplodiploid nature of *M. croceipes* allows for plastic sex allocation, where females can theoretically adjust the ratio of fertilized (female) to unfertilized (male) eggs based on host quality (Makatiani et al. 2013). While we did not observe sex allocation at the point of oviposition, the nonsignificant trend toward male-biased emergence in the development experiment suggests potential differential mortality rather than active choice (Trivers and Willard 1973; Veller et al. 2016). Because female parasitoids require more resources to develop, “salty” host environments may represent a sub-optimal environment that disproportionately impacts female survival (Korpelainen 1990; Ode and Heinz 2002; Rad et al. 2024). This potential overriding of initial sex determination due to a non-conductive atmosphere inside the caterpillar could have significant population-level

implications with a shift toward male bias ratios that reduces the reproductive potential of subsequent generations, potentially weakening the long-term efficacy of biological control during herbivore outbreaks (Wogin et al. 2013). Since we recorded equal cocoon formation and wasp emergence percentages across treatments, salinity appears to primarily influence the timing, rather than the absolute success of parasitoids, with its developmental trajectory reshaped by the host’s physiological response to salinity. Our findings align with broader evidence that high salinity induces developmental delays and increased mortality across diverse insect taxa (Alford et al. 2017; Quicke et al. 2023; Rahman et al. 2023; Pawar et al. 2025b; Vincent et al. 2025). For endoparasitoids like *M. croceipes* that are intimately tied to host physiology, salinity-driven shifts in host nutritional quality or osmotic balance can directly affect parasitoid growth and survival (Moore et al. 2022).

A key factor to consider is that egg-laying choice and development were tested in separate experiments. This approach allowed us to isolate the maternal choices of adult parasitoids from the performance of their offspring, preventing the confounding effects of these two distinct life stages. However, this separation also limited our ability to infer about cumulative effects that might occur if a parasitoid were subjected to salinity stress continuously from the point of host seeking through to adult emergence. Additionally, while we used plant-based olfactometer trials, our performance assays utilized artificial diets. While the artificial diet allowed us to isolate the direct impacts of salt ingestion and osmotic stress on *H. zea* and *M. croceipes*, we acknowledge that this may not fully replicate the plant-mediated effects of soil salinity. Our previous work on this system demonstrated that salinity levels do not significantly influence the induction of key plant secondary metabolites, such as trypsin inhibitors and polyphenol oxidase (Pawar et al. 2025b). Thus, the artificial diet serves as a proxy for the primary physiological challenge of salt ingestion that herbivores and parasitoids would encounter in saline environments.

Our results suggest that salinity leads to a complex shift in tri-trophic dynamics. We propose a scenario where “bottom-up” forces (plant resistance via salinity) and “top-down forces” (parasitism) act in opposition. While high salinity impedes herbivore growth (Pawar et al. 2025b), the same stress creates a refuge from parasitism with reduced parasitoid attraction and delayed development. Consequently, for herbivores that can tolerate moderate salinity, they may experience lower parasitism pressures. Furthermore, delayed host development increases their window of vulnerability to predation or parasitism while lengthening generation times for parasitoid wasps. In salinity-prone agroecosystems, this desynchronization could lead to a failure of biocontrol agents to track pest populations by releasing herbivores from “top-down” control (Amadou et al. 2019). This highlights

the influence of considering how soil salinization can potentially lead to mismatched biocontrol efficacy making integrated pest management strategies that account for abiotic heterogeneity necessary.

Author contributions

SVP, BS, RM, and GF conceived and designed research. SVP, RM, and MP conducted behavior experiments. SVP, SMP, and JA contributed to volatile experiments. SVP, BS, SMP, and MKB analyzed data. SVP wrote the manuscript. All authors read and approved the manuscript.

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Data availability The data generated and analyzed by the authors during the current study are freely available from the corresponding author upon request.

Declarations

Competing interests The authors declare no competing interests.

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