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Abstract

In nature, plants interact with multiple organisms, below and aboveground. Although interactions of plants with single biotic stressors are well characterized, knowledge of how the immune system responds to multiple biotic stressors is lacking. It is known that the two most important pathways involved in the plant immune defenses

are jasmonic acid (JA) and salicylic acid (SA). The crosstalk between these plant hormonal signaling pathways seems to fine-tune the plant responses to different stressors. In this study, we characterized maize (*Zea mays*) hormonal interactions under the attack of two economically important pests: the bacterial pathogen that causes Goss's bacterial wilt and leaf blight (*Clavibacter michiganensis* subsp. *nebraskensis*), and the chewing insect, fall armyworm (*Spodoptera frugiperda*). Our results indicate that the Goss's wilt-resistant maize plants when pretreated with bacteria became more vulnerable to the subsequent attack by the fall armyworm larvae. Furthermore, plant hormone analysis demonstrated that the antagonistic interactions of JA-Isoleucine (JA-Ile), biologically active form of JA, and SA in maize plants contributed to enhanced plant susceptibility to herbivory. Collectively, our results suggest that plant hormonal interactions may play a major role in maize defense against multiple biotic stressors. Furthermore, this study will improve our understanding and ability to predict plant-induced hormone responses in an economically important crop.

Keywords: Fall armyworm, Goss's bacterial wilt and leaf blight, Maize, Phytohormones

Introduction

Plants are frequently challenged by various biotic stressors such as insect and vertebrate herbivores, and pathogens such as fungi, viruses, and bacteria. These attacks can occur either simultaneously or sequentially. In response to these stressors, plants have a multitude of defense mechanisms including constitutive and inducible defenses (Howe and Jander 2008; Louis and Shah 2013; Zust and Agrawal 2017; Erb and Reymond 2019). Constitutive defenses include both preformed physical barriers and chemical factors, whereas inducible defenses include the induction of signaling cascades, which consequently lead to the production of metabolites and/or plant hormones (Chen 2008; Howe and Jander 2008; Pieterse et al. 2012; Nalam et al. 2019). Unfortunately, knowledge of the molecular mechanisms underlying the interactions of multiple biotic stressors in the same plant species is lacking. This information is critical for development of host plants with robust host resistance that is stable under multiple biotic and abiotic stressors. Among the few studies evaluating multiple stressors on host plant response, it is suggested that response of the plant immune system and expression of plant hormonal signaling pathways depend on the mechanism feeding behavior/pathogen ingress (i.e., biotrophic/necrotrophic pathogens) (Thaler

et al. 1999, 2010, 2012; Ali and Agrawal 2012; Moreira et al. 2018). The two most important hormonal signaling pathways associated with induced plant defenses are jasmonic acid (JA) and salicylic acid (SA). The crosstalk between these plant hormonal signaling pathways is a well-studied phenomenon, and it has been shown that expression of these hormones is correlated with negative or positive pest performance in plants, depending on the plant/pest system. However, very little information is available on the molecular mechanisms underlying the interactions of multiple biotic stressors in herbaceous monocot plants, including maize (*Zea mays L.*).

Clavibacter michiganensis subsp. *nebraskensis* (CMN) (Vidaver & Mandel) and *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae) are important corn pests. CMN is a maize pathogen that has been historically confined to the U.S. Midwest. This gram-positive bacterium primarily infects maize plants through wounds caused by wind-driven rain, hail, and other mechanical damage causing wilt and leaf blight symptoms. A recent study described the results of a survey of agronomic practices and other problems that occurred in fields from which samples tested positive for CMN and detected an effect in the bacterial infection by the presence of insects (Langemeier et al. 2017). When CMN infection occurs early during seedling stages, they can cause systemic vascular infections of their host plants and reside as biotrophic pathogens in the xylem vessels (Eichenlaub and Gartemann 2011). In addition, the bacteria can overwinter in crop residues (Jackson et al. 2007). Yields can be reduced up to 50% when susceptible hybrids are infected, and currently there is no commercial resistant maize hybrid available that provides complete protection against this pathogen (Claflin 1978; Jackson et al. 2007).

