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Interactions Between Water-Stress and Maize Resistance to Spider Mites with Varied Host Specialization

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INTERACTIONS BETWEEN WATER-STRESS AND MAIZE RESISTANCE TO SPIDER MITES WITH VARIED HOST SPECIALIZATION

by

Gunbharpur S. Gill

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Biology

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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Interactions between water-stress and maize resistance to spider mites with varied host specialization

by

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Utah State University, 2020

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An increase in the frequency and intensity of abiotic and biotic stresses due to climate change is predicted to cause major declines in agricultural production worldwide. Of particular concern is water-stress, which not only reduces crop yield by harming the growth and development of plants but also by triggering outbreaks of herbivorous pests that thrive in such conditions. Spider mites, in particular, outbreak in water-stressed maize crops and have been reported to cause severe yield losses. Selection of plants resistant to herbivores is a critical pest management approach; however, it is unclear how water-stress affects resistance in maize against spider mites with varied host specialization. In chapter II, I examined the effects of water-stress on population growth of a generalist herbivore, two-spotted spider mite (*Tetranychus urticae* Koch, TSM), and a specialist herbivore, Banks grass mite (*Oligonychus pratensis* Banks, BGM), on a model maize inbred line (B73) in greenhouse and field settings. Here, I evaluated maize (B73) defense protein responses to water-stress and mite (TSM and BGM) herbivory. I found that water-stressed maize had enhanced populations of mites, generally. Optimally irrigated plants responded to TSM and BGM herbivory with similar plant defense changes. However, combinations of plant water-stress and TSM herbivory resulted in modest increases in two protease activities (chitinase and trypsin inhibitors), a result not observed with BGM. In chapter III, I evaluated the effect of maize resistance on mite behavior by testing a susceptible (B73), and two resistant (B75 and B96) maize lines. I found that resistant lines had reduced oviposition and altered more behaviors for TSM, while BGM, a specialist on maize, responded less to maize resistance. In chapter IV, I investigated the effect of water-stress on maize resistance to spider mites by evaluating B73, B75 and B96 maize lines with varied resistance. Plant defense responses were also tested to evaluate the effects of water-stress and herbivory on maize lines. While mite populations increased on B73 exposed to water-stress, resistant maize (B75 and B96) exposed to water-stress maintained plant resistance to mites. B75 and B96 had high chitinase and trypsin inhibitor activities. However, trypsin inhibitor activity only increased when combining TSM with water-stress, a result not observed with BGM.

My research provides an understanding of the interactions of water-stress and maize resistance on spider mite outbreaks, and the plant responses to abiotic and biotic stresses. This information is essential considering extreme variation in climate conditions and the development and use of spider mite management tools.

(302 pages)

PUBLIC ABSTRACT

Interactions between water-stress and maize resistance to spider mites with varied host specialization

Gunbharpur S. Gill

Spider mites are well-documented pests of many agricultural crops including cereals such as maize. In hot and dry conditions, when crop plants are under water-stress, spider mite populations can rapidly increase within weeks and can cause severe yield losses. One approach to manage pests, such as spider mites, is through the development and selection of plants that can resist pests. Screening of maize lines has provided evidence of spider mite resistance; however, it is unclear how plant water-stress may affect the ability of maize to sustain spider mite resistance. In addition, it is important to understand how plants respond to a combination of water-stress and the stress of herbivory. The frequency and severity of water-stress conditions are predicted to increase due to climate change. Therefore, understanding the effects of water-stress on maize resistance to spider mites is of critical importance. First, I evaluated the effects of water-stressed maize on the population growth of two species of spider mite, the twospotted spider mite (TSM) that feeds on a wide variety of plants and Banks grass mite (BGM) that feeds specifically on grasses, including maize. In addition, I evaluated plant responses to water-stress and herbivory for each mite species. I found that plants exposed to water-stress had increased spider mite populations. Interestingly, plants responded more when there was a combination of water-stress and TSM herbivory. I followed this with two studies, where I evaluated maize resistance to each mite species and tested whether water-stress affected resistance. I found that TSM was sensitive to maize resistance as its populations remained low, however, BGM feeding and reproduction was apparently unaffected by resistant maize. Furthermore, water-stress did not reduce maize resistance to spider mites. Together, my results show that maize resistance could be an important tool for spider mite management, specifically for TSM, and that this approach can be sustained in maize as water-stress conditions continue to be the new normal.

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CHAPTER I

LITERATURE REVIEW

Introduction

Climate change is predicted to increase the frequency of hot and dry conditions that lead to extreme drought incidences (IPCC, 2014). In 2018, 67% of the continental United States experienced low water availability and drought conditions (United States Drought Monitor, 2018), one of the major factors that can cause major yield losses to economically important crops (Rippey, 2015). Water-stressed plants typically have reduced cell growth, leaf size, stem extension, root proliferation and overall growth (Farooq et al., 2009a). Beyond the direct effect of water-stress on plants, plants exposed to water-stress can trigger outbreaks of herbivorous pests that thrive in such conditions leading to additional major crop damage (Bloudoff-Indelicato, 2012; Cammell and Knight, 1992). Spider mites, usually minor pests, outbreak under water-stress conditions and have been reported to cause crop losses as high as 47% (Bacon et al., 1962; English-Loeb, 1990; Li et al., 2009). The maize cropping system is one of many crops that faces herbivory from spider mites with varied host specialization (Aeschlimann, 1987; Bacon et al., 1962; Bui et al., 2018; Bynum Jr. et al., 2015; Helle and Sabelis, 1985a; Kamali et al., 1989a). Host plant resistance, the capacity of plants to avoid, recover and tolerate the damage caused by pests (Sharma and Ortiz, 2002), is one approach that may assist in reducing spider mite pressure. However, water-stress has been shown to alter host plant resistance leading to plants that may be more susceptible to pest pressure (Ojwang et al., 2010; Sharma et al., 1999). These interactions are further complicated considering that herbivore host specialization and their ability to deal with plant resistant traits can affect the effectiveness of host plant resistance (Ali and Agrawal, 2012). This dissertation investigates the interactions between water-stress and maize resistance on spider mite outbreaks and how maize plants respond to abiotic (water-stress) and biotic (spider mite herbivory) stresses. This chapter provides a literature review focused on spider mites generally and their impact in the maize system, water-stress effects on plants and herbivores, and the combined interactions of abiotic and biotic stressors on plants and herbivores. Chapter II investigates the effects of water-stress on population growth of a generalist herbivore, two-spotted spider mite (*Tetranychus urticae*, TSM), and a specialist herbivore, Banks grass mite (*Oligonychus pratensis*, BGM), on a model maize inbred line (B73) in greenhouse and field settings. It is formatted for submission to the peer-reviewed journal Environmental and Experimental Botany, and is entitled, *Varying responses to combined water-stress and herbivory in maize for spider mite species that differ in host specialization*. Chapter III investigates the effect of maize resistance on mite behavior by testing a susceptible (B73), and two resistant (B75 and B96) maize lines. It is formatted for submission to the peer-reviewed journal, Environmental and Experimental Botany, and is entitled, *Behavioral responses of a generalist and specialist spider mite to maize with varied host plant resistance*. In chapter IV, I evaluated the effect of water-stress on maize resistance to spider mites by evaluating B73, B75 and B96 maize lines with varied resistance. Plant defense responses were also tested to evaluate the effects of water-stress and herbivory on maize lines. It is formatted for submission to the peer-reviewed journal, Environmental and Experimental Botany, and is entitled, *Maize resistance to spider mites is not disrupted with water-stress*.

Spider mites as a pest of maize

The twospotted spider mite (*Tetranychus urticae*, TSM) and the Banks grass mite (*Oligonychus pratensis,* BGM) are two major pests of maize that have been associated with major crop losses (Aeschlimann, 1987; Bacon et al., 1962; Bui et al., 2018; Bynum Jr. et al., 2015; Helle and Sabelis, 1985a; Kamali et al., 1989a). These spider mite species are very small, about 0.6 mm in length, and feed on the underside of leaves by piercing plant tissue with a specialized mouthpart (stylet) to suck and consume cell contents (Grbic et al., 2007; Mondel and Ara, 2006; Rioja et al., 2017). They overwinter in soil, litter or weeds, and can disperse by crawling or wind currents (Alston and Reding, 2011; Ruckert et al., 2015). Both species have a similar life cycle of 6-10 days from egg to adult depending on humidity and temperature (Crooker, 1985). In optimum low humidity (20-40%) and high temperature (above 36°C), the population size of both TSM and BGM can increase up to ~70-fold per generation, and their generation period can decrease to as short as ten days (Grbic et al., 2007; Perring et al., 1984a).

TSM is an extreme generalist because it feeds on more than 1100 plant species, while BGM is a specialist that restricts its feeding to grasses (Bui et al., 2018). TSM is a significant pest of maize, and BGM, in addition to maize, has also been observed to damage sorghum (*Sorghum bicolor* (L.) Moench) and wheat (*Triticum aestivum* L. subsp. *aestivum*) crops (Foster et al., 1977; Holtzer et al., 2013). Spider mite feeding damage has been reported to cause major losses in silage as well as grain yields in maize (Archer and Bynum, 1993). Specifically, during the grain filling period, if conditions are hot and dry, spider mite populations can rapidly increase within weeks compounding yield losses by as much as 47% (Archer and Bynum, 1993; Bacon et al., 1962; English-

Loeb, 1990).

Often, TSM and BGM are considered a minor pest of maize, as populations of these spider mites stay below economic threshold levels (Archer and Bynum, 1993). For spider mites, the economic threshold is when mite injury is visible in the lower third of plants, and mites can be found in the middle third of the plant (Archer and Bynum, 1993). Spider mites can outbreak as a result of several factors (English-Loeb, 1990; English-Loeb, 1989). In hot and dry conditions, predation and reproduction rates of many spider mite predators decrease, making them unable to suppress mite populations (Berry et al., 1991; Bynum et al., 2004; Pickett and Gilstrap, 1986). In addition, water-stressed plants may increase concentrations of sugars, amino acids and protein, such that plant tissues have more readily available nutrients for mites, and hence boost their overall growth and development (Dworak et al., 2016; White, 1969). Plant water-stress also affects spider mites by changing leaf microclimate (Downing, 2013; Ferro and Southwick, 1984). Here, water-stressed plants decrease stomatal conductance to reduce water losses, which consequently increases the temperature and decreases the relative humidity within the leaf microclimate (Ferro and Southwick, 1984). Such changes in leaf microclimate (i.e., higher temperature and lower humidity) can benefit spider mites (Perring et al., 1984a; Rott and Ponsonby, 2000). Further, dust accumulation on leaves, especially in dry conditions can create microhabitats that favor spider mites but not their natural enemies (Capinera, 2001; Kinn et al., 1972; Muhammad, 2015).

