RESEARCH PAPER

Response of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) to salt-stressed maize plants

Zai-Ling WANG[1,2] (iD), Muhammad HASEEB[3] and Run-Zhi ZHANG[1,2]

[1] Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing, China
[2] University of Chinese Academy of Science, Bejing, China
[3] Center for Biological Control, College of Agriculture and Food Sciences, Florida A&M University, Tallahassee, Florida, USA

Correspondence
Muhammad Haseeb, Assistant Professor, Center for Biological Control, College of Agriculture and Food Sciences, Florida A&M University, 1740 South Martin L. King, Jr. Blvd., 308 South Perry Paige Bldg., Tallahassee, FL 32307-4100.
Phone: 1+(850) 412 7057
Fax: 1+(850) 412 7263
Email: muhammad.haseeb@famu.edu
Runzhi Zhang, Department of Entomology, Institute of Zoology, Chinese Academy of Sciences, #1-5 Beichen West Rd., Chaoyang, Beijing 100101, China.
Phone: 86-10-64807270
Fax: 86-10-64807099
Email: zhangrz@ioz.ac.cn

Abstract

Salt-stressed maize is an economically important crop in many arid and semi-arid regions of the world where soil salinization is most common, and the invasive fall armyworm (FAW) *Spodoptera frugiperda* threatens global maize production. It thus poses a puzzle of whether FAW populations feeding on salt-stressed maize plants are becoming more or less invasive. Here, we evaluated the FAW response to salt-stressed maize plants by examining effects of salt-stressed maize plants on FAW survival, development and fecundity. We found a longer larval development time (salt-stressed, 12.9 ± 0.8 d; non-stressed, 11.3 ± 0.4 d), but unaffected survival rate and pupal mass accumulation in FAW feeding on salt-stressed maize plants. Moreover, the lifetime egg production of FAW females feeding on salt-stressed maize plants (633.5 ± 62.7 eggs) was reduced by nearly half compared with those feeding on non-stressed maize plants (1255.9 ± 70.3 eggs). Overall, FAW showed a negative response to salt-stressed maize plants. Due to limited population increase potential, FAW populations feeding on salt-stressed maize plants should pose less of a problem than ones feeding on non-stressed maize plants do. In practice, salt-stressed maize plants are quite common in arid and semi-arid regions where the relatively high-salinity groundwater is often used to irrigate maize plants, potentially limiting FAW population size. Thus, salt-stressed maize plants would contribute to practical applications of integrated pest management (IPM) strategies in controlling FAW.

Key words: development, fall armyworm, fecundity, IPM, survival

Introduction

About 350 million hectares of land throughout the world are impacted by increasing salt levels (Rengasamy 2006). Due to conversion of wetlands or forests into agricultural land, the redistribution of soil salts leads to salinization. Soil salinization has been found in various climatic and geographic regions even if it is most common in arid regions (Mittal *et al.* 2012). Salt addition not only has left extensive areas of agricultural land degraded, but also has negative impacts on crop plant growth and productivity (Orcutt & Nilsen 2000). In recent years, increasing attention has been given to salt-stressed crop plants as a vital part of agricultural

production. Since herbivores depend on host plants acting as shelter and food source (Dicke & Baldwin 2010; Howe & Jander 2008), salt-stressed crop plants could impact their herbivorous consumers. Salt-stressed plants can impede survival, development and fecundity of herbivores probably due to water limitation (Huberty & Denno 2004), decreased nutritive quality of host as food (Han *et al.* 2014; Inbar *et al.* 2001), or enhanced plant chemical defense (Gutbrodt *et al.* 2011).

Salt-stressed crops are considered to be of not only economic significance in arid and semi-arid regions but also a substantial constraint to herbivorous pest growth (Debouba

et al. 2006). One of the mechanisms may be that herbivores face lower water availability because of the increased salt concentration in plant sap (Romero-Aranda *et al.* 2001; Soria & Cuartero 1997). Sodium chloride (NaCl) is one of the key ingredients in salt-stressed plants triggering loss of intracellular water in herbivores (Mahajan & Tuteja 2005). Besides, herbivores fail to harvest sufficient nutrients probably due to the impact of salt-stressed plants on their nitrogen metabolism, which may reflect osmotic or specific interactions of NaCl in several steps of nitrogen assimilation (Han *et al.* 2016). Enhanced plant chemical defense in salt-stressed plants may also affect herbivores *via* increased accumulation of secondary metabolism (Ballhorn & Elias 2014). However, to date responses of herbivores to salt-stressed plants still remain unclear, the direction of responses (neutral, positive, or negative) depends on the feeding strategy adopted by herbivores (chewing or sap-feeding insects) and feeding specialization (specialist or generalist) (Gutbrodt 2011; Inbar *et al.* 2001).