One threat to the existing plant host resistance to Goss's bacterial wilt disease is pest damage caused by an economically important phytophagous insect in maize, the fall armyworm (FAW)*, S. frugiperda*. FAW is an important pest in maize that has spread through North and South America, and as an invading species in Africa, and more recently in Asia (Montezano et al. 2018; Ganiger et al. 2018). Currently, the management practice to control this pest is the use of resistant hybrids expressing insecticidal protein from the bacterium *Bacillus thuringiensis* (*Bt*). Unfortunately, there is an increasing number of field-evolved reports of resistance in this insect to *Bt* transgenic traits (Tabashnik and Carriere 2017).

It is unknown whether interactions between plant hormonal signaling pathways can be correlated with negative or positive pest performance in maize under the subsequent damages from chewing insects and biotrophic pathogens. A recent study with CMN and parental lines of the maize nested association mapping (NAM) population showed variable levels of resistance to CMN (Hu et al. 2018). In this study, we used the maize NAM founder lines, B73 and Oh7B, that were identified as moderately resistant and susceptible lines, respectively, against CMN (Hu et al. 2018). We further explored how initial infection by the biotrophic pathogen CMN on B73 and Oh7B lines will influence the subsequent attack by a different biotic stressor, a chewing insect. Our results indicate that there is resistance trade-off based on the antagonistic effects between JA-isoleucine (JA-Ile), biologically active form of JA (Howe and Jander 2008), and SA so that infection by Goss's bacterial wilt and leaf blight reflects in the increase of plant susceptibility to subsequent attack by FAW. Understanding the interactions among plant-bacterium-chewing insect can contribute to our comprehension of ecosystem processes and ability to predict the outcome of plant-mediated interactions.

Materials and methods

Bacteria and insects

A strain of the Goss's bacterial wilt and leaf blight pathogen, CMN 225A, was collected from a symptomatic corn sample collected from Nebraska in 2011 as part of a multistate survey across the Midwest (Langemeier et al. 2017) and used in these experiments. This bacterial strain was selected for this study due to its known virulence or aggressiveness in maize studies. This strain has been in culture at the University of Nebraska-Lincoln in a nutrient broth yeast agar (NYB) solid medium and maintained at room temperature for 2 days before inoculation. As a subsequent attacker, newly hatched (for bioassay) and third instar (for phytohormone analysis) larvae of FAW were used to infest maize plants inoculated with CMN. FAW larvae were obtained from a commercial vendor (Benzon Research Inc., PA) on an artificial diet, and were kept at room temperature prior to infestation.

Plant lines and growth conditions

Two NAM founder lines B73 and Oh7B were selected based on their level of resistance to the bacterial pathogen (Hu et al. 2018) and were identified as moderately resistant and susceptible lines, respectively. Both lines were obtained from the U.S. National Plant Germplasm System (USDA Agricultural Research Station, Ames, IA). Plants were grown in all-purpose growing mix Berger BM6 (Hummert International, Earth City, MO), in the Agronomy and Horticulture glasshouse at the University of Nebraska-Lincoln. These plants were grown in 3.8 cm × 21 cm plastic cone-tainers (Hummert International, Earth City, MO). The glasshouse environmental setting was 14-h/10-h (light/dark) photoperiod, 25 – 27 °C, and 50 to 60% relative humidity. All plants for the experiments were used at V3 developmental stage or approximately 2–3 weeks from planting. These aforementioned conditions were applied to address the following research objectives to identify how the initial infection by the biotrophic pathogen CMN on B73 and Oh7B lines will influence the subsequent attack by the chewing insect, FAW, and to further identify the molecular mechanisms involved in maize response to these biotic interactions.

