Tomato Defenses Under Stress: The Impact of Salinity on Direct Defenses Against Insect Herbivores

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Abstract

Plant responses to multifactorial stress combinations are seldom studied, but combinations of abiotic and biotic stresses may cause drastic yield reductions in crops. While an abiotic stress, the salinization of agricultural soil, affects crop production, added pressures of insect herbivores could lead to further losses. In this paper, we investigate the effects of salinity on an insect herbivore, the corn earworm caterpillar (*Helicoverpa zea*), feeding on tomato (*Solanum lycopersicum* cv. Better Boy) plants. We show that salt-stressed tomato plants are poor hosts for *H. zea*, impacting caterpillar growth rates, caterpillar feeding preference, and moth oviposition. We further show that these observations are best explained by reductions in both relative leaf water content and leaf total protein content, along with ionic toxicity and imbalance. We observe that salt stress does not influence anti-insect herbivory defense protein (PPO and TPI) levels. Finally, we observe that salt treatment leads to differences in specific volatiles, with lower emissions of 2-carene, α-phellandrene, β-phellandrene, α-humulene, and β-caryophyllene in salt-treated plants. We demonstrate that salt exposure changes tomato plant quality and chemical composition, which in turn negatively affects insect herbivores feeding on these plants.

Introduction

In their natural environment, plants frequently encounter two or more stresses that can limit their productivity and fitness (Spooner, Peralta and Knapp, 2005; Mittler, 2006; Holopainen and Gershenzon, 2010). These include both abiotic stresses (e.g., soil salinization, drought, extreme temperatures, waterlogging) and biotic stresses (e.g., herbivory (insect or mammalian) and pathogen-borne diseases (bacterial, fungal, or viral) (Gull, Lone and Wani, 2019). Plant stress response pathways are dynamic and influenced by diverse factors such as stress type, location, intensity, duration, and the interplay of interacting stresses (Singh, Dhanapal and Yadav, 2020).

The progressive salinization of cultivable land is an abiotic stress that poses a major threat to global agriculture, causing billions of dollars in losses annually (Pitman and Läuchli, 2002; Ashraf, 2010; Ruan*et al.* , 2010; Jamil *et al.* , 2011; Munns and Gilliham, 2015). It is estimated that more than 50% of cultivable lands will be salinized by 2050 (Ashraf, 2009; Lakhdar *et al.* , 2009; Zhao*et al.* , 2020). Various natural and anthropogenic factors contribute to soil salinization, including low precipitation, saline groundwater contamination, poor irrigation, and seawater intrusion in coastal areas (Shrivastava and Kumar, 2015; Kaya *et al.* , 2022; Zhang *et al.* , 2022; Sahbeni *et al.* , 2023). Salinity stress impacts plants by reducing water uptake in roots, leading to cell dehydration and increased ionic toxicity by Na^+ and Cl^- ions that disrupt osmotic balance, ultimately resulting in reduced plant growth and development (Rengasamy, 2006; Munns and Tester, 2008). Salt stress also impairs photosynthesis, leading to decreased carbon fixation and biomass production, and has been documented to compromise plant yields in several crops such as rice, wheat, barley, and tomato (Parida and Das, 2005; Shabala, Wu and Bose, 2015).

Tomato plants are affected under conditions of high salinity, leading to reduced seed germination and fruit yields (Cuartero *et al.* , 2006). However, some tomato plants are known to be moderately salt sensitive and certain varieties can exhibit salt tolerance properties (Hayward and Long, 1943; Spooner, Peralta and Knapp, 2005; Martinez*et al.* , 2012; Guo *et al.* , 2022). This variation in salt tolerance among tomato cultivars can be attributed to differential expression of specific genes and proteins that regulate homeostasis and stress responses, including the high-affinity K^+/ Na^+ transporter (HKT1like transporters) (Rubio, Gassmann and Schroeder, 1995; Nieves-Cordones *et al.* , 2008; Zhang*et al.* , 2008, 2018), vacuolar Na^+/ H^+ antiporters (NHX1-like transporters) that mediate Na^+ extrusion and sequestration to vacuoles (Apse*et al.* , 1999; Serrano and Rodriguez-Navarro, 2001; Rodríguez-Rosales *et al.* , 2008; Wang *et al.* , 2020; Solis*et al.* , 2022), and the abscisic acid-responsive element binding protein (AREB1 family) (Seok *et al.* , 2017; Yoo *et al.* , 2019). Simply put, plants deal with ionic stress by Na^+ exclusion, Na^+ inclusion and sequestration into vacuoles, or via tissue tolerance. The mechanism of salt tolerance at play depends on the plant species or variety and can lead to varying plant tissue contents based on the mechanism.

Furthermore, excessive salt can trigger the accumulation of reactive oxygen species (ROS). Low ROS concentrations can be involved in signal transduction (Miller *et al.* , 2010), whereas high ROS concentrations can lead to oxidative stress and damage to cellular components such as proteins, lipids, and DNA (Provin and Pitt, 2001; Foolad, 2004; Yang and Guo, 2018). Higher amounts of H_2O_2 and ROS species are commonly seen in plant responses to biotic stress, such as insect herbivory. H_2O_2 accumulation has been reported in salt-stressed maize and tomato plants at 24 and 48 hours post-salt application (Forieri, Hildebrandt and Rostas, 2016; Tandra *et al.* , 2022). A study reported that ROS accumulation under salt stress primed a JA-mediated anti-insect herbivory defense response (Sabina and Jithesh, 2021). As salt stress and herbivory co-occur, plant responses to one stress will have implications for cross-tolerance to another (Capiati, Pais and Tellez-Inon, 2006; Fujita *et al.* , 2006).

Herbivorous pests devour plant tissue, reduce the plant's photosynthetic capacity, and alter plant metabolism, nutrient acquisition and allocation, thus impacting crop yields (Babst *et al.* , 2008; Qu, 2019). The corn earworm caterpillar (*Helicoverpa zea*) is one of the most destructive pests of tomatoes, corn, and cotton, causing annual losses exceeding $1 billion globally (Wilcox, Howland and Campbell, 1956; Capinera, 2000; Blanco *et al.* , 2007; Rhino *et al.* , 2016; da Silva *et al.* , 2020). *H. zea* is known to trigger ROS accumulation and activate the JA-dependent plant defense response pathway in cotton (Bi, Murphy and Felton, 1997) and soybean (Bi and Felton, 1995). The JA-dependent plant defense response alters the production of plant defense metabolites, including alkaloids and protease inhibitors (Wang *et al.* , 2019; Jiao *et al.* , 2022).

Plants use distinct response pathways for individual stressors. However, plants under multifactorial combinations often exploit overlapping and converging pathways via shared proteins or signaling molecules to mount more efficient responses (Sewelam, Kazan and Schenk, 2016).However, the specificity of plant responses to unique stress combinations hinders our comprehensive understanding of their complex interplay and emergent outcomes. It thus becomes difficult to predict how plants will respond to multiple stresses. Furthermore, the performance of herbivorous pests feeding on stressed plants is influenced by plant quality, nutrient composition, and defense chemical levels that can be influenced under stress (Ali *et al.* , 2021). The plant stress hypothesis predicts that stressed plants should have higher herbivore abundance due to a decreased concentration of defense chemicals or changes to plant nutrient: chemical defense ratios (White, 1969, 1984; Joern and Mole, 2005). Conversely, the plant vigor hypothesis predicts that healthier plants (or plant parts) exhibit higher vigor and are better hosts for herbivores than stressed plants due to the higher availability of nutrients (Price, 1991; Cornelissen, Wilson Fernandes and Vasconcellos-Neto, 2008).

The effects of salinity stress on insect herbivores depend upon the specific host plant-insect interaction.