The conventional management of spider mites relies on insecticides and acaricides (Deletre et al., 2014; Marcic, 2012; Prischmann et al., 2005; Ruckert et al., 2018). However, TSM and BGM have reported populations that show pesticide resistance to many major chemical classes (Ay and Gürkan, 2005; Dermauw et al., 2013b; Kwon et al., 2010; Leeuwen et al., 2005; Yang et al., 2001). Additionally, some pesticide applications like neonicotinoids can promote outbreaks of many spider mite species as observed on maize (Ruckert et al., 2018), rose (Gupta and Krischik, 2007), hemlock (Raupp et al., 2004) and boxwood (Szczepaniec and Raupp, 2013). There are a number of natural enemies that suppress spider mites, including predatory mites (e.g., *Phytoseiulus persimilis* Athias-Henriot and *Neoseiulus californicus* McGregor), thrips, predatory bugs (e.g., minute pirate bugs), among others (Rhodes and Liburd, 2006; Grevstad and Klepetka, 1992; McMurtry et al., 1970). Pesticide applications for spider mites can cause adverse impacts on populations of natural enemies (Prischmann et al., 2005). While augementative releases of natural enemies in the maize system is not cost effective (Bynum et al., 2004; Pickett and Gilstrap, 1986), conservation biological control strategies, including reducing pesticide use to encourage predators that assist in suppression is key (Prischmann et al., 2005). Finally, using overhead irrigation that removes dust from leaves and washes off mites, planting drought-tolerant hybrids and utilizing host plant resistance (plant traits that repel, tolerate and recover from pest) would be some additional tactics that are sustainable and could aid in spider mite management (Chandler, 1979; Grinnan et al., 2013; Kinn et al., 1972; Machado et al., 2000; Mansour et al., 1993; Tadmor et al., 1999a).

Host plant resistance in maize for spider mite management

Host plant resistance is defined as the ability of plants to avoid, recover and tolerate the damage caused by pests (Sharma and Ortiz, 2002). Plant resistance to herbivory can be categorized into three resistance types including antibiosis, antixenosis, and tolerance (De Ponti, 1977; Howe and Jander, 2008; Kogan and Ortman, 1978; Painter, 1951; Perring et al., 1982). For resistance associated with antibiosis, the plant produces toxic defense chemicals (secondary metabolites) that negatively affects the fecundity and development of an herbivore (Painter, 1951). Antixenosis or non-preference, however, does not adversely affect the herbivore, rather the plant is less attractive for the herbivore to feed, settle or lay eggs (De Ponti, 1977; Kogan and Ortman, 1978). Often, antibiosis and antixenosis are usually overlapping in nature because many plant traits have both toxic and repellant properties (Stout, 2013). Finally, tolerance does not affect the herbivore directly and is not a less attractive host, but rather the plant recovers, sometimes over compensating in growth, after the herbivore feeds (Painter, 1951). These resistance qualities can be utilized in the management of arthropod pests in managed systems. This is accomplished through breeding programs where screening for resistance involves an evaluation of plant germplasm or parental lines (Eigenbrode and Trumble, 1994; Stoner, 1996).

In maize, antibiosis and tolerance resistance mechanisms have been reported against spider mites (Bynum et al., 2004; Mansour et al., 1993). Antixenosis is also a component of maize resistance as described with corn plant hopper (*Peregrinus maidis* Ashmead) (Singh and Seetharama, 2008). Several studies screened maize inbred lines and identified several candidate plants showing spider mite resistance (Bynum et al., 2004a; Kamali et al., 1989a; Mansour et al., 1993; Tadmor et al., 1999a). For instance, the B96 maize inbred line was shown to reduce the population growth of TSM and carmine mites (*Tetranychus cinnabarinus* Boisduval) and their feeding (Kamali et al., 1989b; Tadmor et al., 1999a). In maize, among other cereals in the Poaceae family, benzoxazinoids are a class of plant defense compounds (Adhikari et al., 2015; Frey et al., 2009; Glauser et al., 2011; Hanhineva et al., 2011). Benzoxazinoids provided resistance against mites, insects, nematodes, fungi as well as bacteria (Ahmad et al., 2011; Bui et al., 2018; Feng et al., 1992; Grün et al., 2005; Niemeyer, 1988; Oikawa et al., 2004; Sicker et al., 2000). The resistant effects of benzoxazinoids are due to the anti-feeding properties driven by inhibition of proteases in the gut of herbivores (Ahmad et al., 2011; Betsiashvili et al., 2015; Castañeda et al., 2009; Feng et al., 1992; Mukanganyama et al., 2003). Of the many benzoxazinoid compounds, DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-1) is the primary compound showing these toxic effects and is stored in a non-toxic form, DIMBOA-glucoside in the cell vacuoles (Meihls et al., 2012; Pereira et al., 2017). While benzoxazinoids are known to be present in young seedlings of plants, they can also be induced by herbivore feeding (Elek et al., 2013; Gianoli and Niemeyer, 1998; Maag et al., 2016). B75 and B96 maize inbred lines have higher DIMBOA levels which offer suppression to spider mites (Bui et al., 2018; Barry et al., 1994; Bing et al., 1990).

While past studies have shown significant progress in evaluating maize plant defenses and developing resistant plants to spider mites, there is further potential for testing resistant plants under water-stress conditions, since such conditions are associated with spider mite outbreaks. This requires an understanding of the basis of plant responses to spider mite, especially considering host specialization (i.e., generalist and specialist).

Plant defense and responses to herbivory

Plants encounter attacks from diverse herbivores within different feeding guilds (e.g., chewing vs. piercing-sucking) and varied host specialization (e.g., generalist vs. specialist) (Howe and Jander, 2008). To defend against herbivory, plants have direct defense mechanisms such as mechanical protection on the leaf surface (e.g., thrones, spikes, thorns, thick epidermis) or production of toxic chemicals (e.g., defensive proteins, phenols, quinones) which deter the growth and development and even cause mortality of different life stages of attacking herbivores (Agrawal, 2011; Fürstenberg-Hägg et al., 2013; Howe and Jander, 2008; Karban and Myers, 1989; Mithöfer and Boland, 2012; Tian et al., 2012). Plants also emit volatiles following herbivore feeding that can lure natural enemies of attacking herbivores (Kaplan, 2012; Kaplan and Lewis, 2015; Kaplan and Thaler, 2010; Kessler and Baldwin, 2000).

Plant responses to herbivory are mediated in part by the jasmonic acid (JA) and salicylic acid (SA) defense pathways (Gill et al., 2016a,b; Howe and Jander, 2008; Kessler and Baldwin, 2002). Induction of these pathways mediates the production (or activation) of many plant defense proteins including polyphenol oxidase (PPO) and trypsin inhibitor (TI) which tend to be associated with JA signaling, and chitinase (CHI) and peroxidase (POD) that tend to be regulated by the SA pathway (Barto and Cipollini, 2005; Cipollini et al., 2004). Elevated activity of these defense proteins can negatively impact herbivore growth and development (Cipollini et al., 2004). For example, plants produce PPO that decreases the nutritional value of plants for arthropod herbivores by alkylating its dietary proteins and amino acids (Constabel and Barbehenn, 2008; Dowd, 1994; Mander and Liu, 2010). In tomato, overexpression of PPO reduced growth and increased larval mortality of *Spodoptera litura* Fabricius (Mahanil et al., 2008). The importance of PPO activity for resistance was also confirmed in resistant wheat cultivars with higher PPO activity for the suppression of *Sitobion avenae* Fabricius compared to susceptible wheat cultivars (Han et al., 2009). POD is another plant defensive protein that not only prevents plants from the harmful effects of Reactive Oxygen Species (ROS) but is also known to create physical barriers for herbivores by lignin formation and cross-linking of cell wall components (Almagro et al., 2009). Higher levels of POD in plants can provide plant resistance to herbivores, as well as increase plant tolerance to abiotic stresses, generally (Dowd and Johnson, 2015; Fazeli et al., 2007; Liang et al., 2017; Shoorooei et al., 2013). Proteins such as CHI and TI also have important plant defense roles. Specifically, CHI is known to degrade the exoskeleton and peritrophic membrane of herbivores, and is induced by arthropods including spider mites (Fürstenberg-Hägg et al., 2013; Kant et al., 2004; Zhu-Salzman et al., 2004). TI, on the other hand, is a protease inhibitor that interferes with herbivore digestion and amino acid acquisition (Arnaiz et al., 2018; Broadway and Duffey, 1988, 1986; Cipollini et al., 2004; Duffey and Felton, 1991; Duffey and Stout, 1996; Fürstenberg-Hägg et al., 2013). Bui et al. (2018) observed broadly similar transcriptomic levels for genes encoding chitinases and protease inhibitors at 1 day for TSM and BGM herbivory. Further, *Nicotiana attenuate* Torr. ex S. Watson plants increased TI activity in response to *Manduca sexta* Linnaeus (Zavala et al., 2004). Herbivores including TSM, *Spodoptera exigua* and *Nicotiana attenuata* were reported to perform better on plants lacking TI activity (Arnaiz et al., 2018; Steppuhn and Baldwin, 2007; Zavala et al., 2004). Although POD, PPO, CHI, and TI are only a subset of plant defenses, it is clear that plants respond to herbivory, and such defense responses can be useful in herbivore suppression and plant survival.

Plant responses to herbivores with varied diet breadth and feeding type

Plant responses may also be tailored to herbivores with different feeding strategies and host specialization (Ali and Agrawal, 2012). In general, plants respond to herbivores with chewing mouthparts with JA and ethylene (ET) related defense pathways, while phloem feeders such as aphid and whitefly induce SA plant responses (Ali and Agrawal, 2012). Spider mites are cell feeders and mirror minor leaf damage similar to what is observed with whitefly and aphid, yet the majority of plants respond with JA based defenses (Ament et al., 2004; Sarmento et al., 2011). Through the co-evolutionary history of plants with herbivores, plants have also evolved an ability to respond uniquely to generalist and specialist herbivores (Alba et al., 2015; Ali and Agrawal, 2012; Ament et al., 2004; Bui et al., 2018; Glas et al., 2014; Lankau, 2007; Manzaneda et al., 2010; Martel et al., 2015; Massad et al., 2011; Sarmento et al., 2011; Schimmel et al., 2018). For example, tomato plants were found to induce plant defenses in response to generalist TSM, but these responses were absent (or suppressed) in response to feeding by the specialist spider mite *Tetranychus evansi* Baker & Pritchard (Alba et al., 2015; Ament et al., 2004; Glas et al., 2014; Martel et al., 2015; Sarmento et al., 2011; Schimmel et al., 2018). Further, *Boechera divaricarpa* A. Nelson responses to the generalist *Trichoplusia ni* Hübner were associated with JA and ET genes, whereas plant responses to specialist *Plutella xylostella* Linnaeus were associated with SA genes (Vogel et al., 2007). *Lindera benzoin* L. Blume responded to the generalist *Spodoptera exigua* with higher POD activity than the specialist *Epimecis hortaria* Fabricius (Mooney et al., 2009).

Despite these unique responses by plants, generalist and specialist herbivores also have ways to respond to those defenses (Ali and Agrawal, 2012; Bui et al., 2018). Generalists appear to be affected the most by plant defenses, while specialist herbivores have evolved mechanisms to tolerate defenses (Ali and Agrawal, 2012; Bui et al., 2018). In general, herbivores with broad diet breadth (i.e., generalists) rely on broad detoxification capabilities to overcome defenses from diverse plant species (Dermauw et al., 2013a, 2013b; Leeuwen et al., 2011; Szczepaniec et al., 2013). In contrast, specialized herbivores typically have long co-evolutionary relationships with their host plants, favoring the ability to detoxify, suppress, and manipulate specific (narrow) defenses of particular hosts (Ratzka et al., 2002; Wheat et al., 2007; Wittstock et al., 2004). Nevertheless, to some extent, even specialist herbivores can be negatively impacted by plant defenses (Adler et al., 1995; Agrawal and Kurashige, 2003; Berenbaum et al., 1989; Cornell and Hawkins, 2003). In particular, specialist herbivores can tolerate low levels of defenses, but as plant defense concentrations/activity increase, some toxins (e.g., digestibility reducers) are believed to be effective against both generalists and specialists (Ali and Agrawal, 2012; Feeny, 1976).