Insect performance after bacterial pretreatment in maize plants assay

The bacterial suspension consisted of a combination of CMN cells scraped from media plates and eluted into sterile distilled water. The concentration of the suspension obtained for infection was adjusted to a concentration of 3×10^9 CFU/ml, which was used in previous experiments to evaluate symptom development in maize. Plant inoculations were performed by slowly injecting 100 µl of the bacterial suspension into the maize stem interspace between the first and second leaf, using 1 ml syringe with 28 gauge and 12.7 mm needle (BD Allergy Syringe). Negative control plants were injected with the same volume of water only and non-inoculated control plants received no injection. Inoculations were performed in the evening and 15 h later, a single FAW neonate larva was transferred to the whorl of each plant. The 15 h-mark was selected based on results of a previous QTL study for resistance to Goss's bacterial wilt and leaf blight (Singh et al. 2019). The

pathogen responsive genes *PR1* and *PR5*, commonly used molecular markers of SA, were expressed within 12 to 15 h after CMN inoculation (Singh et al. 2019). To avoid larval escape, single pot was covered with a plastic cage. The weight of individual larva was measured after 7 days of infestation. There were thirteen biological replications for each treatment (i.e., plants inoculated with a bacterial suspension, negative control plants inoculated with water only, and non-inoculated control plants). These experiments were conducted twice with similar results.

Bacteria and insect interaction for hormone quantification

To characterize phytohormone response under multiple biotic stressors, plants were inoculated/infested in the same manner as described above, followed by phytohormone quantification. For hormone quantification, the same methodology as described previously was used (Varsani et al. 2019; Grover et al. 2020). However, plant samples were collected at two different time points. The first time was 15 h after bacterial/distilled water inoculation and the second time was 24 h after FAW larvae infestation. Plant samples consisted of approximately 2 cm length of the upper stem area, closer to the whorl, and weighing 100–150 mg. The remaining plants were infested with single third instar FAW larva, placed directly in the whorl of the plant. Third instar larvae were used in this experiment as they are in an advanced stage of development and could begin feeding on the plant within a short period of time. Larvae were allowed to feed for 24 h, and then plant tissue sampling was repeated at the same plant area and weight. Each treatment had three to five biological replications depending on sample availability. Maize tissues were ground using a 2010 Geno/Grinder (SPEX SamplePrep) for 40 s at 1400 strokes min^{-1} with liquid nitrogen cooling to keep samples frozen throughout the grinding process. Samples were delivered on dry ice to the Proteomics and Metabolomics Facility at the University of Nebraska-Lincoln for targeted quantification of phytohormones using liquid chromatography-MS/MS, as described previously (Varsani et al. 2019; Grover et al. 2020).

Statistical analysis

Experimental units were a complete factorial arranged in a completely randomized design. Two-way analysis of variance (ANOVA) was conducted with PROC GLIMMIX (SAS 9.4, SAS Institute) to evaluate the effect of plant line, treatment, and interactions between plant variety and bacterial pretreatment on fall armyworm performance after bacterial pretreatment and hormonal quantification. When a significant difference was identified, a post hoc analysis using a Tukey's HSD pairwise comparison was performed to determine where significant differences lie among treatment means. Values from the interactions and from least-squares means of the treatments with $P \leq 0.05$ were considered to be significantly different.