The responses of herbivorous pests to changes in plant quality can vary both within and among feeding guilds (Awmack and Leather, 2002; Huberty and Denno, 2004). Some studies have demonstrated that increased salinity levels can enhance insect pest performance on host plants. Leaf miner (*Tuta absoluta*) development rates on tomato plants have been shown to increase under saline conditions (Han *et al.* , 2016). Another study on the two-spotted spider mite (*Tetranychus urticae*) showed positive correlations between mite fecundity

and population growth on soybean (*Glycine max*) and maize (*Zea mays*) to salt stress (Eichele-Nelson *et al.* , 2017). Green peach aphid (*Myzus persicae*) abundance increased on sweet pepper plants (*Capsicum annuum*) under saline conditions (Polack, Pereyra and Sarandon, 2011). However, some studies show that increased salinity levels decrease herbivore performance on plants. Brown planthopper (*Nilaparvata lugens*) survival parameters such as nymphal development period, adult longevity and oviposition, and population density on rice (*Oryza sativa*) decreased due to lower plant quality (Quais *et al.* , 2019; Ali *et al.* , 2021). A study on wheat showed that the survival parameters of the cherry-oat aphid (*Rhopalosiphum padi*) were negatively affected by salt stress (Ghodoum Parizipour *et al.* , 2021). The soybean looper (*Pseudoplusia includens*) showed lower growth in salt-exposed soybean chloride-includer varieties (Najjar *et al.* , 2018). Literature focusing on salinity stress effects on plant-chewing-insect interactions seems to be highly variable and limited.

Just as plant quality determines insect performance, it also impacts the release of plant volatile organic compounds (VOCs) (Holopainen and Gershenzon, 2010). A study on salt-treated maize reported decreased VOC emissions per plant but not per biomass (Forieri, Hildebrandt and Rostas, 2016). They also observed differential emission of specific VOCs between salt treatments. Plant VOC emissions are used as signals for host selection by moths and can also influence higher tropic levels (Bernays and Chapman, 2007; Karban, 2008; Ninkovic, Markovic and Rensing, 2021). Many times, the establishment of insect pests on a plant begins with an adult moth perceiving appropriate hosts via VOCs and laying its eggs on the host plant (Penaflor *et al.* , 2011). Therefore, along with assessing caterpillar performance on plants, it becomes necessary to investigate moth oviposition preferences to get a comprehensive idea of the plant-insect interaction at play.

In this paper, we discuss tomato (*Solanum lycopersicum*) responses to combined stresses of salinity (NaCl) and insect herbivory by the generalist polyphagous corn earworm caterpillar *Helicoverpa zea*Boddie (Lepidoptera: Noctuidae) (Quaintance and Brues, 1905; Fitt, 1989). We hypothesized that salt-treated plants would negatively affect*H. zea* caterpillar performance and influence their foraging and oviposition behavior. We also speculated that this effect might be influenced by several factors, including reduced water content in plants, decreased total protein levels, ionic toxicity, nutrient imbalances, heightened levels of proteins that defend against herbivores, changes in volatile organic compound (VOC) emissions, or a combination of these elements.

Materials and Methods

Plants

Tomato plants *Solanum lycopersicum* cv. Better Boy (BB) were grown in cubic plastic pots (3.5" x 3.5" x 3.5") filled with Metromix 400 potting mix (Griffin Greenhouse & Nursery Supplies, Tewksbury, MA, USA) in a greenhouse at the Pennsylvania State University (25 +- 2degC, 70% +- 10% R.H., 16L: 8D). Plants were fertilized at the one-leaf stage with Osmocote Plus 15-9-12 Fertilizer (ICL Speciality Fertilizers, Summerville, SC, USA). Tomato plants at the four-leaf stage (roughly 4 weeks old) were used in all experiments.

Plants were subjected to three salt treatments:

1. No salt (0 mM): 200 ml of a 0 mM salt solution (distilled water) is added to the base of the plant.

2. Medium/intermediate salt (100 mM): 200 ml of a 100 mM salt solution is added to the base of the plant.

3. High salt (200 mM): 200 ml of a 200 mM salt solution is added to the base of the plant.

100 mM was chosen as an intermediate concentration and 200 mM as the high concentration based on multiple studies (Foolad, 1996; Zhang and Blumwald, 2001; Dombrowski, 2003; Sun *et al.* , 2010; Munns and Gilliham, 2015; Forieri, Hildebrandt and Rostas, 2016).

Plants were watered with their designated salt solutions every day for three days unless specified otherwise, following which they were used for experiments on the third day. It is worth noting that at the end of the three-day period, the soil salt concentration might be higher than the supplied amount due to salt

accumulation in the soil. By the end of the three-day treatment, salt-treated plants looked visibly stressed, dark green in colour, and showed retarded growth.

Insects

Corn earworm *(Helicoverpa zea)* eggs were purchased from Benzon Research (Carlisle, PA USA) and caterpillars were reared on a wheat-germ-based artificial diet (Peiffer and Felton, 2005) until pupation. Adult moths were provided with a 10% sugar solution, and eggs were collected daily to be used in the experiments.

Caterpillar relative growth rate (RGR) no-choice assay

To determine the resistance of tomato under different salt regimes against *H. zea* , caterpillar relative growth rate (RGR) on plants from different treatments was evaluated (**Figure 1A**). Two types of no-choice assays were conducted:

1. Detached-leaf agar cup-based caterpillar RGR assay: The fourth fully expanded leaf from each salt-pre-treated plant was cut and placed in individual plastic cups lined with 3% agar (to ensure the leaves retained moisture). A single pre-weighed 2nd instar*H. zea* caterpillar was added to each cup. Caterpillars were weighed after three days of feeding.

2. On-plant caterpillar RGR assay: Salt pre-treated plants were placed in individual cages and a single pre-weighed 2ndinstar *H. zea* caterpillar was allowed to feed freely on the plant. Caterpillars were weighed after three days of feeding.

Caterpillar relative growth rate (RGR) was calculated as:

RGR = (W2- W1)/(W1 *(T2-T1)), where W1 and W2 are caterpillar weights at time T1 and T2 respectively.

Caterpillar petri dish choice assay

To determine caterpillar preference for plant tissue with different levels of salt stress, we conducted three two-choice assays and one three-choice assay (**Figure 1B**):

1. No salt-treated plant leaf disc (0 mM) vs. High salt-treated plant leaf disc (200 mM).
2. Medium salt-treated plant leaf disc (100 mM) vs. High salt-treated plant leaf disc (200 mM).
3. No salt-treated plant leaf disc (0 mM) vs. Medium salt-treated plant leaf disc (100 mM).
4. No salt-treated plant leaf disc (0 mM) vs Medium salt-treated plant leaf disc (100 mM) vs High salt-treated plant leaf disc (200 mM) (Pan*et al.* , 2019).

1.5 cm diameter leaf discs were excised from the fourth fully expanded leaf of each treatment plant (0 mM, 100 mM, and 200 mM). One leaf disc from each treatment was placed at opposite ends of a petri dish (10 cm X 1.5 cm) lined with 3% agar. A single 2nd instar*H. zea* caterpillar was placed inside the petri dish, and the petri dishes were sealed with parafilm to prevent the desiccation of herbivores and plant tissue (Marsack and Connolly, 2022). Caterpillars were given thirty minutes to make a choice in the petri dish, after which the leaf disc the caterpillar had settled on was recorded. This was referred to as the "first establish" (FE) parameter. Another parameter called the "first finish" (F1) was reported as the first leaf disc to be totally consumed by the caterpillar (**Supplementary Figure S1**). In the three-choice test, a "second finish" (F2) was also recorded, which was the second leaf disc to be completely consumed by the caterpillar. First and second finishes were recorded for a maximum of five days. After two days of feeding, leaf area consumed or caterpillar consumption rate was determined by photographing the remaining leaf disc area and analyzing images in ImageJ (**Supplementary Figure S2**)(Glozer, 2008; Connolly, Guiden and Orrock, 2017; Orrock *et al.* , 2018; Marsack and Connolly, 2022).

Moth oviposition assay

Gravid female *H. zea* moth oviposition preferences were tested for tomato plants with differing salt exposures (no salt – 0 mM and high salt – 200 mM) (**Figure 1C**). In a cage (24" x 24" x 36"), no-salt-treated and salt-treated plants of similar heights were placed 30 cm apart at opposite ends of the cage. Three pairs of

*H. zea*moths mated for 24 hours before the assay were released in the cage. The total number of eggs on each plant was recorded every day for 3 days (Paudel *et al.* , 2019). A 10% sucrose solution was provided to the moths for feeding during the assay. Dead moths were replaced as needed throughout the experiment, although this was only for 7 out of the total 41 replicates. The plant arrangement inside the cage was randomized to counter location biases in the setup.