Plant interaction with water-stress

Plant responses to water-stress are complex and involve many physiological, biochemical, and molecular changes (Farooq et al., 2009b). Water-stressed plants typically have reduced cell growth, leaf size, stem extension, root proliferation and overall growth (Farooq et al., 2009b). Water-stressed plants prevent water-loss by keeping stomata closed and inhibiting the growth of leaves (Chaves et al., 2003). Water-stress in plants also reduces carbon fixation due to disturbed activity of various enzymes including a decline in Rubisco activity (Bota et al., 2004). As a result of water-stress, chemical signals such as reactive oxygen species (ROS) are generated which causes major injury to plants and deter plant growth (Apel and Hirt, 2004; Farooq et al., 2009b). In particular, the increase in ROS causes protein degradation, lipid peroxidation, and DNA fragmentation which ultimately leads to cell death (Mittler, 2002). To tolerate the damage from increased ROS, plants produce oxidative enzymes such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) (Apel and Hirt, 2004). Also, to withstand water-stress, plants undergo osmotic adjustments and enhance water uptake by expanding a deep root system (Chaves et al., 2003). Despite trying to withstand and avoid water-stress, the consequences of these changes can result in major crop loss. In maize, if the plants are exposed to water-stress within a 2-10 week window before anthesis (flowering period very critical for ear development), the crop can face major yield losses (Eubanks, 2006).

Plant water-stress can also affect the accumulation of mineral nutrients such as nitrogen, phosphorus, calcium, magnesium, sulfur, and chloride (Silva et al., 2011). In particular, water-stress was shown to increase or decrease nitrogen, increase calcium, reduce magnesium, increase sulfur and chloride concentrations (Brown et al., 2006; Mahouachi et al., 2006; Sardans et al., 2008; Silva et al., 2011; Silveira et al., 2001; Singh and Singh, 2004). In maize, water-stress was reported to increase leaf proteins related to photosynthesis carbohydrate metabolism and defenses (Dworak et al., 2016). Water-stress can also lead to increased soluble sugars, however, under severe water-stress conditions soluble sugars may decrease (Pinheiro et al., 2001).

Plant water-stress interactions with herbivores

Yield losses associated with plant water-stress are not only a direct result of abiotic stress but indirectly, water-stress can exacerbate the population growth of herbivores (English-Loeb, 1990; Li et al., 2008; Mattson and Haack, 1987a; Risch, 1987). Several mechanisms have been identified that contribute to plant water-stress leading to increases in associated pest populations including changes in leaf microclimate, plant chemistry and nutrition, as previously described (Ferro and Southwick, 1984). Further, drought can also decrease the rates of expression of genes such as chitinase and protease inhibitors (trypsin inhibitor), which are also known to provide resistance to plants against herbivores (Atkinson and Urwin, 2012; Dowd and Johnson, 2015).

Three hypotheses provide a framework on the plant relationship with stress and herbivore performance and include the plant stress, plant vigor and pulsed stress hypotheses (Huberty and Denno, 2004; Price, 1991; White, 1969). According to the "Plant Stress Hypothesis" water-stress in plants increases the abundance of mobile nitrogen, particularly, essential and non-essential amino acids, which makes them a highly nutritious food source for arthropods (White, 1969). Feeding on nutrition-rich leaves accelerates the development, fecundity, and performance of herbivores (White, 1969). While this hypothesis received support from many studies (Cobb et al., 1997; Louda and Collinge, 1992; Mattson and Haack, 1987b; Oswald and Brewer, 1997), a number of other studies have found inconsistent results (Huberty and Denno, 2004; Joern and Mole, 2005; Koricheva et al., 1998; Staley et al., 2006; Williams and Cronin, 2004). The "Plant Vigor Hypothesis" predicts that healthy plants, those that grow vigorously and without stress (e.g., water-stress), are comparatively more suitable hosts to herbivore as compared to stressed plants due to higher availability of nutrients, higher osmotic potential and lower plant defense mechanisms (Price, 1991). Finally, the “Pulsed Stress Hypothesis” suggested that phloem feeders may perform better on pulsed or intermittent water-stressed plants due to the recovery of turgor and additional availability of phloem (nitrogen) as compared to severely stressed plants (Huberty and Denno, 2004). Also, the studies that tested the impact of water-stress on herbivore performance reported different results according to the feeding guild of herbivores (Gutbrodt et al., 2012; Koricheva et al., 1998; Santamaria et al., 2018; Valim et al., 2016; Ximénez-Embún et al., 2018, 2017b, 2016). For instance, water-stress in plants positively impacted the population growth of cell feeder spider mites (Santamaria et al., 2018; Ximénez-Embún et al., 2018, 2017b, 2016). Studies on chewing herbivores reported that water-stressed plants negatively impacted the population growth of several herbivores including *Plutella* spp. (Gutbrodt et al., 2012; Koricheva et al., 1998; Valim et al., 2016). Adversely, leaf-mining species showed a variable response to water-stress, as population growth of only one species was increased in drought conditions, while three other species showed no consistent response (Staley et al., 2006).

Water-stress can affect plant resistance to pests, and consider the connection plant responses have to multiple stresses. For example, although plant responses such as POD are primarily involved in abiotic stress, these responses can also connect with plant defenses to biotic stresses (Almagro et al., 2009). These interactions can be quite complex as studies investigating several arthropod herbivores across various cropping systems reported that water-stress led to idiosyncratic effects on plant resistance to pests

(Grinnan et al., 2013; Ojwang et al., 2010; Sharma et al., 1999; Verdugo et al., 2016, 2015). Abiotic stresses including water-stress, for example, reduced plant resistance to the green peach aphid (*Myzus persicae* Sulzer) (Verdugo et al., 2015), and resistance was lost for sorghum midge (*Stenodiplosis sorghicola* Coquillett) (Sharma et al., 1999) and bean fly (*Ophiomyia phaseoli* Tyron) (Ojwang et al., 2010). An evaluation of 29 studies focused on aphids across several cropping systems found that resistance in crops exposed to water-stress was decreased (41.4% of studies), increased (34.5%), showed no change (20.1%), or had conditional effects (3.4%) (Verdugo et al., 2016). These varied responses of plants to water-stress on their ability to resist herbivores expands to a number of plants including different genotypes of soybean (*Glycine max* L.) (Grinnan et al., 2013), lucerne (*Medicago sativa* L.) (Johnson et al., 2014) and sweet potato (*Ipomoea batatas* L.) (Mao et al., 2004).

Plant water-stress interactions with herbivores with varied diet breadth

Additional complexity may exist for plants that encounter attacks from herbivores with different host specialization (i.e., generalist and specialist) (Ali and Agrawal, 2012). Plants can have unique interactions with generalist and specialist herbivores, which could further be tailored with additional stressors, such as water-stress (Khan et al., 2010; Mewis et al., 2012; Tariq et al., 2013). Also, since water-stress in plants have been reported to enhance populations of both generalist and specialist herbivores (Khan et al., 2010; Mewis et al., 2012; Tariq et al., 2013), it is important to understand the basis of plant interactions with water-stress and herbivory from generalist and specialist herbivores.

Studies focused on evaluating generalist and specialist herbivores with piercing-sucking mouthparts have shown that generalist herbivores benefit from plant water-stress, while specialists have no effect of plant water-stress (Khan et al., 2010; Mewis et al., 2012; Tariq et al., 2013). For example, water-stress in *Arabidopsis thaliana* L. Heynh., and *Brassica oleracea* L. increased population growth of generalist *Myzus persicae*, while no such effect was observed for the specialist *Brevicoryne brassicae* Linnaeus (Khan et al., 2010; Mewis et al., 2012; Tariq et al., 2013). Indeed, there is evidence of contrasting results as well where the performance of the specialist *Brevicoryne brassicae* was better than the generalist *Myzus persicae* at moderate drought levels on water-stressed plants (Tariq et al., 2012). Interestingly, water-stressed plants can have either increased or decreased defense responses to generalist herbivores (Khan et al., 2011, 2010; Mewis et al., 2012; Tariq et al., 2013, 2012). In contrast, regardless of water-stress, plant defenses responses did not change for specialist herbivores (Khan et al., 2011, 2010; Mewis et al., 2012; Tariq et al., 2013, 2012).

For generalist and specialist herbivores with chewing mouthparts, plant water-stress can negatively impact the performance of generalists and positively impact the performance of specialist herbivores (Gutbrodt et al., 2011; Nguyen et al., 2018). In particular, the specialist *Pieris brassicae* Linnaeus performed better on water-stressed *Alliaria petiolata* (Bieb.) Cavara & Grande than the generalist *Spodoptera littoralis* Boisduval (Gutbrodt et al., 2012). Similarly, Nguyen et al. (2018), showed that water-stress in *Solanum dulcamara* L. increased plant defenses which decreased the performance of the generalist *S. exigua* but not the specialist *Leptinotarsa decemlineata* Say. Contrasting results were shown by Gutbrodt et al. (2011), where water-stressed *B.*

oleracea were preferred by both generalist *S. littoralis* and specialist *P. brassicae* compared to well-watered plants. Further, studies showed that water-stressed plants can have varied responses for generalist and specialist herbivores. For example, *Solanum dulcamara* plants exposed to combined water-stress with generalist *S. exigua* elicited different plant responses as compared to drought combined with specialist *L. decemlineata* (Nguyen et al., 2018).

For generalist and specialist spider mite herbivores that feed on cell contents, water-stress in plants appear to increase the population growth of generalists (e.g., TSM) as well as specialists (e.g., *Tetranychus evansi* and BGM) (Bagarama, 2015; Bui et al., 2018; Gillman et al., 1999; Klubertanz et al., 1990; Kvien et al., 1987; Machado et al., 2000; Santamaria et al., 2018; Sinaie et al., 2019; Ximénez-Embún et al., 2017b, 2016, 2018, 2017a). However, water-stressed plants can respond to generalist and specialist spider mite species with different plant defense responses. In general, water-stress combined with generalist mites increased plant defense mechanisms (Dworak et al., 2016; Sabzi et al., 2019; Santamaria et al., 2018; Ximénez-Embún et al., 2017a). For example, water-stress and TSM herbivory in *Phaseolus vulgaris* L. increased the expression of PAL, LOX, PR3, PR4, and OS defense genes (Sabzi et al., 2019). Similarly, water-stress and herbivory by TSM in *Medicago truncatula* Gaertn. increased levels of local antioxidant and osmoprotective responses (Santamaria et al., 2018). In contrast, water-stress combined with specialist herbivory had a variable response where plant defenses increased (Ximénez-Embún et al., 2016), decreased (Schimmel et al., 2018) or were unclear (Ximénez-Embún et al., 2018). For example, specialist *T. evansi* down-regulated plant defenses, while combined drought and specialist mite herbivory affected defenses differently in a variety of plant accessions (Ximénez-Embún et al., 2018). Some studies also reported that mild water-stress can have negative impacts on the population growth of TSM (English-Loeb, 1990; English-Loeb, 1989; Jongebloed et al., 1992). Specifically, TSM populations were higher on well-watered and severely water-stressed plants and lowest on intermediate stressed bush beans (*Phaseolus vulgaris* L.) (English-Loeb, 1990; English-Loeb, 1989).