Results

Insect performance after bacterial pretreatment in maize plants

There was an overall treatment effect ($P = 0.0034$) and treatment by maize genotype effect ($P = 0.039$) in the mean larval group weight. There was an increase of FAW weight in B73 maize plants that were pretreated with CMN. While the mean larval group weight followed by standard error value in CMN-pretreated B73 plants was 86.29 ± 7.81 mg ($P < 0.0001$), the mean weight from larvae that fed on plants pretreated with water was only 59.38 ± 3.71 mg ($P < 0.0001$). FAW from uninfected plants (control plants) had an average weight of 68.15 ± 3.61 mg ($P < 0.0001$; Fig. 1). The FAW weight between CMN-pretreated plants between genotypes was significantly different ($P = 0.0146$). There was also a maize genotype effect observed in this study ($P = 0.0213$). In the susceptible line Oh7B, the mean larval weight from plants pretreated with CMN was 65.46 ± 3.42 mg ($P < 0.0001$). The mean larval group weight from negative control plants that were inoculated with water and the non-inoculated control plants were 61.46 ± 3.27, and 60.62 ± 2.93 mg, respectively.
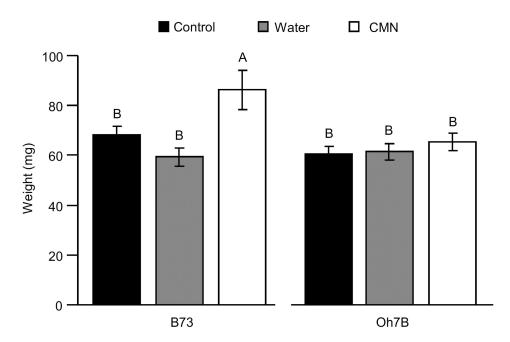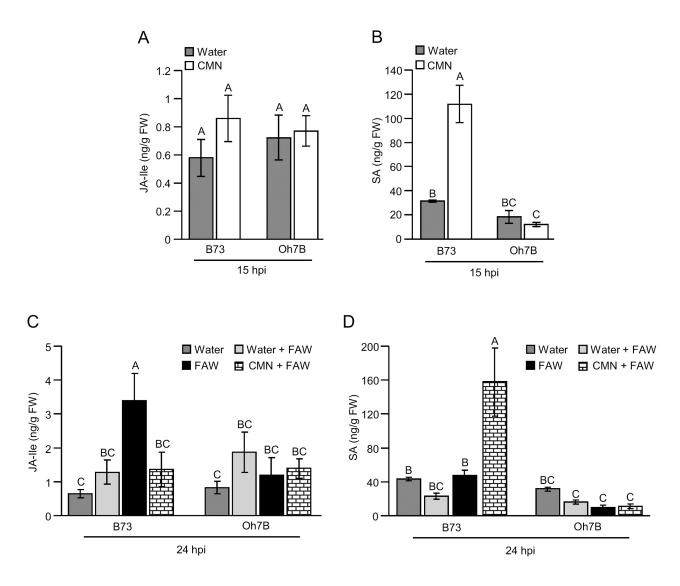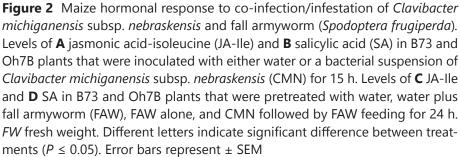
Figure 1 Fall armyworm (*Spodoptera frugiperda*) performance after bacterial pretreatment in maize plants. Fall armyworm (FAW) weight increased in plants treated with *Clavibacter michiganensis* subsp. *nebraskensis* (CMN), causal agent of Goss's bacterial wilt and leaf blight. Moderately resistant (B73) and susceptible (Oh7B) lines were pretreated with either a CMN suspension or water only. Control plants did not receive bacterial pretreatment; water was used as negative control. After 15 h post inoculation, single FAW neonate was transferred to the whorl of each plant. FAW weight was measured after 7 days of feeding. Different letters indicate significant difference between treatments ($P \leq 0.05$). Error bars represent ± SEM

Bacteria and insect interaction for hormone quantification

To characterize if the difference in performance of FAW in bacterial pretreated plants is due to SA and JA-mediated responses, maize plant samples were analyzed for hormone concentrations. The levels of JA-Ile, the biologically active form of JA (Howe and Jander 2008), were not altered in both B73 and Oh7B maize plants after 15 h of CMN inoculation (Fig. 2A). However, SA accumulation was significantly increased in CMN-resistant B73 plants 15 h post inoculation (hpi) of CMN (Fig. 2B). We did not find any significant difference in the levels of SA with and without CMN inoculation on Oh7B plants after 15 hpi (Fig. 2B).