Quantifying plant relative water content (RWC)

Leaf relative water contents (RWC) were estimated using the method as described by Mullan & Pietragalla, 2012). RWC readings of ten plants were taken per treatment.

Quantifying plant nutrient levels

Plants treated with 0 mM, 100 mM, and 200 mM for three days were dried and ground, following which they were sent to the Penn State Analytical Laboratory for ion content analysis (P, K, Ca, Mg, S, Mn, Zn, Cu, B, Al, Fe, and Na contents) (Huang and Schulte, 1985).

Plant defense responses

Defense proteins

To investigate the interactive effect of salt stress and insect herbivory on tomato defense responses, the activity of two jasmonic acid (JA)-inducible plant defense proteins: polyphenol oxidase (PPO: mOD/min/mg tissue) and trypsin proteinase inhibitor (TPI: % inhibition/mg protein) were measured (Tan *et al.* , 2018).

PPO and TPI activity levels were measured in three experiments: salt addition alone over 1, 3, and 5 days, insect herbivory for 3 hours, followed by salt addition, and short term (6 hours, 24 hours) and long term (3 days, 7 days) salt priming followed by insect herbivory.

A two-factorial assay with salt (0 mM, 200 mM) and herbivory (no herbivory, herbivory) was conducted. A single 5^{th}instar *H. zea* caterpillar was allowed to feed inside a clip cage (3.15 cm^2 leaf area) on the fourth fully expanded leaf of the plant as part of the herbivory treatment. Empty clip cages were placed on plants in the no herbivory treatment. Forty-eight hours after tomato plants were subjected to their respective treatments, 50 mg of leaf tissue was collected in liquid nitrogen and stored at -80degC until further analysis. PPO and TPI levels were analysed using a spectrophotometric method (Acevedo *et al.* , 2017). Leaf total protein content was estimated using a Bradford protein assay using a bovine serum albumin standard curve (Bradford, 1976).

Defense Gene Expression

To determine whether salt stress and insect herbivory induced tomato defense responses, the expression of defense-related genes was measured (**Supplementary Figure S4**).

A two-factorial assay with salt (0 mM, 100 mM, and 200 mM) and herbivory (no herbivory, herbivory) was conducted. Following insect herbivory for 3 hours, plants were treated with salt. Treated leaves were flash frozen in liquid nitrogen and stored at -80degC until further analysis.

For quantitative real-time polymerase chain reaction (qRT-PCR), leaves were homogenized in a Geno Grinder 2000 (OPS Diagnostics, USA), and total RNA was purified using TRIZOl. 1 µg of purified RNA was transcribed to cDNA using a High-Capacity cDNA Reverse Transcription Kit (Applied Biosystems, USA). qRT-PCR primers used are shown in**Supplementary Table S2** . qRT-PCR reactions using Power-Track SYBR Green PCR Master Mix (Applied Biosystems, USA) were run on a 7500 Fast Real-Time PCR System (Applied Biosystems, USA) using a previous protocol (Acevedo *et al.* , 2017).

Relative quantification of genes were calculated using the $2^{-C}{}_{\text{T}}$ method (Livak and Schmittgen, 2001), with 0 mM x no herbivory-treated plants as the reference group and ubiquitin as a housekeeping gene to normalize C_{T} values (Rotenberg *et al.* , 2006).

Volatile Organic Compound (VOC) Collection and Analysis

VOCs were collected from each of the plants within the various salt treatments. Individual tomato plants were placed in a 9-liter glass chamber, and VOCs were collected for 12 hours using a push-pull system at a push flow rate of 1 L/min and a pull flow rate of 0.8 L/min, following which plant fresh and dry shoot weights (FW and DW) were recorded. Ten plants were sampled per treatment. Volatiles were collected using adsorbent filters containing 45 mg HayeSep Q (Hutchison Hayes Separation Inc., USA) and were eluted by passing 150 µl dichloromethane through the traps into 2.0 ml glass vials equipped with a 250 µl glass insert. 5 µl of internal standards octane (40 ng μl^{-1}) and nonyl acetate (40 ng μl^{-1}) were added to the samples (Helms *et al.* , 2019).

VOCs were analyzed by GC-MS using an Agilent 7890A gas chromatograph equipped with an Agilent HP-5MS UI (30m x 0.25 mm x 0.25 µm) column coupled to an Agilent 5975C mass spectrometer configured with standard EI tune settings. Splitless injections were performed at an inlet temperature of 250°C using helium carrier gas with a constant flow rate of 0.7 mL/min. After 1 µl sample injection, the column was maintained at 40°C for 2 minutes. The oven temperature was increased by 10°C per minute and held at 300°C for 4 minutes. Target compounds were identified by comparing mass spectra and retention indices published in NIST17, Adams, and the University of Göteborg libraries (Helms *et al.* , 2017; Lin, Chen, *et al.* , 2021). Compounds with quality scores >85 were selected for further analysis. The abundance of each compound per gram of fresh plant tissue was calculated using the internal standard of nonyl acetate. A principal component analysis (PCA) was performed on the analyzed compounds for visual representation.

Statistical Analysis

Data was assessed for normality, and non-normal data was transformed using natural logarithms or square root transformations when necessary. If data transformations were unsuccessful, non-parametric tests were used to determine significance. A one-way ANOVA followed by Tukey's*post hoc* test was used for caterpillar RGR and plant nutrient content analysis. Caterpillar percentage leaf consumption area was compared using paired T-tests between the treatments for the two-choice assays. For the three-caterpillar choice assay, the percentage leaf area consumed was compared using the non-parametric Friedman's test, followed by Dunn's *post-hoc* test. Caterpillar first finishes and establishes were compared using Chi-square tests with 1:1 choice assumption. Differences in the average eggs laid on no-salt-treated and salt-treated plants were compared using a two-way ANOVA (repeated measures model). Plant defense protein levels (PPO and TPI) were analyzed using a mixed-effects model. Volatile emission differences under salt treatment were analysed using a permutational multivariate analysis of variance (PERMANOVA, with salt x herbivory as factors). Student's T-test was conducted between no-salt and salt treatments under herbivory and no herbivory for individual volatile compounds.

Results

Helicoverpa zea avoids salt-treated plants

H. zea caterpillars grow slower on salt-treated tomato plants

H. zea caterpillar relative growth rate (RGR) on plant tissues treated with varying amounts of salt was estimated in a detached leaf agar-cup-based assay as well as an on-plant assay. *H. zea*caterpillar RGR was negatively affected by salt treatment in a detached-leaf agar cup-based assay (**Figure 2A;** $\chi^2 = 8.174, P = 0.0168$, Dunn's *post-hoc* : 0 mM vs 200 mM: $P = 0.0205$, 100 mM vs 200 mM: $P > 0.9999$, 0 mM vs 100 mM: $P = 0.1236$) as well as an on-plant assay (**Figure 2B;**$F_{(2,\ 112)} = 19.63$, $P < 0.0001$, Tukey's*post-hoc* : 0 mM vs 200 mM: $P < 0.0001$, 100 mM vs 200 mM: $P = 0.6173$, 0 mM vs 100 mM: $P < 0.0001$).

H. zea caterpillars prefer to feed on tomato plants treated with a lower concentration of salt

In petri dish-based choice assays, *H. zea* caterpillars preferred to feed on tomato plant leaf discs treated with the least amount of salt. In a two-choice assay, percent leaf area consumed by *H. zea*caterpillars was significantly higher in no-salt (0 mM) plant tissue compared to high salt plant tissue (200 mM) (**Figure 3A;** $t = 4.861$, $df = 34$, $P < 0.001$) and moderate salt plant tissue (100 mM) compared to high salt plant tissue (200 mM) (**Figure 3A;** $t = 4.107$, $df = 25$, $P = 0.0004$). However, caterpillars did not show significant

consumption differences between 0 mM and 100 mM plant tissue (**Figure 3A;** t = 0.3521, df = 35,P = 0.7268). Caterpillars were observed to completely consume plant tissue treated with the least amount of salt first (first finish) (**Figure 3B** ; 0-200: χ^2 = 25,$P < 0.0001$; 100-200: χ^2 = 16.333, $P < 0.0001$; 0-100: χ^2= 4.172, $P = 0.0411$).