Since many maize cultivars are salinity-tolerant in natural ecosystems, salt-stressed maize is an economically important crop in many arid and semi-arid areas where soil and groundwater salinity is arguably the biggest challenge in crop production (Barron *et al.* 2003; Hansen & Indeje 2004; Nouna s 2003; Parida & Das 2005). The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is an invasive pest that principally attacks maize, the underlying economic losses can reach between 15 and 73% worldwide (Fan e 2020; Wu *et al.* 2021a). FAW larvae often penetrate and feed within the maize plant tissues (Ren *et al.* 2020), so they have an extremely close relationship with maize plants. Similar to other herbivores, FAW seems to be impacted by salt-stressed maize plants, and its response (neutral, positive, or negative) to salt-stressed maize plants deserves further study.

In this study, we analyzed the response of FAW to salt-stressed maize plants by studying effects of salt-stressed maize plants on FAW survival, development, and fecundity. As such, we addressed three main questions: 1). Effects of salt-stressed maize plants on larval and pupal survival of FAW, 2). Effects of salt-stressed maize plants on FAW larval and pupal development times, and pupal mass, and 3). Effects of salt-stressed maize plants on FAW fecundity. Our analysis of FAW response to salt-stressed maize plants provides a valuable supplement to ecological theory about responses of herbivores to salt-stressed plants. From an IPM perspective, at present global agriculture is under the increasing threat by FAW (Wu *et al.* 2021b). Given the rapidly escalating economic impact of FAW, understanding effects (neutral, positive, or negative) of salt-stressed maize plants on FAW contributes to practical applications of IPM strategies in controlling FAW.

Materials and methods

Insects

The FAW colony was maintained in the laboratory at the Yellow River Delta experimental station (37.67 N, 118.91 E) of Institute of Zoology, Chinese Academy of Sciences located in Dongying, Shandong Province, China, since Dongying is characterized by salt-affected soils. Larvae were reared on maize plants (the same variety as used in the experiments) in cages (40 × 40 × 200 cm). Subsequently, the emerging FAW adults were paired and introduced into a plastic container (16 × 22 × 8 cm high). We provided a 10% honey water solution once a day. All FAW individuals were reared at 27 ± 1°C, 60 ± 20% RH, and a photoperiod of 12:12 (L:D). Then 3rd-generation emerging 1st-instar larvae were collected for the experiments.

Salt-stressed and non-stressed maize plants

Our preliminary experiments suggested it was hard to monitor FAW individuals feeding directly on maize plants (larvae are fed upon within the whorl), so we instead fed them leaves in Petri dishes to better follow FAW individuals from their emergence as larvae until death. Non-stressed and salt-stressed maize leaves were collected from the greenhouse of the experimental station. The experimental plots had been planted with salt-stressed and non-stressed maize (Jidan 209, a variety resistant to salinity) for 6 consecutive years and not been manured before. The soil had two salinity levels (0 mmol/L and 75 mmol/L) under artificial conditions, and the maize nutrient solution and NaCl levels were renewed every 7 days after the initial nutrient and stress application. No chemical pesticides were applied to the plots during the entire maize-growing season. Over the course of experiments, the youngest fully expanded main stem leaves of maize (the fourth leaf from the shoot apex) were collected at the budding stage. Therefore, FAW individuals feeding on non-stressed and salt-stressed maize leaves were identified as non-stressed and salt-stressed treatments, respectively.