Figure 2 Maize hormonal response to co-infection/infestation of *Clavibacter michiganensis* subsp. *nebraskensis* and fall armyworm (*Spodoptera frugiperda*). Levels of **A** jasmonic acid-isoleucine (JA-Ile) and **B** salicylic acid (SA) in B73 and Oh7B plants that were inoculated with either water or a bacterial suspension of *Clavibacter michiganensis* subsp. *nebraskensis* (CMN) for 15 h. Levels of **C** JA-Ile and **D** SA in B73 and Oh7B plants that were pretreated with water, water plus fall armyworm (FAW), FAW alone, and CMN followed by FAW feeding for 24 h. *FW* fresh weight. Different letters indicate significant difference between treatments ($P \leq 0.05$). Error bars represent ± SEM

We also measured the levels of JA-Ile and SA on both B73 and Oh7B plants after pretreating the maize plants with CMN for 15 h followed by FAW infestation for 24 h. FAW feeding for 24 h on B73 plants triggered the accumulation of JA-Ile compared to water-inoculated B73 control plants (Fig. 2C). Surprisingly, we also found that B73 plants that were pre-inoculated with water followed by FAW infestation had significantly lower levels of JA-Ile compared to B73 plants that were infested with FAW alone. Because the water plus FAW infestation did not exhibit similar significant increase in JA-Ile compared to FAW feeding alone on B73 plants, these data should be treated with caution. Water inoculation on B73 plants may have resulted in an earlier accumulation of JA-Ile, which was no longer detectable at the timepoints that was chosen for this experiment (i.e., 24 h after FAW infestation). Alternatively, the injection of water with needle on B73 plants may have trigged the SA accumulation that contributed to reduced accumulation of JA-Ile after 24 of FAW feeding. However, this is less likely, because we observed no significant differences in SA levels in B73 plants after water inoculation and with and without FAW feeding (Fig. 2D). Compared with the FAW feeding alone, we found a significant decrease in the levels of JA-Ile on CMN-resistant B73 plants that were exposed to the combination of CMN and FAW infestation (Fig. 2C). No significant changes were found in the levels of JA-Ile in the CMN-susceptible Oh7B plants with and without CMN pretreatment and FAW feeding for 24 h (Fig. 2C). Similarly, no significant differences were found in the levels of SA in the Oh7B plants with and without CMN pretreatment and FAW feeding for 24 h (Fig. 2D). In addition, there were no significant changes in the SA levels in the CMN-resistant B73 plants with and without water inoculation followed by FAW feeding for 24 h (Fig. 2D). However, CMN-resistant maize B73 plants exposed to the combination of CMN and FAW feeding for 24 h exhibited significant increase in SA levels compared to plants that were treated with water alone, water plus FAW, and FAW alone (Fig. 2D).

Discussion

Plants encounter various biotic stressors; however, very little is known about how these interactions play out in the ecosystem and whether

co-infection modifies plant resistance or susceptibility. Broadly, knowledge on host response to interactions involving insects and pathogens is lacking. This is the first study on maize using tri-partite interaction assays between biotrophic pathogens and chewing herbivores. Our results showed that inoculation of CMN increased weight of the subsequent attacker FAW in the maize B73 line. In Bacher et al. (2002), females of the boring weevil, *Apion onopordi,* showed enhanced performance in weed creeping thistle plants, *Cirsium arvense*, pretreated with the biotrophic rust fungus, *Puccinia punctiformis.* In contrast, *Brassica nigra* plants that were pretreated with either egg extract from a chewing herbivore, *Pieris brassicae*, or the biotrophic bacterium, *Xanthomonas campestris,* had a negative impact on the herbivore growth (Bonnet et al. 2017). However, there was no attempt to elucidate the plant defense mechanism(s) that could explain these results.

In the present study, we further explored the hormonal mechanism that maize plants use against combined biotic stressors. JA and SA are mainly known to play major roles in regulating plant defense responses against pathogens and insects (Pieterse et al. 2012). Biotrophic pathogens and some piercing/sucking insects, generally induce SA signaling accompanied by the production of pathogenesis-related (PR) proteins, whereas JA-mediated responses are predominantly against necrotrophic pathogens and chewing insects (Thaler et al. 2012). Maize hormonal profiling in this study suggests that the induction of plant defense responses after CMN infiltration is correlated with the induction of SA and the infestation of FAW with the induction of JA-Ile in the CMN-resistant maize line (B73; Fig. 2).