In a three-choice assay, the percentage leaf area consumed by *H. zea* caterpillars decreased significantly from 64.97 ± 5.873% in 0 mM to 39.67 ± 4.255% in 100 mM to 16.99 ± 1.298% in 200 mM treatments (**Figure 3C;** χ^2 = 37.93, $P < 0.0001$, Dunn's*post-hoc* all $P < 0.05$). *H. zea*caterpillars did not choose to feed or establish on any leaf preferentially at first (**Figure 3D;** First establish (FE): χ^2 = 1.310, df = 2, $P = 0.5194$); however, they showed differences in feeding over time. Caterpillars finished 0 mM leaves first, followed by 100 mM leaves (**Figure 3E;** First finish (F1): χ^2 = 35.429, df = 2, $P< 0.0001$; Second finish (F2): χ^2 = 20.222, df = 2, $P< 0.0001$). Refer to **Supplementary Figure S1** and**Supplementary Figure S2** for photographs of first finishes and leaf area consumption in the assay.

Gravid female *H. zea* moths oviposit preferentially on plants not treated with salt

H. zea gravid female moths showed a significant preference for no-salt-treated plants compared to salt-treated plants. After one day, the average number of eggs laid on no-salt-treated plants (12.56 ± 2.894) did not significantly differ from the average number of eggs laid on salt-treated plants (7.122 ± 1.641) (**Figure 4:** Day 1, $P = 0.2879$). However, there were significantly higher eggs laid on no-salt-treated plants (Day 2: 22.37 ± 3.6; Day 3: 30.66 ± 4.276) vs salt-treated plants (Day 2: 11.12 ± 1.995; Day 3: 14.95 ± 2.820) on the second (**Figure 4:** Day 2,$P = 0.0243$) and third days of oviposition (**Figure 4:** Day 3, $P = 0.0092$). Day ($F_{(1.42,\ 113.6)} = 45.27$, $P < 0.0001$) and salt treatment ($F_{(1,\ 80)} = 7.472$, $P = 0.0077$) accounted for a significant source of variation in the data. A significant interaction between day and salt treatment ($F_{(2,\ 160)} = 7.131$, $P = 0.0011$) was also observed, which would be apparent as the total number of eggs laid increases daily.

Salt application decreases relative water content and total protein content of plants

Salt addition significantly decreased leaf relative water content (RWC) from 78 ± 2.25% in 0 mM plant leaves to 64.92 ± 4.45% in 200 mM plant leaves (**Figure 5A;** $P < 0.05$). Salt addition significantly decreased leaf total protein content from 0.012 ± 0.0007 mg/ml/mg dry weight in 0 mM leaves to 0.0095 ± 0.0010 mg/ml/mg dry weight in 200 mM leaves (**Figure 5B** ; $P < 0.05$).

Salt-treatment of tomato plants does not change anti-insect herbivory protein levels

Salt addition alone does not influence PPO and TPI levels

There was no significant interaction between day and salt application on PPO and TPI levels (all $P > 0.05$). Furthermore, PPO and TPI levels did not significantly differ with salt application (all$P > 0.05$). There was a significant main effect of day on PPO levels ($F_{(1.432,\ 24.34)} = 7.446$, $P = 0.0062$), wherein PPO levels significantly increased from Day 1 to Day 3 in no-salt-treated leaves (**Figure 6A;** Šídák's multiple comparisons test, $P = 0.0351$). There was also a significant main effect of day on TPI levels ($F_{(1.927,\ 30.83)} = 9.239$,$P = 0.0008$), wherein TPI levels significantly decreased from Day 1 to Day 5 in no-salt-treated leaves (**Figure 6B;** Šídák's multiple comparisons test, $P = 0.0156$). Salt addition alone does not lead to significant changes in leaf PPO and TPI levels.

Salt addition after insect herbivory does not increase PPO and TPI levels more than that from herbivory alone

Salt was added to plants subjected to prior insect herbivory. There was no significant interaction between salt and herbivory on PPO and TPI levels (all $P > 0.05$). Furthermore, salt application did not affect PPO levels regardless of insect herbivory ($F_{(1,21)} = 0.0038$, $P > 0.05$). However, PPO levels were significantly higher in herbivory tissue than in no herbivory tissue, regardless of the salt application (**Figure 7A;** $F_{(1,\ 21)} = 83.17$, $P < 0.0001$). Salt application showed a significant main effect for TPI levels (**Figure 7B;** $F_{(1,\ 12)} = 8.261$, $P = 0.0140$). TPI levels were significantly higher in herbivory tissue than no herbivory tissue, regardless of

salt application (**Figure 7B;** $F_{(1, 8)} = 53.94$, $P < 0.0001$). Salt addition after insect herbivory does not increase PPO and TPI levels more than that by insect herbivory alone.

Salt addition over short and long durations does not prime plants for an increased-induced PPO and TPI response to insect herbivory

There was no significant interaction between salt and herbivory on PPO and TPI levels at all time intervals (all $P > 0.05$). Furthermore, salt application had no effect on PPO and TPI levels, regardless of insect herbivory (all $P > 0.05$). Herbivory, however, led to a significant increase in the PPO activity and TPI levels, regardless of salt application (**Figure 8A** : PPO;**Figure 8B** : TPI; all $P < 0.05$). There were no significant increases in PPO levels after herbivory at 7 days of salt treatment ($P > 0.05$). Salt addition over short and long durations did not prime tomato plants for a faster-induced response in terms of PPO and TPI levels to insect herbivory.

Na^+ ions accumulate in tomato plants upon salt treatment

Salt treatment of leaves led to increased leaf Na^+content in a dose-dependent manner (**Figure 9;** $F_{(2, 15)} = 262.2$, $P < 0.0001$). The Na^+ content in leaves was 786.8 ± 63.83 mg/kg in 0 mM treated leaves, 6575 ± 358.3 mg/kg in 100 mM leaves, and 10497 ± 374.8 mg/kg in 200 mM treated leaves.

Volatile Organic Compounds (VOCs)

Even though emission of specific VOCs (**Supplementary Table S4**) like 2-carene (**Figure 10A;** t = 2.43, df =18, $P = 0.0258$), [?]-phellandrene (**Figure 10B;** t = 3.514, df = 18,$P = 0.0025$), β-phellandrene (**Figure 10C;** t = 2.571, df = 18, $P = 0.0192$), [?]-humulene (**Figure 10D;** t = 2.504, df = 18, $P = 0.0221$), and β-caryophyllene (**Figure 10E;** t = 2.637, df = 18, $P = 0.0167$) decreased post salt treatment, total volatile emission per biomass (ng/g FW) post salt treatment remained unchanged (**Figure 10F;** $P > 0.05$). The overall blend of the plant volatiles was not significantly different between no salt and salt treatments (**Figure 10G;** PERMANOVA ($F_{(1,9)} = 2.122$, $P = 0.1125$).

Discussion

The data presented here demonstrates how exposure of tomato plants to an abiotic stress (salinity), can influence a biotic stress (insect herbivory). Our findings reveal that the bottom-up effects of salinity stress exert discernible influences on *H. zea* biology, including caterpillar growth rates, tissue selection, and moth oviposition. These effects are potentially mediated by reduced leaf relative water content, leaf total protein content, plant nutrient status, and ionic imbalances, and not entirely via anti-herbivore defense proteins, or the emission of specific plant volatiles. Usually, co-occurrence of multiple stressors can result in either individual dominant, additive, or synergistic effects (Holopainen and Gershenzon, 2010).