Effects of salt-stressed maize plants on FAW survival, development, and fecundity

For each of the non-stressed and salt-stressed treatments, 100 FAW individuals were selected. Each newly emerging (< 12 h) 1st-instar FAW larva was introduced into a Petri dish (9 cm diameter) including 30 g fresh non-stressed (0 mmol/L) or salt-stressed (75 mmol/L) maize leaves, the leaves were supplied at 24 h intervals. Subsequently, the larvae were monitored daily, the larval development time

and larval survival (survival rate of larvae reaching pupal stage) were recorded. When last-instar larvae were ready to pupate, they were separately transferred to a plastic cup with 30 g no-salt treated or salt treated leaves. Each plastic cup contained the same amount of loam without (0 mmol/L) or with (75 mmol/L) soil salinity, the loam soil kept at 50% moisture level. Then we monitored the plastic cup daily, and recorded the pupal development time, and pupal survival (survival rate of pupae reaching adult stage). Pupal mass of each individual was measured by analytical balance BS124S (Sartorius, Goettingen, Germany) when it had pupated completely. Emerging FAW adults from the same treatment were paired and introduced into a new plastic cup. Adult individuals were provided with a honey water solution diluted at 10% once a day and monitored daily. The female adults were followed from emergence to death by recording the number of eggs laid. Thus, the lifetime egg production and adult lifespan were recorded. All experiments were performed at 27 ± 1°C, 60 ± 20% RH, 12 L:12D photoperiod in the lab incubators KBF720 (Binder, Tuttlingen, Germany). The test was replicated three times, and a total of 300 FAW individuals for non-stressed or salt-stressed treatment were tested for this experiment.

Data analysis

Descriptive statistics were given as the mean values and standard errors of the mean. All traits were analyzed using independent-sample t-tests. In all tests, P values < 0.05 were considered significant. All statistical analyses were conducted using the SPSS 20.0 software (IBM, Armonk, NY, USA).

Results

### Effects of salt-stressed maize plants on FAW survival

In the larval stage, the survival rate of FAW individuals feeding on salt-stressed maize plants was not significantly impacted (non-stressed, mean ± SE = 86.0 ± 6.1%; salt-stressed, 80.0 ± 8.4%; $t = 0.579$, $df = 4$, $P = 0.594$). Similarly, there was no difference in pupal survival between non-stressed (79.1 ± 5.1%) and salt-stressed (75.3 ± 2.9%) treatments ($t = 0.653$, $df = 4$, $P = 0.55$) (Fig. 1).
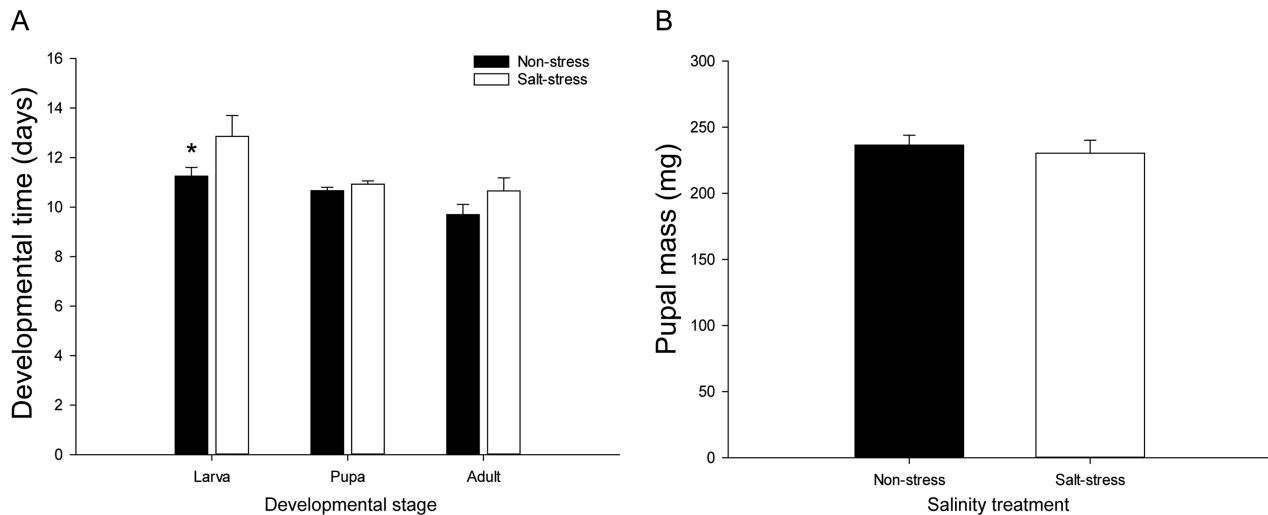
Effects of salt-stressed maize plants on FAW development