The effects of drought stress and mite feeding was also measured on photosynthetic rates (Haile and Higley, 2003) and leaf abscission (Smitley and Peterson, 1996). In particular, Haile and Higley (2003), reported that the photosynthetic rate reduction was greater when TSM fed on well-watered compared to water-stressed plants on soybean (*Glycine max*). Hence, tolerance of plants to generalist TSM increased in water-stressed plants. Smitley and Peterson (1996), reported that on honeylocust trees (*Gleditsia triacanthos* L.), combined water-stress and specialist honeylocust spider mite (*Platytetranychus multidigitali* Ewing) increased leaf abscission as compared to a single stress alone.

The objectives of this dissertation were to 1) determine the effects of water-stress on population growth of TSM and BGM, and plant defense protein responses to mite (TSM and BGM) herbivory, 2) evaluate the effects of maize resistance on mite behavior by testing a susceptible (B73), and two resistant (B75 and B96) maize lines, and 3) investigate the effects of water-stress on maize resistance to spider mites by evaluating B73, B75 and B96 maize lines with varied resistance.

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CHAPTER II

VARYING RESPONSES TO COMBINED WATER-STRESS AND HERBIVORY IN MAIZE FOR SPIDER MITE SPECIES THAT DIFFER IN HOST SPECIALIZATION[1]

Abstract: Water-stress commonly affects crops grown in arid and semi-arid regions. Apart from the direct impact of this abiotic stress on yield, a diverse community of herbivores can outbreak under these conditions, and plant responses to abiotic stress may alter plant defense responses that deter herbivores. Outbreaks of both generalist and specialist spider mites are strongly associated with hot and dry conditions in the field. To understand how water-stress impacts maize responses to spider mites, we conducted parallel greenhouse and field experiments with maize plants (B73 inbred line) subjected to optimal irrigation and water-stress conditions [50-60% and 5-10% volumetric water content (VWC) in the greenhouse, and 25-32% and 10-15% VWC, in the field, respectively]. In addition to recording B73 responses to water-stress alone, we measured the population growth of the generalist herbivore twospotted spider mite (*Tetranychus urticae* Koch, TSM) and the specialist herbivore Banks grass mite (*Oligonychus pratensis* Banks, BGM) on optimally watered and water-stressed plants. We also measured plant defense protein activities [peroxidase (POD), polyphenol oxidase (PPO), chitinase (CHI) and trypsin inhibitor (TI)] at 1, 3, and 7 days post-mite introduction for each irrigation treatment. For B73 plants exposed to water-stress, we observed increases in leaf temperature, leaf water potential, POD activity, as well as decreases in stomatal conductance and stem height. Populations of both mite species increased more rapidly on

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water-stressed B73 plants. While optimally irrigated B73 plants responded with similar plant defense activity to both mite species, combinations of plant water-stress and TSM herbivory resulted in modest increases in CHI and TI activity that were not observed for the respective treatments with BGM. Our results support the physiological factor of elevated leaf temperature in water-stressed plants as an underlying contributor to spider mite outbreaks in maize, and suggest a role for species-specific factors, possibly associated with herbivore host plant breath, in impacting plant responses to herbivory in combination with an abiotic stress.

1. Introduction

Rising temperatures and increasing drought stress associated with climate change constrain global agricultural production (Downing, 2013; Misra, 2014; Smith and Gregory, 2013). More than 67% of the continental United States experienced low water availability and drought conditions in 2018 (United States Drought Monitor, 2018), factors that can cause major yield losses to economically important crops (Rippey, 2015). In maize (*Zea mays* L.) yield losses of nearly 27% were observed in the United States in the major drought episode of 2012 (Rippey, 2015). In plants, suboptimal water (hereafter “water-stress”) affects diverse physiological responses (i.e., leaf temperature, stomatal conductance, and leaf water potential) and overall plant growth (Bradford and Hsiao, 1982; Kramer, 1983; Niu et al., 2006; Ruckert et al., 2018; Shahenshah and Isoda, 2010). Furthermore, water stress has often been associated with pest outbreaks in agricultural and urban systems (Barbosa et al., 2012; Brodbeck and Strong, 1987; Dale and Frank, 2017, 2014; Hebertson and Jenkins, 2008; Mattson and Haack, 1987b; Meineke and

Frank, 2018; Risch, 1987; Ruckert et al., 2015; Stavrinides et al., 2010). While the effects of water-stress on plant physiology are comparatively well-characterized (Bruce et al., 2002; Fitter and Hay, 2012; Osakabe et al., 2014; Xu et al., 2010), fewer studies have investigated the interactions between water-stress and biotic stressors on plant defense responses (English-Loeb, 1989; Khan et al., 2011; Mewis et al., 2012; Santamaria et al., 2018; Tariq et al., 2013b; Ximénez-Embún et al., 2016).

Several expectations have been proposed to explain plant-arthropod interactions under water-stress conditions. The *Plant Stress Hypothesis* posits that metabolic changes (i.e., increases in free sugars and essential amino acids) stimulated by water-stress raise leaf nutritional quality and promote growth and development of arthropod herbivores (White, 1969). In contrast, the *Plant Vigor Hypothesis* proposes that water-stressed plants have increased defensive compounds and reduced overall plant growth that is unfavorable for herbivores (Price, 1991). An additional factor is that while the ability of herbivores to grow on water-stressed plants depends on their ability to utilize leaf nutrition and to overcome plant defenses, this in turn can depend on the degree of host plant specialization (Gutbrodt et al., 2011; Huberty and Denno, 2016).

Many plants are attacked by a diverse community of herbivores that includes both generalist herbivores with broad host ranges, and specialist herbivores with narrow ones (Ali and Agrawal, 2012). Plants have evolved general responses to herbivory (and other biotic challenges) mediated in part by the jasmonic acid (JA) and salicylic acid (SA) defense pathways (Gill et al., 2016a,b; Howe and Jander, 2008; Kessler and Baldwin, 2002). Induction of these pathways mediates the production (or activation) of many phylogenetically well conserved plant defense proteins including polyphenol oxidase

(PPO) and trypsin inhibitor (TI) that tend to be associated with JA signaling, and chitinase (CHI) and peroxidase (POD) that tend to be regulated by the SA pathway (Barto and Cipollini, 2005; Cipollini et al., 2004). Elevated activity of these defense proteins can negatively impact herbivore growth and development (Cipollini et al., 2004). For instance, PPO and POD decrease the nutritional value of plants for arthropod herbivores (Mander and Liu, 2010), while CHI may degrade the exoskeleton and peritrophic membrane of arthropods, and TI, a protease inhibitor, can retard digestion and amino acid acquisition (Arnaiz et al., 2018; Broadway and Duffey, 1988, 1986; Cipollini et al., 2004; Duffey and Felton, 1991; Duffey and Stout, 1996; Fürstenberg-Hägg et al., 2013). Additionally, at the level of plant species and families, specialized defensive proteins and metabolites induced by phytohormone signaling (or ones constitutively expressed) can deter both generalist and specialist herbivores, and may have a disproportionate impact on generalists (Bui et al., 2018).

The diverse nature of plant defense responses to herbivory, and the selection on herbivores to overcome them, has led to complex evolutionary scenarios that remain incompletely understood (Ali and Agrawal, 2012; Ballhorn et al., 2010; Bui et al., 2018; Gols et al., 2008; Lampert, 2012; Mooney et al., 2009; Poelman et al., 2008; Reymond, 2004; Vogel et al., 2007a). While generalist herbivores may rely on broad detoxification capabilities to overcome plant defenses of their diverse hosts (Dermauw et al., 2013a, 2013b; Leeuwen et al., 2011; Szczepaniec et al., 2013), specialist herbivores typically have long co-evolutionary histories with their host plants, potentially favoring the ability to detoxify, suppress, and manipulate the specific (narrow) defenses of particular hosts (Ratzka et al., 2002; Wheat et al., 2007; Wittstock et al., 2004). Nevertheless, how these dynamics are impacted by ubiquitous abiotic factors like water-stress introduces added complexity (English-Loeb et al., 1997; Fazeli et al., 2007; Lee et al., 2007; Ruckert et al., 2018; Thipyapong et al., 2004). For instance, POD activity is increased by drought-stress alone in plants including maize and tomato (Fazeli et al., 2007; Ruckert et al., 2018). Studies of the joint impacts of water-stress and herbivory among arthropod herbivores that vary in diet-breadth have often revealed idiosyncratic plant responses (Khan et al., 2011, 2010; Mewis et al., 2012; Nguyen et al., 2018), but they have provided evidence that plant responses to generalist and specialist herbivores in water-stressed plants can vary.

Two spider mite species, the extreme generalist twospotted spider mite (*Tetranychus urticae*, TSM) and the specialist Banks grass mite (*Oligonychus pratensis*, BGM), are well-documented pests on maize, a major global food crop (Archer and Bynum, 1993; Bacon et al., 1962; Bynum et al., 2015; FAO, 2018; Peairs, 2014; Peairs and Both, 2010; Ruckert et al., 2015). In particular, economic damage by spider mites is associated with drought-stress in field settings, with up to 47% yield loss reported under conditions of water-stress (Archer and Bynum, 1993; Bacon et al., 1962; Bynum et al., 2015; FAO, 2018; Peairs, 2014; Peairs and Both, 2010; Ruckert et al., 2015). Recently, Bui et al. (2018) characterized transcriptomic changes of the maize inbred line B73, from which the maize reference genome was generated (Schnable et al., 2009), to herbivory by TSM and BGM. Genes associated with both JA and SA synthesis and signaling responded robustly to spider mite herbivory, as did POD activity. While Bui et al. (2018) observed no (or little) difference in B73 responses to herbivory between these two mite species that vary radically in their host range breadth, this study was limited to greenhouses, molecular responses were predominantly examined over a narrow time course (≤ 24 hours), and assays were performed only with optimally watered plants. Here, we asked how water-stress impacts B73's response to TSM and BGM in both greenhouse and field experiments. We anticipate our findings will suggest mechanisms for elevated performance of spider mites on drought-stressed maize plants, and reveal potential differences in plant defense responses to the generalist TSM as compared to the specialist BGM in the field setting under water-stress conditions.

2. Materials and methods

2.1. Experimental design

2.1.1. Greenhouse Experiment

We conducted a 3 × 2 factorial design experiment using three levels of mite type [Control (no mite), TSM and BGM] and two levels of water (optimal irrigation and water-stress) with repeated measures (1, 3, and 7 days) in the greenhouse. This experiment was performed at Utah State University's Research Greenhouse in Logan, UT.

Experimental units consisted of plastic containers (25.4 cm × 50.8 cm × 17.8 cm, Sterilite®, MA) filled with potting soil (Sunshine Mix #3, Sun Gro Horticulture, MA) arranged in a complete randomized design (Supp. Fig. 1). We planted six maize plants (B73 inbred line) per container, where each container represented a replicate and each plant represented a subsample. Each treatment (mite × water) was replicated four times. Maize plants were kept under greenhouse-controlled conditions (25±2 °C, 60±5% RH, 16:8 hr (L:D) photoperiod) and fertigated at a rate of 4.8 kg/100L of 21N-5P-20K Peters Excel Water Soluble Fertilizer mixture (ICL Specialty Fertilizers, SC, USA) in water.