Many studies report a positive correlation between water stress and insect herbivory (Thaler and Bostock, 2004). Drought stress is known to drive insect outbreaks in certain cases (Mattson and Haack, 1987; Bao*et al.* , 2019; Lantschner, Aukema and Corley, 2019). The "plant stress hypothesis" states that insects would find it easier to grow on stressed plants due to the lower ability of plants to defend themselves. A study on leaf miners revealed that leaf miners exhibited accelerated development and shorter developmental times on tomato plants under elevated salinity (Han *et al.* , 2016). The carmine spider mite (*Tetranychus cinnabarinus*) showed faster development on strawberry cultivars under salinity stress (Cakmak and Demiral, 2007). In a no-choice assay, we observed a decrease in *H. zea*caterpillar growth rates with an increasing level of salinity in their plant diet (**Figure 2**). We did not observe any changes in leaf area consumption by caterpillars feeding on no salt and salt-treated substrates (unpublished results). This would indicate that lower caterpillar growth rates are not due to lower tissue consumption but are due to other factors. This observation substantiates the "plant vigor hypothesis," suggesting *H. zea* prefers plants grown in non-saline conditions, as they would be healthier and exhibit a "higher vigor." Salt priming of *Arabidopsis thaliana* seeds led to elevated ROS and glucosinolates, which was correlated to lower performance of the generalist common cutworm caterpillar (*Spodoptera litura*) (Xiao *et al.* , 2019). Another study demonstrated that *Spodoptera exigua* larvae were less likely to damage tomato plants treated with > 50 mM NaCl, consumed less leaf tissue, displayed decreased

pupation rates, and had shorter lifespans (Marsack and Connolly, 2022). It is evident from many such studies that the indirect influence of salinity stress on insects is contingent upon various factors, including the insect feeding guild and plant species.

Several factors, such as the levels of anti-insect herbivore defense proteins, leaf water content, leaf nutrient changes, and ionic toxicity, may collectively contribute to the observed reduction in *H. zea*caterpillar growth rates. Dombrowski 2003 reports salt stress-induced accumulation of proteinase inhibitor II (*PIN2*) transcripts and amplified tomato responses to wounding via the wound-signalling gene*LOXD* transcripts. To investigate the interactive effect of salt stress and insect herbivory on tomato defense responses, we measured the activity of two jasmonic acid (JA)-inducible plant defense proteins: polyphenol oxidase (PPO) and trypsin proteinase inhibitor (TPI) (Tan*et al.* , 2018). However, in spectrophotometric assays, we did not observe any impact of salt addition on tomato PPO and TPI levels (**Figure 6**). Similarly, a prior study (Winter *et al.* , 2012) failed to detect salt-stress-induced proteinase inhibitor transcripts or herbivore-induced plant volatiles (HIPVs). It is possible, however, that 200 mM NaCl depicts a highly stressful concentration where plants choose to maintain nutrient homeostasis and growth rather than investing resources in defense metabolites (Abrol, Vyas and Koul, 2012). Investigation of low concentration salt priming could provide more insights into this hypothesis (Xiao *et al.* , 2019). Gene expression studies showed that *GAME4* (glycoalkaloid metabolism gene 4) and *AspPI* (aspartic proteinase inhibitor) gene expression increases significantly under herbivory and high salt (**Supplementary Figure S4)** , indicating that salt could prime plants for a higher induced response to insect herbivory through certain defenses such as glycoalkaloids or aspartic proteinase inhibitors. A study in maize showed that although salinity alone did not induce defense gene expression (*Zm-Bx1* and *Zm-SerPIN*), joint salinity and insect herbivory did (Forieri, Hildebrandt and Rostás, 2016). There are some indications of crosstalk between salinity and insect herbivory pathways, although the precise defenses and genes involved need to be investigated further.

Consistent with prior studies, we observed a substantial reduction in leaf relative water contents following salt treatment (**Figure 5**) (Cuartero and Fernández-Muñoz, 1998; Wang, Haseeb and Zhang, 2021). A study (Lin, Paudel, *et al.* , 2021) reported *M. sexta*larvae consumed lower amounts of plant tissue under severe drought stress. *M. sexta* larvae showed compensatory feeding in later instars by insects feeding more on low-water-containing diets (probably to make up for water deficiencies) (Ojeda-Avila, Woods and Raguso, 2003). While lower water contents in diet could account for lower caterpillar growth rates, additional factors such as altered nutrient availability and ionic toxicity can have additive or synergistic effects.

According to a study in soybean, salt-stressed plants are photosynthetically less productive and would lead to lower insect growth due to their lower nutritional quality (Najjar *et al.* , 2018). Many plants, in their bid to tolerate salt stress, typically possess the capacity to selectively exclude Na^+ and Cl^- ions while facilitating water uptake (Munns, 2005). For example, the halophyte *Hordeum marinum* starts accumulating Na^+ and Cl^- ions only after exposure to 450 mM NaCl (Garthwaite, von Bothmer and Colmer, 2005). However, a study on transgenic salt-tolerant tomato plants reported salt accumulation in tomato leaves at much lower concentrations (Zhang and Blumwald, 2001). Additionally, another study demonstrated the accumulation of Na^+ in older tomato leaves, possibly as a protective mechanism to shield younger leaves from salt stress (Khelil, Menu and Ricard, 2007). A study under low salt conditions (5 mM) showed an increase in Na^+, Cl^-, C, S, Zn^{2+}, and Cu^{2+} in *A. thaliana* shoots (Hongqiao *et al.* , 2021). In line with these studies, we detected an accumulation of Na^+, Zn^{2+}, Ca^{2+}, Mg^{2+}, and Mn^{2+} ions in salt-stressed leaves (**Figure 9, Supplementary Figure S3**). Notably, the micronutrients Zn^{2+} and Mn^{2+} are components of superoxide dismutases (Cu-Zn SOD and Mn-SOD) that catalyze H_2O_2 formation from superoxide radicals. The observed accumulation of Zn^{2+} and Mn^{2+} ions with increasing salt treatment may be indicative of their role in enhancing NaCl tolerance, as demonstrated by prior research in *A. thaliana* (Wang *et al.* , 2004; Liu*et al.* , 2015). Like some other studies, our study also shows that K^+ uptake is hampered possibly through high-affinity K^+ transporters, whereas Ca^{2+} and Mg^{2+} levels increase with salt application, possibly as salt tolerance mechanisms by the plant (Carter *et al.* , 2005; Fuchs *et al.* , 2005; Valdez-Aguilar, Grieve and Poss, 2009; Nieves-Cordones *et al.* , 2010; Koksal *et al.* , 2016; Akter and Oue, 2018). It is interesting to note that many insects seek salts actively, and the accumulation of sodium can offset the negative effects of plant secondary metabolites on

insect herbivores (Joern, Provin and Behmer, 2012; Kaspari, 2020; Marroquin, Holmes and Salazar, 2023). However, a high level of Na^+ ions could disrupt the insect's osmotic balance, interfering with the excretory, nervous, digestive, and respiratory systems (Silver and Donini, 2021).*Helicoverpa armigera* larvae grew better on an artificial diet with a lower amount of sodium, indicating that higher sodium concentrations could be toxic to insects (Xiao *et al.* , 2010). We also observed lower caterpillar growth on a salt-containing artificial diet (**Supplementary Figure S5**), which indicates that higher salt levels (Na^+ and Cl^- ions) in the diet are detrimental to insect growth.

We do not disregard the influence of other chemical defenses or essential nutrients that are not measured here on *H. zea*caterpillar performances. For instance, glycoalkaloids such as tomatine increase in salt-stressed plants and could potentially lead to decreased caterpillar growth and deter caterpillar feeding (Friedman, 2002; Han*et al.* , 2016; Dong *et al.* , 2020). Studies also report that salinity affects the production of phenolics, terpenoids, and cyanogenic glycosides in different plants, all of which can affect insect growth (Wahid and Ghazanfar, 2006; Mahmoudi *et al.* , 2010; Ballhorn and Elias, 2014; Wang *et al.* , 2015; Marroquin, Holmes and Salazar, 2023). Tomato plants under salt stress would need to significantly increase their alkaloid production within three days for this hypothesis to hold. Interestingly, we observed that salt treatment alone did not lead to upregulation of *GAME4* , an upstream gene in the steroidal alkaloid biosynthesis pathway (Dzakovich, Francis and Cooperstone, 2022). We did, however, see a higher induced response of*GAME4* in herbivore-damaged salt-stressed plants, which indicates some salinity-based priming against insect herbivory. Analyzing alkaloid contents would help validate this hypothesis. However, Thaler & Bostock 2004 report that salt stress by itself does not alter JA-inducible responses, which could be why we did not see any differences in gene expression and enzyme levels between salt treatments in no herbivory tissue.

Lastly, it is important to note that the effects of salt stress on insect herbivores can vary depending on the insect species and the severity of the salt stress. Some insect species can be more salt-tolerant than others. Our findings collectively emphasize that in salt-stressed plants, factors such as nutrient imbalances, ionic toxicity, and lower relative water contents (alone or in conjunction) (Martinez *et al.* , 2012) cause lower *H. zea* herbivore performances than alterations to anti-insect herbivore defense protein levels.

