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ARTICLE ADDENDUM

Insect stings to change gear for healthy plant: Improving maize drought tolerance by whitefly infestation

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ABSTRACT
Since plants first appeared about 1.1 billion years ago, they have been faced with biotic and abiotic stresses in their environment. To overcome these stresses, plants developed defense strategies. Accumulating evidence suggests that the whitefly [*Bemisia tabaci* (Genn.)] affects the regulation of plant defenses and physiology. A recent study demonstrates that aboveground whitefly infestation positively modulates root biomass and anthocyanin pigmentation on brace roots of maize plants (*Zea mays* L.). In agreement with these observations, indole-3-acetic acid (IAA) and jasmonic acid (JA) contents and the expression of IAA- and JA-related genes are higher in whitefly-infested maize plants than in non-infected control plants. Interestingly, the fresh weight of whitefly-infested maize plants is approximately 20% higher than in non-infected control plants under water stress conditions. Further investigation has revealed that hydrogen peroxide (H_2O_2) accumulates in whitefly-infested maize plants after water stoppage. Taken together, these results suggest that activation of phytohormones- (i.e., IAA and JA) and H_2O_2-mediated maize signaling pathways triggered by aboveground whitefly infestation promotes drought resistance. They also provide an insight into how inter-kingdom interactions can improve drought tolerance in plants.

Abbreviations: ABA, abscisic acid; ET, ethylene; ETI, effector-triggered immunity; GA, gibberellin; H_2O_2, hydrogen peroxide; IAA, indole-3-acetic acid; JA, jasmonic acid; PTI, PAMP-triggered immunity; SA, salicylic acid

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In natural settings, plants are exposed to numerous pathogens and insects. To overcome the potentially damaging effects of these agents, plants have developed defensive machineries against potential invaders.[1] Plants have non-self-recognition mechanisms for pathogens and insects, and have elaborated two types of immune systems including pathogen-associated molecular pattern (PAMP)-triggered immunity (PTI) and effector-triggered immunity (ETI).[2-6] In addition, accumulating evidence suggests that the plant hormones salicylic acid (SA), jasmonic acid (JA), ethylene (ET), abscisic acid (ABA), gibberellin (GA), auxin, cytokinin, and brassinosteroid are important as downstream components of PTI and ETI.[7-12]

Previous results have demonstrated that, in pepper plants, aboveground whitefly (*Bemisia tabaci* Genn.) infestation activates defense responses against two bacterial pathogens in leaf and root.[13] Recently, whitefly-infested *Nicotiana benthamiana* plants have shown to produce SA as a way to attenuate *Agrobacterium* infection.[14] Whitefly infestation positively modulates tobacco defense responses, and infested plants show reduced crown gall formation by *Agrobacterium*.[14] SA produced by stems following whitefly infestation can be translocated into belowground tissues, and SA is a key factor affecting host plant responses to *Agrobacterium* pathogenicity.[14]

Up to now, although many studies have reported that whitefly infestation can affect the plant defense machinery, the mechanisms via which plant defenses in monocot plant species are modulated by whitefly infestation have been barely addressed. To fill this gap, we investigated previously whether whitefly infestation results in molecular, biochemical, and physiological changes in maize plants. Maize seeds (*Zea mays* L. cv. Mibaek^{2nd}) are grown to the V2 stage, and the seedlings were infested with whitefly (approximately 15 whiteflies per maize plant) for 4 weeks in a plastic container at 28 ± 2°C.[15] The results show distinct changes in maize growth and development in leaf and root, and significant increases in root biomass, but not in aboveground shoot biomass, following whitefly infestation.[15]

The increase in root biomass after infestation aboveground with whitefly was accompanied by the production of indole-3-acetic acid (IAA) in maize roots.[15] Endogenous IAA production levels are statistically higher in whitefly-infested maize roots at 24 and 48 h than those in control plants.[15] This observation is supported by pepper transcriptome data showing that auxin-related genes and nutrient transporter genes are up-regulated in whitefly-infested roots.[16] It is likely that aboveground whitefly infestation transports signals/molecules into roots and the rhizosphere,