Compared to FAW individuals feeding on non-stressed maize plants (11.3 ± 0.4 d), those feeding on salt-stressed maize plants exhibited a longer larval development time (12.9 ± 0.8 d) ($t = 17.59$, $df = 289.884$, $P < 0.001$). However, salt-stressed maize plants did not impact the pupal development time (non-stressed, 10.7 ± 0.1 d; salt-stressed, 10.9 ± 0.1 d; $t = 1.378$, $df = 145$, $P = 0.17$) and the adult lifespan (non-stressed, 9.7 ± 0.4 d; salt-stressed, 10.7 ± 0.5 d; $t = 1.438$, $df = 130.095$, $P = 0.153$) of FAW (Fig. 2(A)). Our study also showed the unaffected pupal mass in FAW feeding on salt-stressed maize plants (non-stressed, 236.5 ± 7.5 mg; salt-stress, 230.3 ± 9.8 mg; $t = 1.778$, $df = 108.746$, $P = 0.078$; Fig. 2(B)).

Effects of salt-stressed maize plants on FAW fecundity

FAW fecundity was significantly and adversely affected by salt-stressed maize plants ($t = 6.626$, $df = 48$, $P < 0.001$).
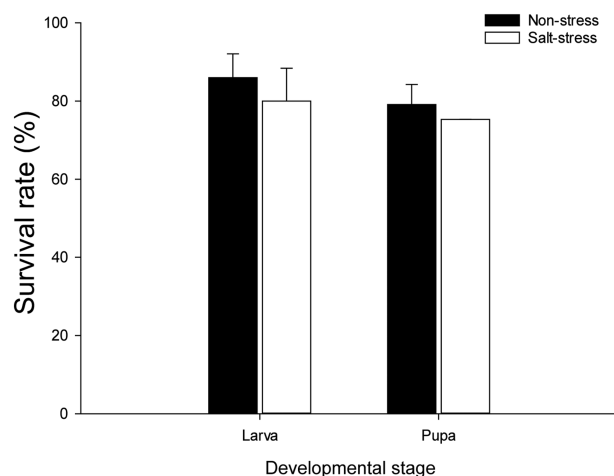
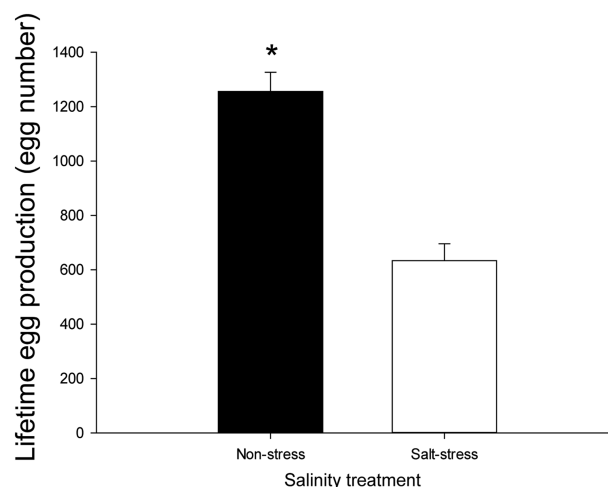**Figure 1** Larval and pupal survival of FAW feeding on non-stressed and salt-stressed maize plants (mean±SE).

Figure 2 FAW development after feeding on non-stressed and salt-stressed maize plants (mean±SE). **(A)** Larval and pupal development times, and adult lifespan. **(B)** Pupal mass. The asterisk indicates significant difference in development time between non-stressed and salt-stressed treatments (independent t-tests, $P < 0.05$).

The mean lifetime egg production of a FAW female feeding on non-stressed maize plants was 1255.9 ± 70.3 eggs, whereas that of a FAW female feeding on salt-stressed maize plants was reduced by nearly half (633.5 ± 62.7 eggs) (Fig. 3).