In petri dish-based choice assays, *H. zea* caterpillars avoided plants treated with salt (**Figure 3**). The initial behavior of the insect caterpillars revealed a random selection of leaves for feeding, as evident by the "first establish" parameter. This indicates that cut leaf-disc-based volatile or visual cues do not influence insect behavior. However, as time progressed, a discernible shift occurred, with caterpillars increasingly favoring leaves treated with lower salt concentrations for consumption. This caterpillar feeding preference was seen in caterpillar leaf area consumption as well as the "first finish" parameter. The observed change in caterpillar feeding preference complemented caterpillar growth rates, suggesting that caterpillars preferred to feed on no-salt-containing diets, which would result in a higher growth rate. Insect preference for plants under lower salinity is also observed in other studies (Quais *et al.* , 2020; Ali *et al.* , 2021; Marsack and Connolly, 2022).

Like the caterpillars, we observed a clear preference of *H. zea*moths for no-salt-treated plants (**Figure 4**). Conversely, a study on monarch butterflies showed no difference in female oviposition between no-salt and salt-treated plants (Mitchell *et al.* , 2019). The "optimal oviposition theory" or "mother knows best hypothesis" suggests that female moths exhibit a preference for laying their eggs on plant hosts that will maximize the fitness and performance of their offspring (Jaenike, 1978; Valladares and Lawton, 1991; Courtney and Kibota, 2017). Female moths utilize various parameters to determine suitable host plants for oviposition. For many noctuid lepidopterans, olfactory cues have been identified as crucial in locating and selecting host plants (Jost and Pitre, 2002; Rojas, Virgen and Cruz-López, 2003; McCallum *et al.* , 2011). These cues include volatile compounds emitted by plants, which can either attract or repel moths based on their preferences and adaptations (De Moraes, Mescher and Tumlinson, 2001; Bruce, Wadhams and Woodcock, 2005). For example, isothiocyanates act as oviposition stimulants for the diamondback moth *Plutella xylostella* (Renwick *et al.* , 2006), and pyrrolizidine alkaloids stimulate oviposition in the cinnabar moth (*Tyria jacobaeae*) (Macel and Vrieling, 2003). Studies report that salt stress changes the emission of three terpenes, (Z)-beta-ocimene, 2-carene, and β-phellandrene, which have been quantitatively correlated

with salt concentration (Tomescu *et al.* , 2017). Green leaf volatiles such as (Z)-3-hexenal and terpenoids like β-phellandrene and α-pinene have been implicated in attracting lepidopteran moths for oviposition (Huang *et al.* , 2020; Agbessenou *et al.* , 2022; Sisay *et al.* , 2023). Like the abovementioned studies, we also observed decreased levels of β-phellandrene as well as 2-carene, α-phellandrene, β-caryophyllene, and α-humulene in salt-treated plants (**Figure 10**). Insect responses to plant volatiles depend on the insect species, the specific volatile compound in the volatile blend, and the concentration of relevant volatiles. Decreased constitutive emissions of β-phellandrene might cause lower *H. zea* moth oviposition on salt-treated plants. We did not observe any differences in total volatiles emitted per gram of fresh weight between stressed and unstressed plants, as corroborated by some other studies (Loreto and Delfine, 2000; Teuber *et al.* , 2008; Forieri, Hildebrandt and Rostás, 2016). However, the total volatiles emitted by the whole plant could be a more ecologically relevant unit.

Furthermore, moths may also rely on visual and tactile cues, including leaf shape, color, and texture, as indicators of plant quality for egg-laying (Rojas and Wyatt, 1999; Jakobsson *et al.* , 2017; Keerthi *et al.* , 2023). Plant physical characteristics, such as the presence and density of trichomes and leaf hairs, can likewise influence moth oviposition choices. For example, oviposition by *P. xylostella* on *A. thaliana* decreases with an increasing density of leaf trichomes (Handley, Ekbom and Ågren, 2005). The presence of glandular trichomes on a wild potato species (*Solanum berthaultii*) acts as a deterrent to oviposition by the potato tuber moth (*Phthorimaea operculella*) (Malakar and Tingey, 2000). However, some studies have reported that moths tend to lay eggs on plant parts exhibiting higher trichome densities and concentrated defense chemicals (Thomson, 1987). Additionally, the nutritional composition of host plants, including nitrogen levels, sugar content, and secondary metabolites, plays a vital role in shaping moth oviposition decisions (Heisswolf, Obermaier and Poethke, 2005; Chen, Ruberson and Olson, 2008; Gripenberg *et al.* , 2010). We did not observe any changes to leaf trichome density under salt stress (unpublished results). However, salt stress, leading to lower water availability, may potentially increase the concentration of chemicals in trichomes. Trichomes could also lose turgor and decrease in size, thus influencing moth oviposition. The influence of trichome-level changes on *H. zea* oviposition decisions cannot be ignored and remain to be investigated.

Lastly, moth host finding and consequently oviposition can also be altered due to local changes in relative humidity (Godfrey and Holtzer, 1991; Wolfin *et al.* , 2018). Salt stress would lead to stomatal closure and reduced transpiration, which would in turn reduce local humidity. We observed statistically non-significant decreases in leaf relative humidity under salt treatment for 5 days (preliminary data). These differences, although statistically non-significant, could still be ecologically significant for an ovipositing *H. zea* moth.

Conclusion

The presence of salt as an abiotic stressor in agricultural soils is a serious problem, with research focusing primarily on plant tolerance to salt. However, the inclusion of biotic stressors, such as insect pest infestations, leads to varied plant responses. Understanding plant responses under interacting stresses is vital to developing better crop varieties and insect control. Moreover, salinity-influenced changes to plant quality and composition affect insect herbivores feeding on these plants.

In our study, we observed that a notorious pest, *Helicoverpa zea,*performed poorly on salinity-affected tomato plants. Although our study focused exclusively on a leaf-chewing, generalist herbivore, it would be interesting to investigate how different insect feeding guilds (specialist leaf chewers, phloem feeders, gall makers, leaf miners, etc.) respond to soil salinization. Our work demonstrates the need to study how insect pests are indirectly affected by environmental changes, as this has implications for their survival and performance in agricultural settings. Thus, along with deciphering the molecular basis behind plant responses to multiple stresses, we also need to understand their ecological implications so that we can formulate accurate IPM strategies.

For future work, we wish to investigate salinity-based changes to plant indirect defenses. Salinity can influence other trophic levels in plant-insect interactions, including predators, parasitoids, and local microbiota. Insect quality as a food source for predators or a potential host for parasitoids and microbes drives predator and

parasitoid choices, which would in turn affect insect population dynamics in the field.

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Figures

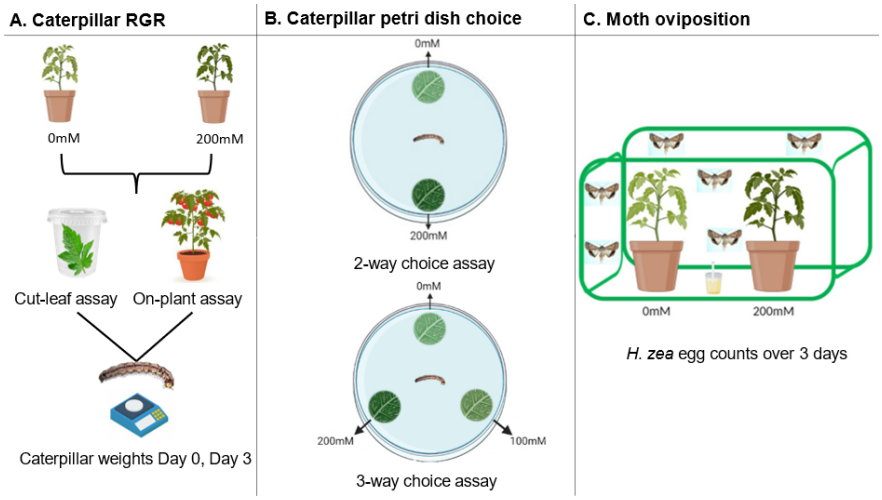

Figure 1: A. Caterpillar RGR no choice assay setup, B. Caterpillar petri dish-based choice assay setup, C. H. zea moth oviposition experimental setup.