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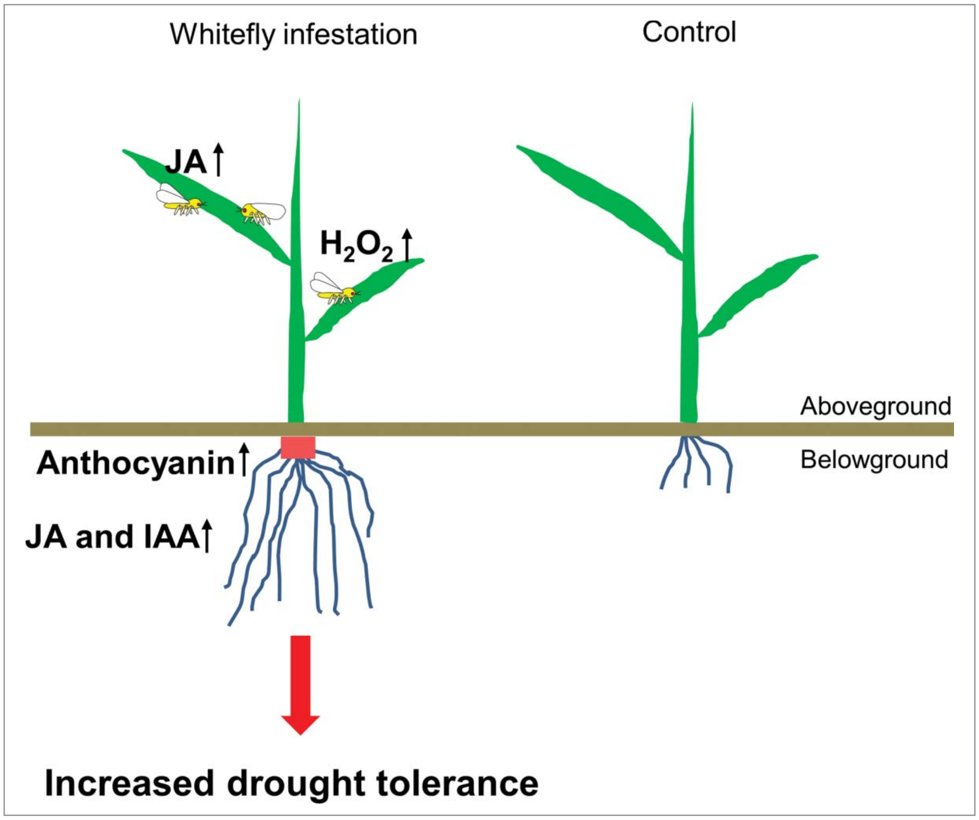

Figure 1. Schematic representation of maize physiological and biochemical changes upon whitefly infestation. Anthocyanin production is dependent on JA production after whitefly infestation. IAA may be required to increase root biomass. Hydrogen peroxide production is a major regulator of water stress. Drought tolerance is a consequence of the physiological and biochemical changes that occur in maize upon whitefly infestation.

in which certain transporters/receptors respond by talking up nutrients to increase root biomass.

Maize plants infested by whitefly produce higher amounts of JA in both leaf and root than control plants.[15] Previous reports revealed that whitefly mainly manipulates the SA-mediated plant defense machinery in *Arabidopsis*, pepper, and tobacco.[13,14,17] By contrast, JA is the main regulator in maize plants whose accumulation is triggered by aboveground whitefly infestation.[15] This discrepancy may have several explanations. First, it is possible that the plant-derived hormone triggered by aboveground whitefly infestation may be plant species specific (monocot vs. dicot). Second, mechanical and technical issues (i.e., time of sampling and strength of whitefly infestation) may affect the production of endogenous plant hormones. For example, in tobacco, whitefly can heavily colonize host plant tissues (150 whiteflies per leaf), whereas, in maize, only a few whiteflies (15 whiteflies per plant) participate in infestation. Third, SA and JA may have antagonistic effects toward each other in plants exposed to certain (a)biotic stresses. Further investigation will be required to determine the relative contributions of JA and SA to plant host defenses activated by whitefly infestation.

Interestingly, anthocyanin pigmentation occurs on the roots and crown parts of maize plants after whitefly infestation.[15] The genes involved in the biosynthesis of anthocyanin in maize plants are highly upregulated in whitefly-infested roots.[15] As explained above, whitefly-infested plants show higher levels of JA production, which may contribute to the activation of anthocyanin production.[18-19] Whitefly-infested maize plants are more tolerant of drought stress.[15] JA and ABA are implicated in the regulation of plant responses to drought stress, including the activation of reactive oxygen species (ROS) and stomata closure.[20] ABA contents are not detectable in whitefly-infested maize plants.[15] Taken together, these studies suggest that JA is required for both anthocyanin production and the elicitation of drought resistance after whitefly infestation.

The above findings are summarized in Fig. 1. Briefly, the increase in the levels of plant-derived major hormones (JA and IAA) following exposure to aboveground whitefly plays a pivotal role in the regulation of maize physiology, resulting in increases in root biomass and anthocyanin production, and increased drought tolerance. Hydrogen peroxide production is a good indicator of the drought tolerance elicited in response to whitefly feeding. The results summarized in this study clearly suggest that interactions can occur between a biotic stimulus (a sucking insect whitefly), a host plant (maize), and abiotic stress (drought stress). The underlying mechanism(s) via which aboveground whitefly infestation affects maize physiology and defense need to be further investigated.

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