Characterizing both susceptible and resistant lines in these types of multi-pest-pathogen interaction studies provide insight into how changes in secondary pest performance may be related to primary pest-induced changes in plant susceptibility. In maize, we demonstrated that increased pest performance was due to differences in the host plant genetic variability and related to differences in the induction of SA hormone levels between the resistant and susceptible maize plants to CMN. Previously, it was shown that SA-responsive transcripts tend to accumulate quicker and to higher levels in leaves of resistant plants than in susceptible plants (Martinez de Ilarduya et al. 2003). Similarly, our results indicated that CMN-resistant maize plants had elevated levels of SA compared to susceptible plants (Fig.

2B). As different maize varieties are genetically distinct, it would be useful for future studies to evaluate interactions in additional maize genotypes to determine if these changes in pest susceptibility correlate with hormone levels.

In nature, plants are likely to experience multiple biotic stresses that elicit phytohormonal responses interacting to yield a synergistic or antagonistic effect that may ultimately shape the plant phenotype and/or resistance. However, evidence of reciprocal antagonism reported in studies measuring molecular aspects of the host response might not be reflective of all species of herbivores and pathogens (Moreira et al. 2018). Results presented in this study suggest that the CMN infection followed by FAW herbivory can affect maize JA and SA-induced pathways antagonistically. While levels of JA-Ile increased in FAW treatment alone, they did not change upon CMN infection and the sequential attack of FAW. Meanwhile, concentration of SA increased significantly under combination of FAW and CMN treatments when compared to CMN alone (Fig. 2). The increase in SA concentration levels could cause the suppression of JA-Ile levels resulting in the increase of plant susceptibility to chewing herbivores. Indeed, it was previously shown that application of exogenous SA and its functional analogs, such as aspirin, 2,6-dichloroisonicotinic acid (INA), activates expression of PR genes (Uknes et al. 1992; White 1979), and blocks the JA signaling process (Doherty et al. 1988; Pena-Cortes et al. 1993), suggesting that crosstalk between JA and SA could exist. Interestingly, Engelberth et al. (2011) proposed that the SA–JA antagonism is absent in maize. In that study, insect elicitor-induced JA was more than two-fold upregulated in exogenous SA-pretreated maize plants. Using artificial elicitors is an alternative to test plant responses; however, it does not take into consideration the wide range of elicitors produced by multiple stressors (e.g., co-infection by bacteria and insects) that consequently interfere with the plant immune response.

One of the factors that can interfere in the reproducibility of types of assays is that the antagonism between JA and SA depends on the concentration and timing of elicitation of each pathway (Thaler et al. 2002). To provide more complete picture of the hormone mechanism in these assays, it would be important to test these pest interactions and the phytohormone levels at different time points and plant developmental stages. Additionally, it would be important to extend

these types of studies in other environmental conditions. Similar to other interaction studies, these assays were conducted in semi-controlled environments where maize plants were in early stages and exposed to controlled delivery of disease inoculum volume. Calub et al. (1974) indicated that inoculation timings performed on 2-week-old seedlings routinely resulted in increased disease severity to Goss's bacterial wilt and leaf blight compared to inoculations performed on older seedlings. However, when a resistant hybrid was used, inoculation timing had little impact on either disease severity or yield. Furthermore, in other less controlled environments, such as in the field, other factors (e.g., abiotic factors) may also play a role in modulating plant defenses (Liu et al. 2013; Riemann et al. 2015). It is well known that these phytohormones can be elicited under poor environmental conditions as well, such as drought. JA, in particular, can also be involved with other volatile compounds such as ethylene, for instance, under nitrogen deficiency (Schmelz et al. 2003). Taken together, these studies suggest that external factors can also contribute to a greater variation of hormone production under natural conditions and can ultimately indirectly promote variation in plant susceptibility to pests.

Finally, the results of this study are relevant to growers and seed producers. For growers, it is important to scout the field early to the presence of Goss's bacterial wilt and leaf blight symptoms. For seed producers, the presence of secondary pests can impact the durability of the resistance used in the field. Evaluating parental lines that are commonly used in the background for generation of maize hybrids, to a potential secondary pest attack, especially those pests that have a significant ecological presence in the area, can benefit the long-term efficacy of the technology.

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