Discussion

Our analysis indicated that FAW overall showed a negative response to salt-stress maize plants. The larval development time greatly increased and the lifetime egg production significantly decreased after FAW fed on salt-stressed maize plants, thus posing a puzzle of why effects of salt-stressed maize plants on FAW are so evident. One explanation lies in

possible reduced water availability to FAW, salt-stressed maize plants may impact FAW metabolism due to water limitation. Similar to FAW, salt-stressed tomato plants can cause weak performance of *Macrolophus pygmaeus* through water limitation (Han *et al.* 2015a). A second and more plausible explanation is that the reduced amount of nutrients in plant sap may restrict FAW growth. Because of reduced plant water potential, photosynthesis of salt-stressed maize plants is often inhibited, thereby causing disruptive use of nitrogen and water (Flores *et al.* 2000, 2003, 2014; Gouia *et al.* 1994; Parida & Das 2005; Soares *et al.* 2018; Wang *et al.* 2003). A last possible explanation for negative responses of FAW is increased concentrations of secondary metabolites in salt-stressed maize plants. Increased production of

Figure 3 Fecundity of FAW females feeding on non-stressed and salt-stressed maize plants (mean ± SE). The asterisk indicates significant difference in lifetime egg production between non-stressed and salt-stress treatments (independent t-tests, $P < 0.05$).

1,4-benzoxazin-3-one aglycones, a secondary metabolite in maize plants, can enhance plant chemical defense *via* toxic activities (Forieri *et al.* 2016; Mahmoudi *et al.* 2010; Shao 2015; Wahid & Ghazanfar 2006; Wang *et al.* 2015), potentially reducing FAW performance.

In this context, we found a prolonged larval development time of FAW feeding on salt-stressed maize plants. Salt-stressed maize plants may cause FAW water deficit similar to a form of physiological drought (Tucker *et al.* 2011). In that case, FAW larvae may face difficulties gaining sufficient water from salt-stressed maize plants, potentially increasing their larval developmental time for water compensation. We also found the decreased egg production of FAW feeding on salt-stressed maize plants. The excessive accumulation of Na^+ and Cl^- ions and cyanide in salt-stressed maize plants may lower the suitability of leaf as food for insects (Manaa *et al.* 2011). FAW may not harvest sufficient nutrients from salt-stressed maize plants, so FAW may fail to supply sufficient nutrients to its offspring, resulting in a reduced fecundity.

Interestingly, FAW feeding on salt-stressed maize plants showed a longer larval development time but unaffected pupal mass. It has been acknowledged that herbivores typically pupate with a higher mass accumulation if they have elongated plant resource consumption (Han *et al.* 2016). FAW larvae may have to compensate for low leaf water content by prolonging their feeding period, and meanwhile develop this "slow" feeding strategy to adapt to lower plant food suitability, which means taking more time for larval development to compensate for nitrogen deficiency. Therefore, FAW feeding on salt-stressed maize plants may spend more time for larval development to keep itself in sufficient nutrients, ensuring normal pupal mass. Moreover, we did not find the reduced larval and pupal survival of FAW feeding on salt-stressed maize plants, possibly indicating salt-stressed maize plants negatively impact FAW through water shortage and nutrient deficiency, rather than through lethally toxic activities.

In conclusion, salt-stressed maize plants caused significant impacts to FAW development and fecundity, suggesting salt-stressed maize plants could contribute to practical applications of IPM strategies in controlling FAW. This highlights the importance of considering the salt-stressed maize crops when an IPM package has been designed to manage FAW. In practice, a longer development time and a reduced egg production in FAW feeding on salt-stressed maize plants, may raise concern regarding lower plant damage by this pest when salt-stressed maizes are grown. Our results would predict that because of limited population increase potential, FAW populations feeding on salt-stressed maize plants should pose less of a problem than ones feeding on non-stressed maize plants do. Actually, salt-stressed maize plants are quite common in arid and semi-arid regions where the relatively high-salinity groundwater is often used to irrigate maize plants, potentially limiting FAW population size. However, the laboratory results cannot be directly extrapolated to field populations as laboratory experiments are simplified systems (Ren i 2019; Wu *et al.* 2018; Zhang *et al.* 2009). The availability of negative responses of FAW to salt-stressed maize plants needs to be confirmed with further field investigations, so monitoring FAW field population dynamics in multiple generations is necessary. Additionally, impacts of salt-stressed maize plants on FAW may cascade up to higher trophic levels (biocontrol agents of FAW), which has been displayed on some types of resources like nitrogen (Chen x 2010; Han *et al.* 2015b; Van *et al.* 2015). Therefore, effects of salt-stressed maize plants on biocontrol agents of FAW also should be examined in future studies.

Acknowledgments

Data availability statement

Data available on request from the authors.

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