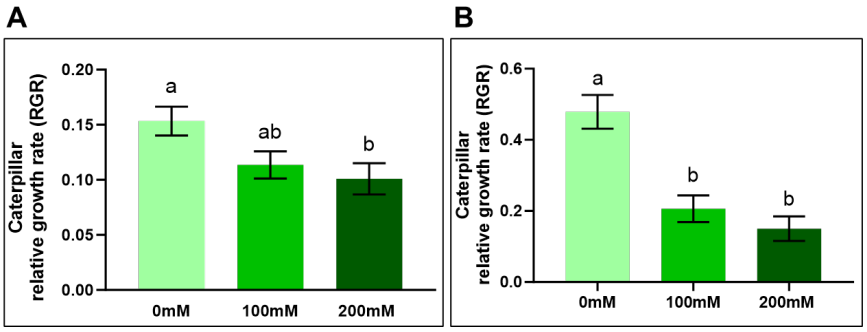

Figure 2: H. zea caterpillar relative growth rate (RGR) feeding on tomato plants with varying levels of salinity. A. Detached leaf agar-cup based caterpillar RGR estimation. B. On-plant based caterpillar RGR estimation. Bars represent mean (± SEM) (A: n = 39, Kruskal-Wallis, Dunns post-hoc; B: n = 36, one-way ANOVA, Tukey's post-hoc, different letters indicate significant differences $P < 0.05$).

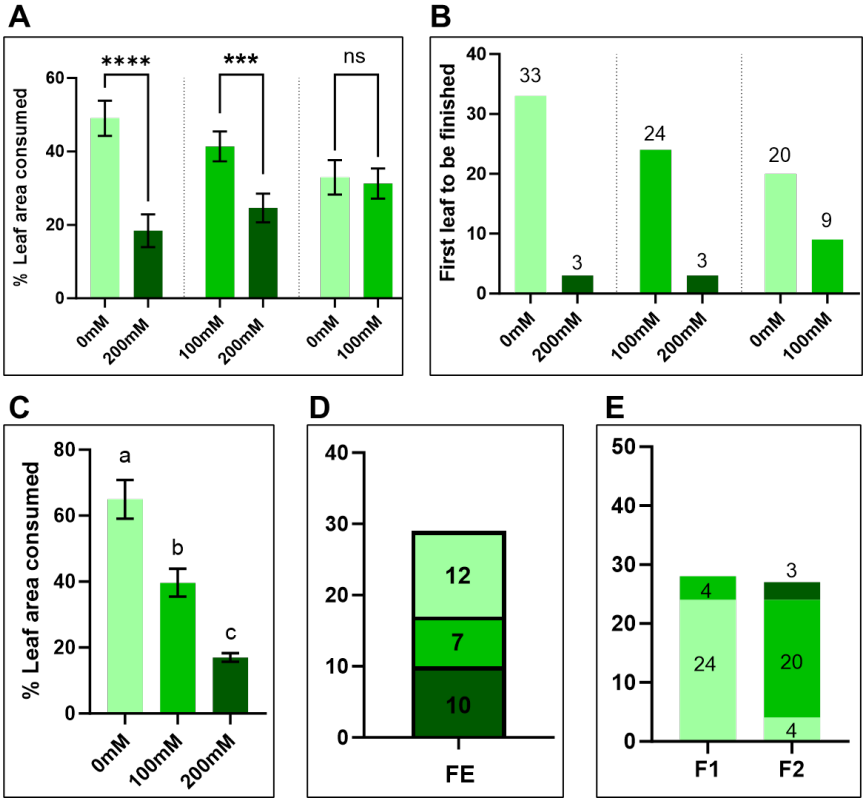

Figure 3: Petri dish-based two-choice and three-choice H. zea feeding preference assay on tomato plant leaf discs treated with varying levels of salinity. A. Bars represent mean (± SEM) percentage leaf area consumed after 48h of caterpillar feeding in paired two-choice assays. (0-200 n = 36, 100-200 n = 26, 0-100 n = 36). B. First leaf to be finished in a dual choice given to insect caterpillars. (0-200: n = 36, 100-200: n = 27, 0-100: n = 29). Three-choice assay (n = 29): C. Bars represent mean (± SEM) percentage leaf area consumed after 48h of caterpillar feeding (n = 29, Kruskal-Wallis, Dunns post-hoc, different letters indicate significant differences $P < 0.05$). D. First leaf that a caterpillar is recorded on after thirty minutes (first establish – FE). E. First (F1) and second leaf (F2) to be finished.

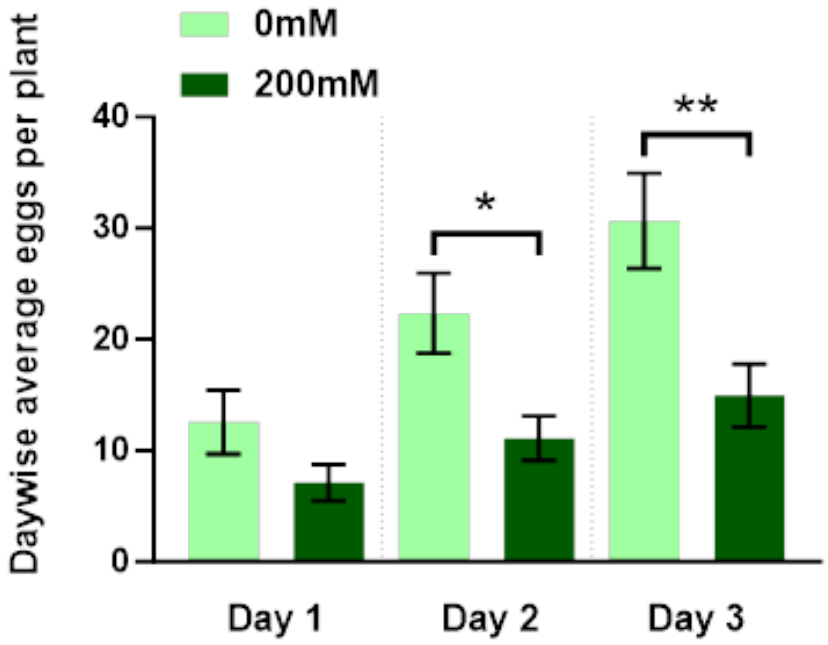

Figure 4: Female H. zea moth oviposition on no salt and high salt-treated plants. Bars represent mean (± SEM) numbers of H. zea eggs laid/ plant /day (n = 41, two-way ANOVA, Tukey's post-hoc, * $P < 0.05$, ** $P < 0.01$).

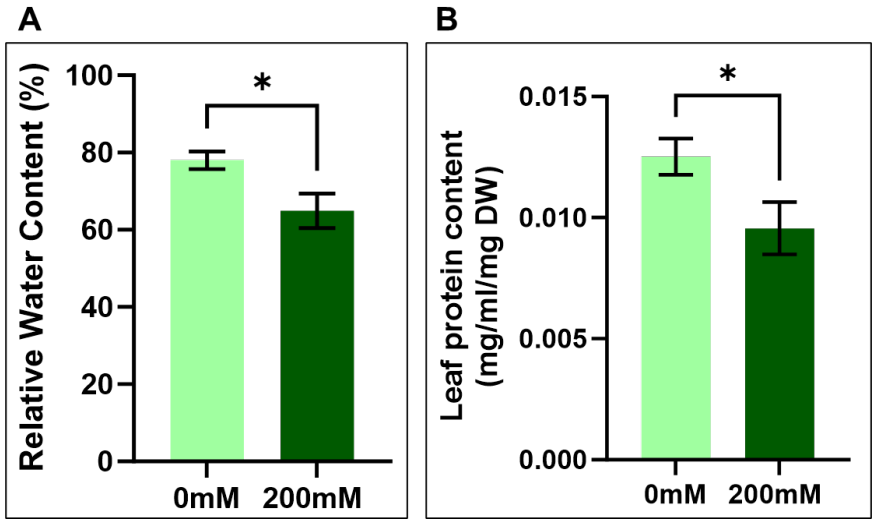

Figure 5: Salt addition decreases A. leaf Relative Water Content (RWC %) and B. leaf total protein content in tomato plants (mg/ml/mg DW). Bars represent mean (± SEM) (n = 10, student's T-test, *$P < 0.05$)