We used drip tape [DIG Corporation (CA, USA), 12.7 mm and 6.35 mm diameter tubing with 3.8 L/hr compensating emitters] to irrigate the plants throughout the experiment. After six weeks, plants were switched from fertigation to irrigation to establish optimal irrigation or water-stress levels. Acclima 315 L soil sensors (Acclima, ID, USA) were used to monitor the volumetric water content (VWC) of soil. All replicates (containers) were irrigated evenly at the level equivalent to field capacity of potting soil (50-60 % VWC) for seven weeks after sowing. When plants were 8-weeks old, containers were randomly assigned to either optimal irrigation (maintaining 50-60 % VWC at field capacity) or water-stress (reducing irrigation to 5-10 % VWC above permanent wilting point) treatments (Fig. 2-1) (Fitter and Hay, 2012). Water-stress and optimal irrigation levels were quantified by measuring stomatal conductance (mmolm^{-2}s^{-1}) and leaf temperature (°C) using a leaf porometer (Model SC-1, Meter Group, WA), leaf water potential (bar) using a pressure chamber instrument (Model 615, PMS Instrument Company, OR), and stem height (cm) by using a measuring tape (Table. 2-1). Here, leaf temperature, stomatal conductance and stem height were measured at 3 and 7 days, while leaf water potential was measured after sample collection at 7 days post mite introduction.

When plants were 8-weeks old, two sticky barriers were made with Tanglefoot (Scotts Miracle-Gro Company, OH, USA) non-phytotoxic wax around the under- and upper-side of the 8th leaf as described by Bui et al. (2018). Each barrier was positioned at 7.5 cm from the leaf center, creating a 15 cm long arena spanning the middle leaf region.

Twenty adult female mites (mated BGM or TSM) from laboratory colonies sustained on B73 maize [28±2 °C, 50±5% RH, 16:8 hr (L:D) photoperiod] were introduced into the leaf arena. Mites were transferred to leaves by vacuuming twenty mites each into filtered pipette tips attached with a rubber hose to a low power vacuum. The widest end of the pipette tips were then secured to the upper leaf surface with tape to allow mites to exit the pipette tips and settle on the undersides of the leaves, the preferred feeding site. Mites moved onto the leaf surface within approximately an hour of inoculation.

Leaf subsamples (leaf area inside the Tanglefoot arena) from two randomly selected plants per treatment were collected at 1, 3, and 7 days post mite introduction. Each leaf sample was immediately placed in an envelope and flash-frozen using liquid nitrogen, and stored in a freezer (-20 °C) until processing. Each leaf sample was inspected using a stereomicroscope (Leica S6 D Greenough, NJ, USA) to count the number of eggs and all mite stages. Frozen leaf samples were kept cold during mite evaluation by placeing samples on an aluminum tray over ice. Subsequently, all nymph and adult mites were removed from leaf samples using a motorized brush (Princeton 9850R-0, Princeton Artist Brush Company, NJ, USA) before processing leaves for defense protein bioassays (see section 2.2).

2.1.2. Field Experiment

Mirroring the greenhouse study, we conducted a 3 × 2 factorial experiment of the same design, treatments, and sample intervals in the field. This experiment was conducted at the Greenville Research Station at Utah State University, North Logan, UT.

Experimental units were represented by Lumite cages (1.8 m L × 1.8 m W × 1.8 m H) (Lumite, GA, USA), arranged in a complete randomized design within varied water treatments (Supp. Fig. 3). A total of 24 cages were arranged in four rows, where cages were spaced 2 m apart and each row was 4 m apart to establish two irrigation treatments. We planted six seeds (B73 inbred line) per cage, where each cage was a replicate and each plant a subsample. Each treatment (mite × water) was replicated 4 times. Granular fertilizer (16N:16P:8K:3Fe; Turf Maker) was used twice (0.03 Kg/ sq. m) prior to and at 8-weeks after seeding.

Drip tape (Toro EAP 5101245-600, 15 mm diameter, 30 cm emitters, Q-100: 2.8×10^{-5} m^3s^{-1}/30m at 0.3 bar) on the soil surface was used to irrigate plants. Soil sensors (Acclima 315 L) were used to monitor the VWC of soil. All replicates (cages) were irrigated at field capacity of field soil (25-32 % VWC) up to 6.5 weeks after sowing (Fig. 2-1). After 6.5 weeks, 12 cages were randomly assigned to the optimal irrigation (25-32 % VWC, field capacity) treatment, while the remaining 12 cages were assigned to the water-stress treatment by discontinuing irrigation until the VWC was reduced to 10-15 % VWC, while keeping plants above the permanent wilting point (Fitter and Hay, 2012). Similar to the greenhouse experiment, we measured stomatal conductance (mmol$m^{-2}s^{-1}$), leaf temperature (°C), leaf water potential (bar), and stem height (cm) to assess the impact of water-stress (Table. 2-1).

Following the greenhouse protocol, the 8th leaf on 8-week old plants was selected for establishment of Tanglefoot arenas of 15 cm in length. Twenty adult female BGMs or TSMs were introduced to the leaf arenas for each mite species treatment using the pipette tip method previously described (Supp. Fig. 2). Leaf subsamples within the Tanglefoot arena from two randomly selected plants per treatment were collected at each sampling time (1, 3, and 7 days), immediately placed in envelopes and flash-frozen using liquid nitrogen and stored in a freezer (-20 °C) until processing. The numbers of adult mites and eggs (BGM and TSM) were recorded from leaf samples using a stereomicroscope (Leica S6 D Greenough, NJ, USA) as described for the greenhouse experiment. All mite stages were removed from leaf samples before processing leaves for defense protein bioassays as described above.

2.2. Plant defense bioassays

Leaf samples were analyzed for four plant defense proteins: polyphenol oxidase (PPO), trypsin inhibitor (TI), peroxidase (POD), and chitinase (CHI) (Barto and Cipollini, 2005). Following methods adapted from Ruckert et al. (2018), leaf samples were pulverized in liquid nitrogen to create a fine powder. Plant tissue (500 mg) was then mixed with 1 mL of 0.05 M sodium phosphate buffer (Han et al., 2015) and centrifuged at 12000 RPM for 12 mins to obtain the cell lysate (supernatant), which contained soluble proteins. The activities of POD, PPO and CHI were analyzed using a microplate reader (Biotek EPOCH, VT, USA). The activity of TI was analyzed by using radial diffusion techniques (Cipollini and Bergelson, 2000). PPO and POD were quantified as $\Delta \mathrm{Abs}_{470\mathrm{nm}}$ min^{-1}mg extract protein^{-1}, CHI was quantified as $\Delta \mathrm{Abs}_{405\mathrm{nm}}$ mg extract protein^{-1}, and TI was quantified as μg TI mg extract protein^{-1}.

2.3. Statistical Analysis:

Data from plant physiological measurements including leaf temperature, stomatal conductance, and stem height from 3 and 7 days were averaged and analyzed along with leaf water potential using t-tests (Proc TTEST procedure; SAS 9.4 M4 University edition) to compare water (optimal irrigation and water-stress of B73) treatments.

Mite (TSM and BGM) population sizes and defense protein activity measurements in the greenhouse and field experiments were analyzed using a generalized linear model (Proc Glimmix; SAS 9.4 M4 University edition). When analyzing mite population growth, two levels of mites (TSM and BGM) and two levels of water (optimal irrigation and water-stress) with repeated measures (1, 3, and 7 days post mite introduction) were used. When analyzing defense protein assays, three levels of mite [Control (no mite), TSM and BGM] and two levels of water (optimal irrigation and water-stress) with repeated measures (1, 3, and 7 days post mite introduction) were used. Square-root transformation was used for mite population growth, POD, PPO and CHI data to conform to the assumption of normality and heteroscedasticity. When interactions were not significant, significant main effects were analyzed using Tukey's HSD post hoc test. When three-way interactions were significant, LSMESTIMATE statement (Proc Glimmix) with Tukey-Kramer adjustment was used for further analysis. For instance, when defense protein activity revealed a three-way interaction (water × mite × time) each mite species was independently analyzed at each time period comparing water-stress and optimal irrigation.

3. Results

3.1. Greenhouse

3.1.1. Effect of water-stress on mite population growth in B73 maize

Subjection of B73 plants to water-stress elicited significant differences, as compared to optimal irrigation, for all plant physiological responses examined (Table 2-1). Specifically, under water-stress, leaf temperature and leaf water potential were elevated by 3.6 ± 0.42 °C and 2.53 ± 0.34 bar, respectively, as compared to optimally irrigated plants (Table 2-1). Additionally, stomatal conductance and stem height were significantly reduced on water-stressed B73 plants by 143.4 ± 14.14 mmolm$_{-2}$S$_{-1}$ and 20.06 ± 1.68 cm, respectively, as compared to optimally irrigated B73 (Table 2-1).

In general, mite populations increased on B73 plants regardless of water level over the 7 days; however, the magnitude of mite population growth over the duration of the experiment was significantly greater on water-stressed as compared to optimally irrigated B73 plants (water × time interaction: $P = 0.005$; Table 2-2). More specifically, while populations of both BGM and TSM increased on water-stressed as compared to optimally irrigated plants, the magnitude of increase for TSM was greater than for BGM, leading to a significant water × mite interaction (Fig. 2-2, Table 2-2). A significant mite × time interaction ($P = 0.018$) also revealed that while both TSM and BGM populations increased for the duration of the experiment, the rate of population growth was initially greater for TSM, as compared to BGM, at 3 days post introduction. An increase in BGM population growth after 3 days was observed, such that by 7 days population levels were similar to those observed for TSM (Fig 2-2, Table 2-2).

3.1.2. Effect of water-stress and mite herbivory on the activity of plant defense proteins

When B73 plants were subjected to water-stress, POD activity significantly increased by 1.17-fold relative to that of optimally irrigated plants (Table 2-3, Fig. 2-4a); PPO activity, however, significantly decreased by 0.8-fold (Table 2-3, Fig. 2-4b). In contrast, spider mite herbivory did not result in significant changes in POD or PPO activity (Table 3).

Water-stress alone did not significantly impact CHI activity in the greenhouse (Table 2-3). In contrast, spider mite herbivory resulted in a significant decrease in CHI activity on B73 as compared to plants without mites (Table 2-3, Fig. 2-4c). Specifically, average CHI activity across the experiment was reduced by 0.78-fold and 0.72-fold for the TSM ($P = 0.05$, Tukey HSD) and BGM ($P = 0.01$, Tukey HSD) treatments, respectively, compared to plants with no mites (Fig. 2-4c). Across all treatments, CHI activity in B73 plants decreased by 0.75-fold over the 7 day period of the experiment (Table 2-3, Fig. 2-4c).

For TI activity, the water × mite × time interaction was significant (Table 2-3, Fig. 2-4d), and appeared to be driven, in part, by increased TI activity when B73 plants were subjected to a combination of water-stress and mite herbivory; however, the effect was species-specific over the 7-day period. To further assess the interaction, we analyzed TI activity for each mite species independently, comparing water-stress to optimal irrigation, at each time period. At 1 and 3 days post mite introduction, the combination of water-stress and herbivory from either mite did not significantly affect TI activity. At 7 days post mite introduction, however, the combined effect of water-stress and TSM herbivory increased TI activity on B73 plants by 2.4-fold as compared to herbivory on optimally irrigated plants ($P = 0.04$, LSMESTIMATE Tukey adjustment). In contrast, the combined effect of water-stress and BGM herbivory resulted in a decrease of 0.6-fold for TI activity, as compared to herbivory and optimal irrigation, at 7 days post mite introduction

($P = 0.02$, LSMESTIMATE Tukey adjustment).