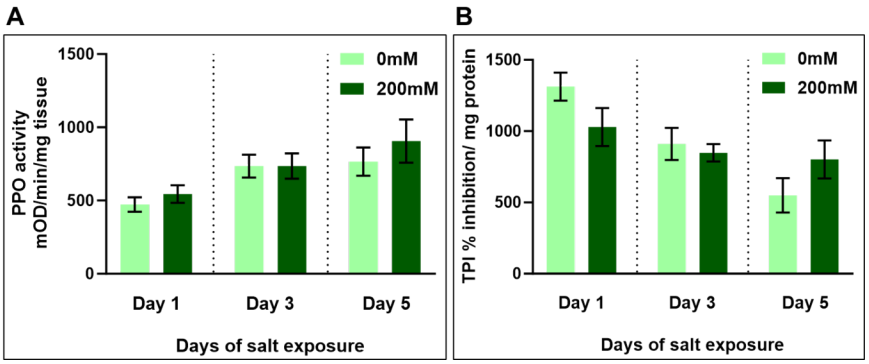

Figure 6: Effect of salt addition on A. PPO activity and B. TPI levels in tomato leaves 1, 3, and 5 days after salt treatment. Bars represent mean (± SEM) (n = 9, mixed-effects analysis * P < 0.05).

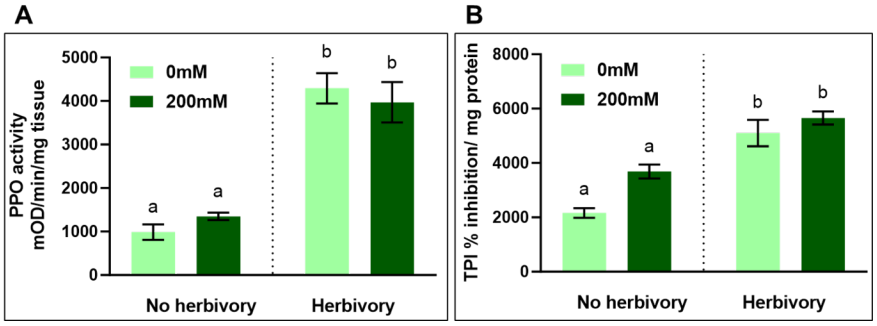

Figure 7: *H. zea* herbivory followed by salt treatment does not significantly change A. PPO activity and B. TPI levels in tomato leaves further than that by herbivory alone. Bars represent mean (± SEM) (n = 7, mixed-effects analysis, different letters indicate significant differences $P < 0.05$).

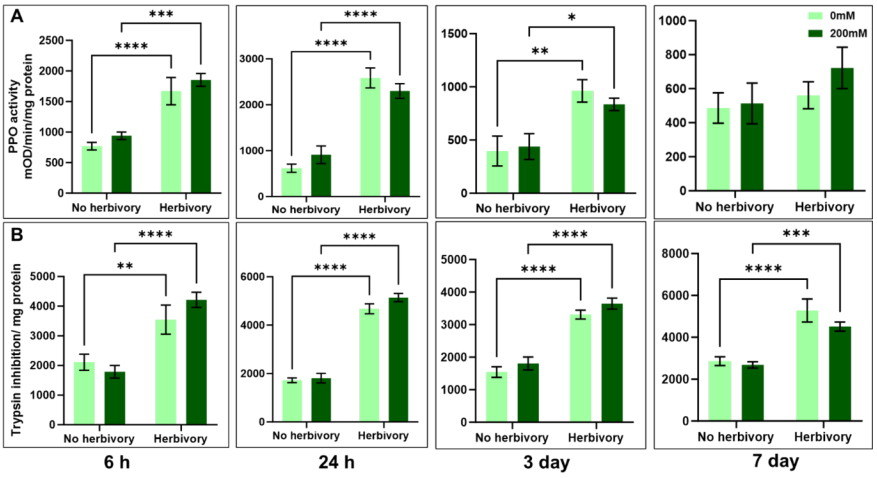

Figure 8: Short term (6 h, 24 h) and long term (3 days, 7 days) salt pre-treatment does not prime plants for an increased induced response in terms of A. PPO and B. TPI levels to *H. zea*herbivory. Bars represent mean (± SEM) (n = 8-11, mixed-effects analysis, * $P < 0.05$, ** $P < 0.01$, ***$P < 0.001$, **** $P < 0.0001$).

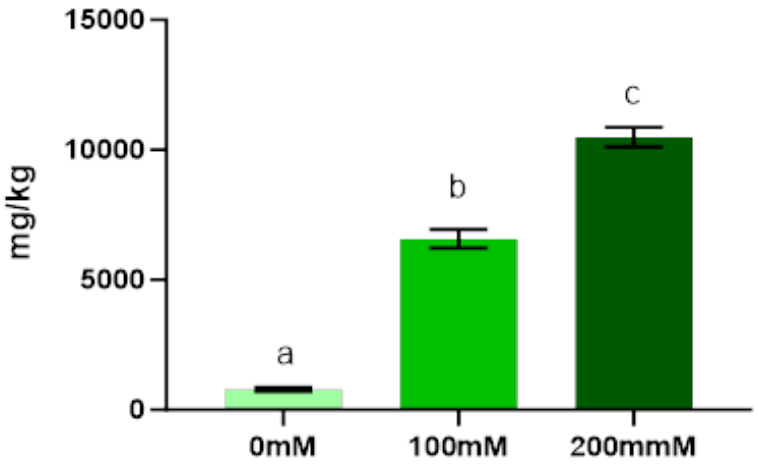

Figure 9: Na content (mg/kg) of tomato plant leaves treated with 0 mM, 100 mM, and 200 mM of NaCl. Bars represent mean (± SEM) (n = 6, one-way ANOVA, Tukey's *post-hoc* test, different letters indicate significant differences $P < 0.05$).

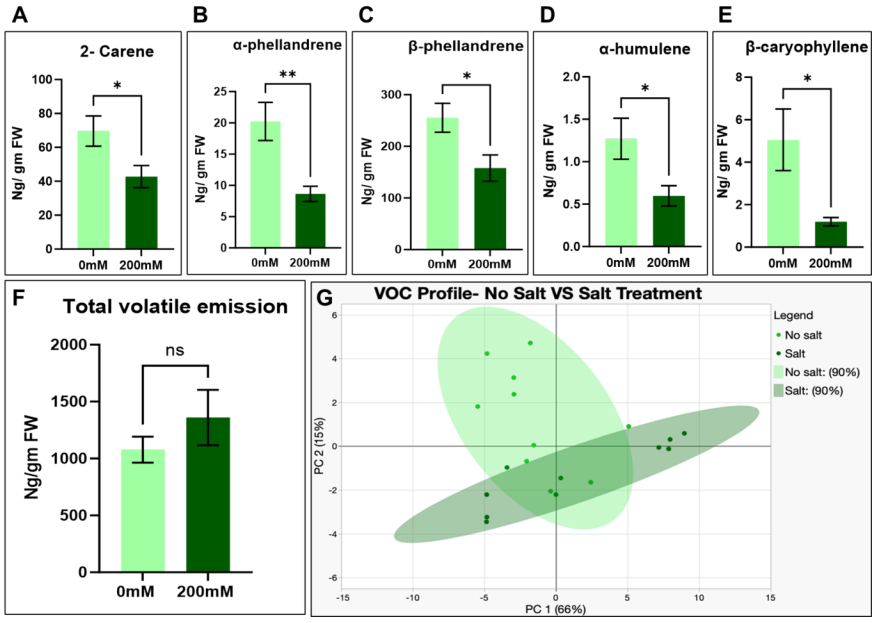

Figure 10: (A-E). Differences in specific VOC emission (ng/g fresh weight) by tomato plants under no salt and salt treatments. Bars represent mean (± SEM) (n = 10, Students T-test, * $P < 0.05$, ** $P < 0.01$). (F) Total volatile emission (ng/g fresh weight) of 0 mM and 200 mM treated plants. (G) PCA plot of the volatile blend from no salt and salt-treated plants.