3.2. Field

3.2.1. Effect of water-stress on B73 on mite population growth

Mirroring findings in the greenhouse, water-stress in the field significantly impacted all plant physiological responses that we examined (Table 2-1). For instance, for water-stressed B73 plants, leaf temperature and water potential increased by an average of 3.12 ± 0.43 °C and 8 ± 1.65 bar, respectively, as compared to optimally irrigated plants (Table 1). Stomatal conductance and stem height were also significantly reduced on water-stressed B73, by 69.1 ± 16.29 mmolm$_{-2}$s$_{-1}$ and 46.35 ± 5.34 cm, respectively, as compared to optimally irrigated B73 (Table 2-1).

For mite populations across the experiment's duration, the water × time interaction term was highly significant ($P < 0.001$, Table 2-4, Fig. 2-3). While mite populations increased on B73 plants regardless of irrigation status over 7 days, mite populations increased more rapidly on water-stressed as compared to optimally irrigated B73 plants (Table 2-4, Fig. 2-3).

3.2.2. Effect of water-stress and spider mite herbivory on plant defense protein activity

While water-stress alone did not affect POD activity of B73 in the field (Table 2-5), the mite × time interaction was significant (Table 2-5, Fig. 2-5a). A modest increase in POD activity for TSM herbivory was observed at 3 days, while for BGM herbivory POD activity levels were not significantly different as compared to the TSM or no mite control treatments (Table 2-5, Fig. 2-5a).

When B73 plants were subjected to water-stress, PPO activity increased by 1.38-fold as compared to plants provided optimal irrigation (Table 2-5). In addition, spider mite herbivory significantly increased PPO activity in B73 plants as compared to those with no mites (Table 2-5, Fig. 2-5b). Specifically, PPO activity was increased by 1.96-fold and 2.09-fold in response to herbivory from TSM ($P = 0.01$, Tukey HSD) and BGM ($P = 0.01$, Tukey HSD), respectively (Fig. 2-5b).

For CHI activity, the water × mite × time interaction term was significant (Table 2-5, Fig. 2-5c). The interaction appeared to be driven, at least in part, by an increase in CHI activity when B73 plants were subjected to a combination of water-stress and mite herbivory; however, the effect was mite-specific. To further investigate this interaction, we analyzed CHI activity for each mite species independently in relation to the control (no mites) at each time period comparing water-stress and optimal irrigation. At 1 day post mite introduction, optimally irrigated plants exposed to TSM increased CHI activity by 1.81-fold as compared to the no mite control ($P = 0.02$, LSMESTIMATE Tukey adjustment). At the same time point, plants exposed to the combination of water-stress and TSM herbivory increased CHI by 1.96-fold as compared to herbivory on optimally irrigated plants ($P < 0.01$, LSMESTIMATE Tukey adjustment). However, the increase in CHI activity in optimally irrigated or water-stressed plants was only apparent at 1 day post mite introduction, and CHI activity levels were uniformly low at later time points (Fig. 2-5c). In contrast, regardless of water-stress and time, no significant difference in CHI activity was observed on B73 plants exposed to BGM herbivory (Table 2-5, Fig. 2-5c).

Similar to the result for CHI activity, for TI activity the water × mite × time interaction was also significant (Fig. 2-5d, Table 2-5), and appeared to be driven by similar factors as assessed by the same follow-up analyzes as performed for CHI activity. At 1 day post mite introduction, B73 plants exposed to the combination of water-stress and TSM herbivory increased TI activity by 2.48-fold as compared to herbivory on optimally irrigated plants ($P < 0.01$, LSMESTIMATE Tukey adjustment) (Fig. 2-5d, Table 2-5). This increase in TI activity, however, was only observed at this time point. Regardless of water-stress and time, no significant effect on TI activity was observed in response to BGM herbivory on B73 plants (Fig. 2-5d).

4. Discussion

Climate change projections for increased drought frequency in many regions of the world highlight the importance of understanding of how water-stress impacts additional stresses plants face, including herbivory (Atkinson and Urwin, 2012; Rejeb et al., 2014; Suzuki et al., 2014). In our experimental designs in both the greenhouse and the field, we found that water-stressed B73 maize plants had reduced stem height, increased leaf water potential, decreased stomatal conductance, and elevated leaf temperatures. These responses are typical of reduced irrigation for maize and other plants (Bradford and Hsiao, 1982; Kramer, 1983; Niu et al., 2006; Ruckert et al., 2018; Shahenshah and Isoda, 2010), confirming water-stress induction, a prerequisite for examining the interaction with spider mites, for which outbreaks are typically associated with drought conditions. As compared to optimally irrigated plants, we found that on water-stressed B73 plants the population growth of both TSM and BGM was elevated (Fig. 2-3). This finding is consistent with earlier work with water-stress and BGM herbivory on maize hybrids (Machado et al., 2000; Ruckert et al., 2018), and with findings on TSM herbivory and water-stressed bush beans (*Phaseolus vulgaris* L.) (English-Loeb, 1990), barley (*Hordeum vulgare* L.) (Santamaria et al., 2018) and tomato (*Solanum lycopersicum* L.) (Ximénez-Embún et al., 2017a). Of several potential factors that may explain mite outbreaks on water-stressed maize, an increase in leaf temperature and change in leaf microclimate appear to generally favor mite population growth by increasing their fecundity and reducing the generational period (Perring et al., 1984b; Rott and Ponsonby, 2000).

In addition to assessing mite reproduction on B73 plants under both optimal irrigation and water-stress conditions, we assessed the activity of several proteins implicated in deterring herbivores. In some cases, as for PPO and POD, activities have also been shown to be modulated by water-stress alone in some plant species (English-Loeb et al., 1997; Fazeli et al., 2007; Lee et al., 2007; Ruckert et al., 2018; Thipyapong et al., 2004), potentially priming water-stressed plants to higher tolerance of other stressors (Mahanil et al., 2008; Thipyapong et al., 2004). In general, we found that significant fold changes in protein activity in response to water-stress alone for B73 plants were modest. While several activities responded significantly to water-stress in at least one of the experimental settings, fold-changes were typically equal or less than two, and in some cases, differed in direction (up- or down-regulated) between greenhouse and field experiments (e.g., as for PPO).

We found that changes in the activity of defensive proteins in response to mite herbivory, with or without water-stress, were also generally modest. Previously, in a greenhouse study, Bui et al. (2018) observed that at 1 day, POD activity in B73 plants was increased in response to both TSM and BGM herbivory in optimally watered plants (Bui et al.'s study included only a 1 day timepoint, and no water-stress). Consistent with this study, we observed that TSM herbivory, albeit not BGM herbivory, was significantly associated in the field with elevated POD activity. The lack of a significant effect for BGM in the field, or either mite in the greenhouse, differs from Bui et al. (2018), and might be explained by their use of a much higher mite density for infestation as well as a larger number of replicates at their single 1 day timepoint (providing increased power to detect an effect). Nevertheless, in a limited number of conditions, we did observe apparent differences in B73 plant responses between TSM and BGM. The most striking was at the 1 day timepoint in the field for CHI and TI activity, as in optimally irrigated plants the activity of CHI was elevated for TSM as compared to BGM herbivory, and the relative increase in activities of both CHI and TI was much higher under water-stress. Interestingly, the elevated CHI and TI activities were transient, and returned to levels observed for all other conditions (timepoints and mite species) by day 3. In their earlier study, Bui et al. (2018) observed broadly similar transcriptomic levels for genes encoding chitinases and protease inhibitors at 1 day between TSM and BGM herbivory, although they did not assay CHI and TI activities directly. The Bui et al. (2018) study was in the greenhouse, however, where we also found no differences in CHI and TI activities in response to either TSM or BGM herbivory in the current study (a contrast to our findings in the field study, Fig. 4c-d). Many factors differ between greenhouse and field settings and assessing the factor (or factors) underlying the differential responses in B73 plants for CHI and TI activities between the greenhouse and field will require further study.

There are several instances where generalist herbivores induce plant defenses that differ from those induced by specialist herbivores. For example, marked defense responses in tomato were observed following TSM herbivory, but these responses were absent (or suppressed) in response to feeding by the specialist spider mite *Tetranychus evansi*, or in response to feeding by another mite herbivore, *Aculops lycopersici* (Alba et al., 2015; Ament et al., 2004; Glas et al., 2014; Martel et al., 2015; Sarmento et al., 2011; Schimmel et al., 2018). Our finding that TSM, but not BGM, induced elevated activities of CHI and TI in the field, especially under water-stress, mirrors the findings with these other generalist or specialist mite herbivores on dicots. However, while the TSM generalist induced stronger plant responses than the BGM specialist on B73 plants at day 1 in the field, especially under water-stress, we cannot rule out that (unknown) aspects of TSM and BGM biology apart from those related to host plant breadth underlie the observation (e.g., behavioral differences, rapidity of feeding initiation, etc.). Regardless, as observed for BGM, TSM population growth on B73 plants was elevated in the field under water-stress, suggesting that the transient upregulation of CHI and TI activity was an ineffective defense response to TSM in the B73 inbred line. While the sequence of the BGM genome is not known, analysis of the TSM genome revealed significant expansion of gene families involved in xenobiotic detoxification (Leeuwen et al., 2011), providing a possible explanation for the ability of TSM to cope with elevated plant defenses.

As opposed POD, PPO, CHI, and TI activities, which are broadly conserved across the plant phylogeny, maize also produces specialized anti-herbivore compounds. Among these, benzoxazinoids such as 4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) and its derivatives are well documented in deterring chewing insect herbivores, especially generalist species (Bosak et al., 2013; Bui et al., 2018; Cambier et al., 2000; Houseman et al., 1992; Meihls et al., 2013). Previously, Bui et al. (2018) demonstrated that TSM population growth was elevated on maize plants with mutations in the benzoxazinoid biosynthetic pathway. In contrast, BGM population growth was not impacted, suggesting that BGM has evolved specialized defense mechanisms to overcome this major class of specialized compounds found in maize and several other major grass (Poaceae) crops. In seedlings, constitutive production of benzoxazinoids is high in maize, and rapidly decreases with plant age, although benzoxazinoid production can be induced by herbivore damage in more mature plants in at least some maize lines (Bosak et al., 2013; Cambier et al., 2000). In our study, which used older plants to mirror spider mite infestations of maize in field settings (Ruckert et al., 2015), TSM populations increased rapidly in both the greenhouse and field on B73 plants under optimal watering, and even more dramatically when water-stress was introduced. While we did not assay benzoxazinoid levels, our findings potentially suggest that B73 plants are unable to mount effective benzoxazinoid defenses against TSM at the developmental stage we used, regardless of water-stress.

Concluding remarks

Limited earlier work examining maize defense responses to TSM and BGM on well-watered plants suggested that induced plant defense responses were similar. In this study, we extended this work to test the hypothesis that an abiotic stress would impact this relationship. We found that water-stress – a key determinant of spider mite outbreaks in agriculture – differentially influenced maize defense responses to the two herbivores, although the effects we observed were modest in magnitude or duration. For our study, we used B73, an important maize inbred line used for development of elite maize germplasm, the source of the reference genome for the species (Schnable et al., 2009), and the common inbred parent for advanced sets of genetic mapping populations in maize (McMullen et al., 2009). While several earlier studies revealed that the majority of maize lines are highly susceptible to TSM herbivory, a small set of lines have nonetheless been reported to be highly resistant (Kamali et al., 1989a; Mansour et al., 1993; Tadmor et al., 1999a); furthermore, variation in benzoxazinoid defenses have been shown to vary substantially among maize inbred lines (Barry et al., 1994; Bing et al., 1992, 1990; Meihls et al., 2013). Our work establishes responses of B73 plants to spider mites and water-stress, and the interaction, thereby providing baseline data for a susceptible maize line that can inform future studies with TSM-resistant maize lines.

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Table 2-1

Effect of water treatments (optimal irrigation and water-stress) on height, leaf temperature, stomatal conductance and leaf water potential in the greenhouse and field experiments.

Experiment	**Variable**	**Optimal irrigation (mean ± SE)**	**Water-stress (mean ± SE)**	**DF**	**T**	***P***
Greenhouse	Leaf temp (°C)	24.17 ± 0.41	27.77 ± 0.35	94	-6.68	<0.001
	Leaf water potential (bar)	3.00 ± 0.14	11.00 ± 0.5	46	-15.31	<0.001
	Stomatal conductance (mmolm$_{-2}$S$_{-1}$)	244.20 ± 13.54	100.80 ± 3.23	94	10.30	<0.001
	Stem height (cm)	62.43 ± 1.36	42.37 ± 0.89	94	12.29	<0.001
Field	Leaf temp (°C)	25.79 ± 1.20	28.91 ± 0.91	94	-2.06	<0.001
	Leaf water potential (bar)	4.65 ± 0.44	8.00 ± 0.78	43	-3.58	<0.001
	Stomatal conductance (mmolm$_{-2}$S$_{-1}$)	260.60 ± 11.29	191.50 ± 9.75	94	4.63	<0.001
	Stem height (cm)	176.34 ± 4.51	130.00 ± 2.81	94	8.72	<0.001

SE: standard error of the mean; DF: degrees of freedom; T: T value; *P*: p-value.

Table 2-2
ANOVA results of the effect of water treatments (optimal irrigation and water-stress) on population growth of mites (TSM and BGM) at time post mite introduction (1, 3 and 7 days) in the greenhouse experiment.

Factor	**DF**	**F**	***P***
Water	1,12	29.76	<.001
Mite	1,12	0.56	0.399
Water × Mite	1,12	7.29	0.016
Time	2,24	455.92	<.001
Water × Time	2,24	24.91	0.005
Mite × Time	2,24	8.11	0.018
Water × Mite × Time	2,24	0.99	0.809

DF: degrees of freedom; F: F-value; *P*: p-value.

Table 2-3
ANOVA results of the effect of water treatments (optimal irrigation and water-stress) and mite (TSM and BGM) herbivory on the activity of B73 plant defense proteins at time post mite introduction (1, 3 and 7 days) in the greenhouse experiment.

Category	**Factor**	**DF**	**F**	***P***
Peroxidase (POD)	Water	1,18	6.59	0.019
	Mite	2,18	2.05	0.158
	Water × Mite	2,18	3.44	0.054
	Time	2,36	1.46	0.246
	Water × Time	2,36	0.72	0.492
	Mite × Time	4,36	0.17	0.950
	Water × Mite × Time	4,36	0.59	0.673
Polyphenol oxidase (PPO)	Water	1,18	7.74	0.012
	Mite	2,18	0.45	0.644
	Water × Mite	2,18	1.19	0.327
	Time	2,30	1.38	0.268
	Water × Time	2,30	0.53	0.595
	Mite × Time	4,30	0.15	0.959
	Water × Mite × Time	4,30	0.75	0.566
Chitinase (CHI)	Water	1,18	0.08	0.930
	Mite	2,18	4.33	0.013
	Water × Mite	2,18	1.10	0.183
	Time	2,36	8.59	<.001
	Water × Time	2,36	1.44	0.187
	Mite × Time	4,36	1.32	0.335

	Water × Mite × Time	4,36	0.99	0.441
Trypsin Inhibitor (TI)	Water	1,18	6.83	0.017
	Mite	2,18	3.23	0.063
	Water × Mite	2,18	2.76	0.090
	Time	2,25	13.26	<.001
	Water × Time	2,25	1.04	0.367
	Mite × Time	4,25	0.78	0.550
	Water × Mite × Time	4,25	3.73	0.016

DF: degrees of freedom; F: F-value; *P*: p-value.

Table 2-4
ANOVA results of the effect of water treatments (optimal irrigation and water-stress) on population growth of mites (TSM and BGM) at time post mite introduction (1, 3 and 7 days) in the field experiment.

Category	**Factor**	**DF**	**F**	***P***
Population growth	Water	1,12	10.54	0.001
	Mite	1,12	1.55	0.995
	Water × Mite	1,12	0.05	0.094
	Time	2,24	20.74	<.001
	Water × Time	2,24	3.22	<.001
	Mite × Time	2,24	1.46	0.357
	Water × Mite × Time	2,24	0.53	0.226

DF: degrees of freedom; F: F-value; *P*: p-value.

Table 2-5
ANOVA results of the effect of water treatments (optimal irrigation and water-stress) and mite (TSM and BGM) herbivory on the activity of B73 plant defense proteins at time post mite introduction (1, 3 and 7 days) in the field experiment.

Category	**Factor**	**DF**	**F**	***P***
Peroxidase (POD)	Water	1,18	0.36	0.555
	Mite	2,18	9.37	0.002
	Water × Mite	2,18	3.48	0.053
	Time	2,36	21.03	<.001
	Water × Time	2,36	1.75	0.188
	Mite × Time	4,36	3.76	0.012
	Water × Mite × Time	4,36	1.64	0.185
Polyphenol oxidase (PPO)	Water	1,18	10.31	0.005
	Mite	2,18	17.70	<.001
	Water × Mite	2,18	2.99	0.076
	Time	2,36	0.52	0.597
	Water × Time	2,36	0.92	0.408
	Mite × Time	4,36	2.10	0.101
	Water × Mite × Time	4,36	1.86	0.139
Chitinase (CHI)	Water	1,18	3.50	0.078
	Mite	2,18	10.48	0.001
	Water × Mite	2,18	6.32	0.008
	Time	2,36	14.83	<.001
	Water × Time	2,36	0.15	0.862
	Mite × Time	4,36	17.95	<.001

	Water × Mite × Time	4,36	4.88	0.003
Trypsin Inhibitor (TI)	Water	1,18	7.77	0.012
	Mite	2,18	24.02	<.001
	Water × Mite	2,18	5.24	0.016
	Time	2,36	10.97	0.002
	Water × Time	2,36	2.29	0.116
	Mite × Time	4,36	10.21	<.001
	Water × Mite × Time	4,36	5.67	0.001

DF: degrees of freedom; F: F-value; *P*: p-value.

Fig. 2-1. Volumetric soil water content for water treatments in the greenhouse and field experiments. Water treatments began 6 days and 9 days prior to mite introduction in the greenhouse (a) and field experiments (b), respectively, and continued for one week. The solid line represents optimal irrigation and the dashed line represents water-stress conditions.

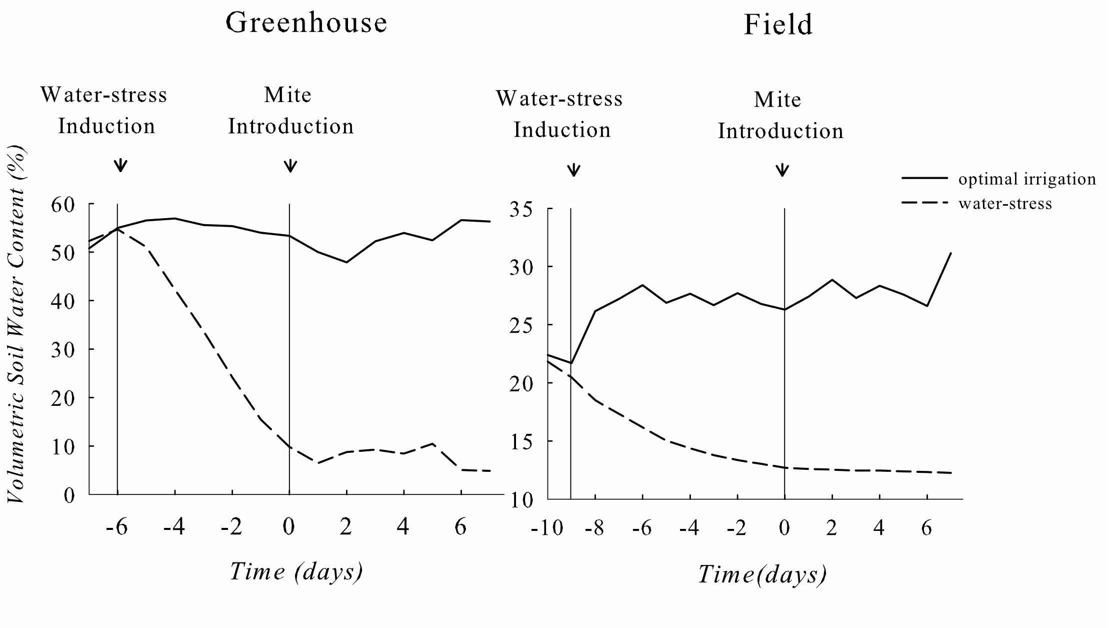


Fig. 2-2. Effect of water treatments (optimal irrigation and water-stress) on population growth of mites (TSM and BGM) at time post mite introduction (1, 3 and 7 days) in the greenhouse experiment. Mean (± SE) generalist TSM and specialist BGM population growth (eggs, larvae, and nymphs combined) on optimally irrigated and water-stressed maize is shown. The solid line with filled triangle symbols represents the number of offspring under optimal irrigation, and the dashed line with empty triangle symbols represents the number of offspring under water-stress.

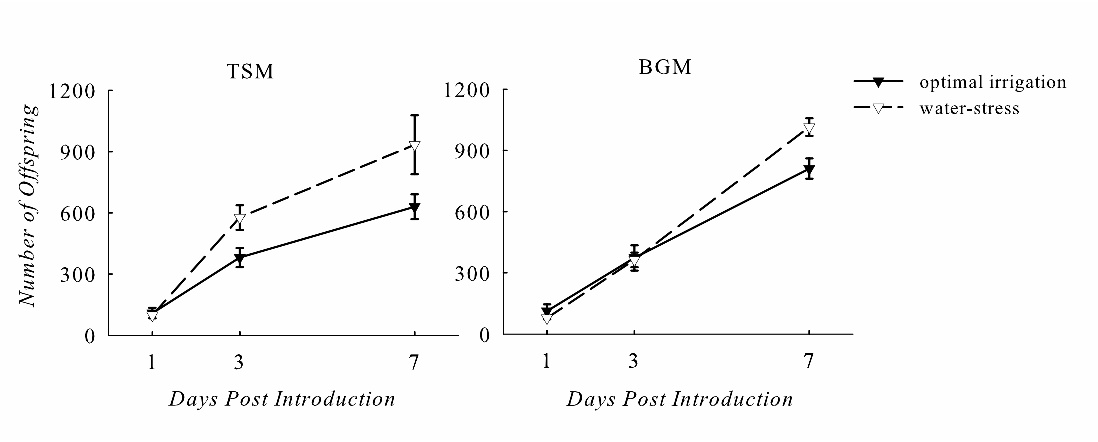


Fig. 2-3. Effect of water treatments (optimal irrigation and water-stress) on population growth of mites (TSM and BGM) at time post mite introduction (1, 3 and 7 days) in the field experiment. Mean (± SE) generalist TSM and specialist BGM population growth (eggs, larvae, and nymphs combined) on optimally irrigated and water-stressed maize are shown. The solid line with filled triangle symbols represents the number of offspring under optimal irrigation, and dashed line with empty triangle symbols represents the number of offspring under water-stress.

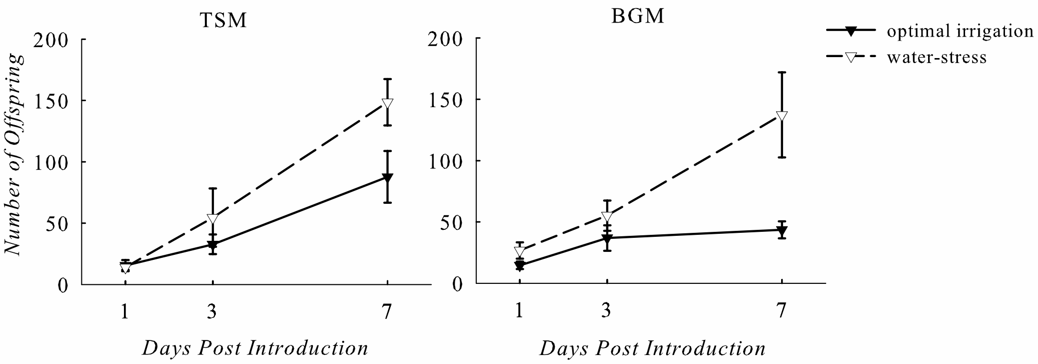


Fig. 2-4. Effect of water treatment (optimal irrigation and water-stress) and mite (TSM, left panels, and BGM, right panels) herbivory on the activity of B73 plant defense proteins at time post mite introduction (1, 3 and 7 days) in the greenhouse experiment. (a) POD, (b) PPO, (c) CHI, and (d) TI. Circles represent controls (no mites), and triangles represent mites. Solid lines with filled symbols represent optimal-irrigation and dashed lines with empty symbols represent water-stress.

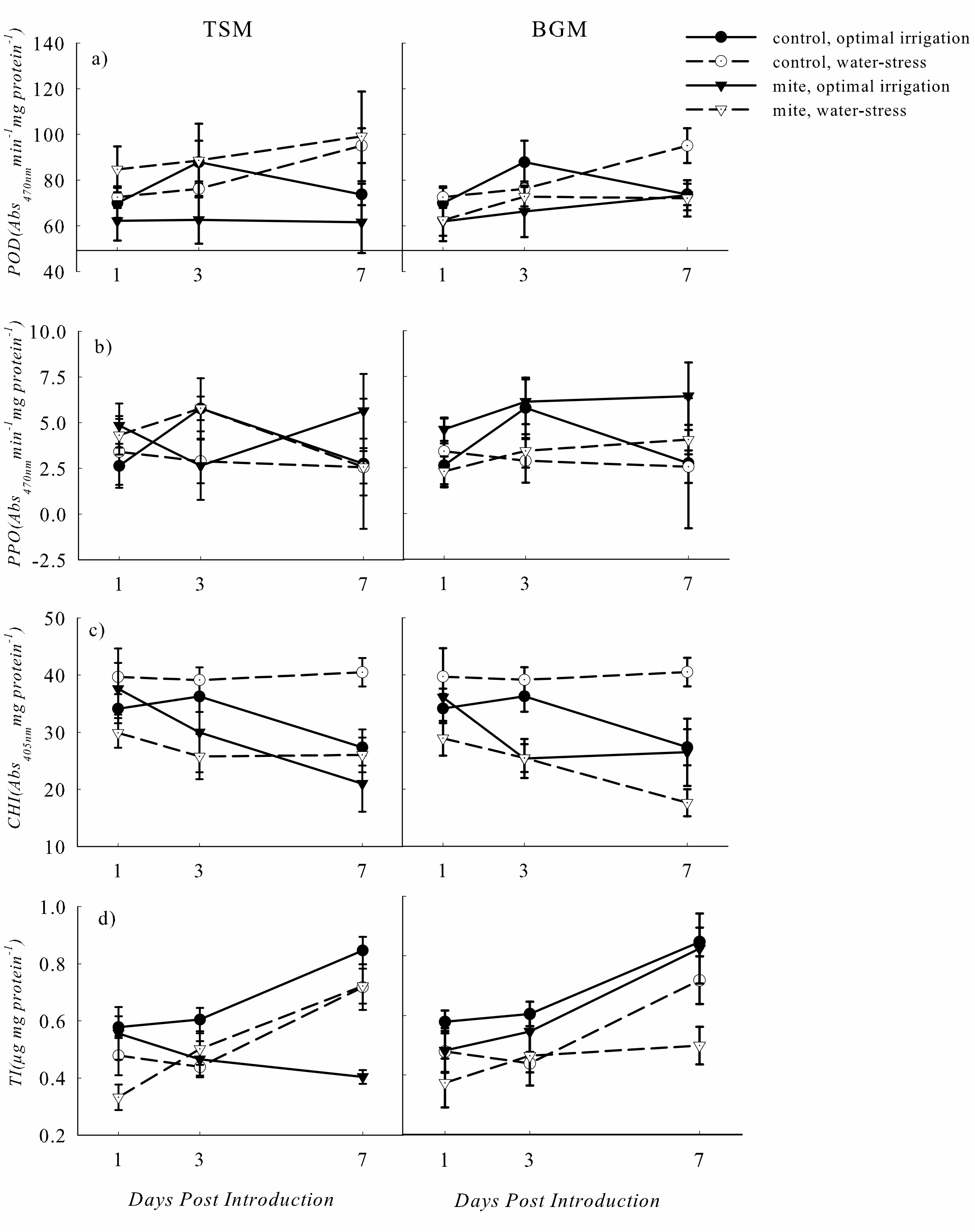
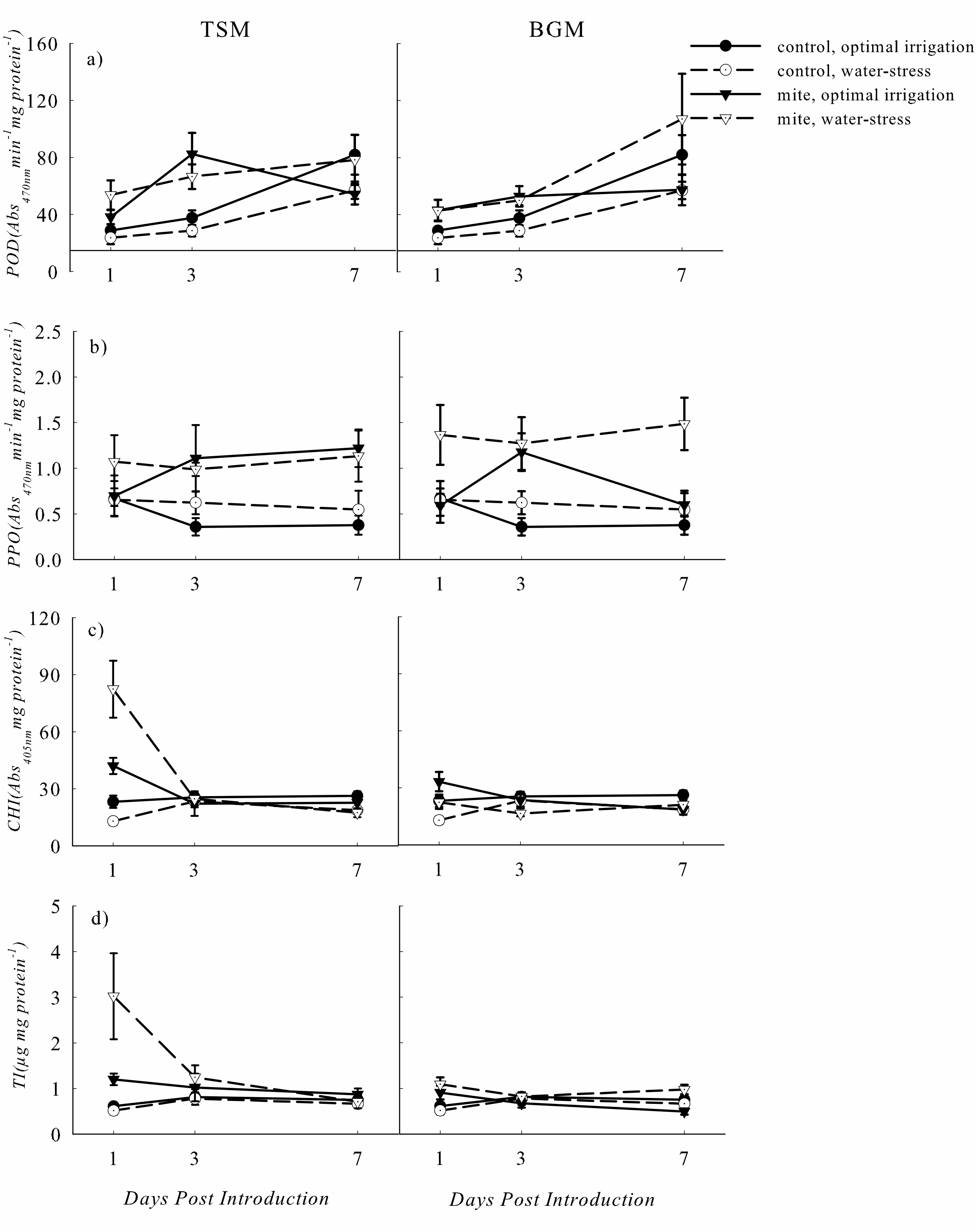


Fig. 2-5. Effect of water treatment (optimal irrigation and water-stress) and mite (TSM, left panels, and BGM, right panels) herbivory on the activity of B73 plant defense proteins at time post mite introduction (1, 3 and 7 days) in the field experiment. (a) POD, (b) PPO, (c) CHI, and (d) TI. Circles represent controls (no mites), and triangles represent mites. Solid lines with filled symbols represent optimal-irrigation and dashed lines with empty symbols represents water-stress.



CHAPTER III

BEHAVIORAL RESPONSES OF A GENERALIST AND SPECIALIST SPIDER MITE TO MAIZE WITH VARIED HOST PLANT RESISTANCE

Abstract: Plants are attacked by diverse herbivorous pests with different host specializations. While host plant resistance provides a way to decrease pest pressure, there is a need to understand the range to which host plant resistance affects behaviors of generalist and specialist herbivores. Here, we investigated the behavioral changes in a generalist herbivore, two-spotted spider mite (TSM), and a specialist herbivore, Banks grass mite (BGM), by introducing them to no-choice Tanglefoot leaf-arenas (2×2 cm$_2$) of three maize inbred lines (B73, B75, and B96). The model inbred line, B73, is susceptible to spider mites while B75 and B96 are considered mite resistant lines because of higher levels of benzoxazinoids (special defense compounds in maize). Video tracking was used to record TSM and BGM walking, probing, feeding, resting, web-building and their travel distance on arenas of each line. Mite oviposition was also recorded after 72 hours. B75, a resistant line, decreased the feeding behavior of both mite species compared to B73 (susceptible control) and B96. Moreover, TSM appeared to be sensitive to both resistant lines (B75 and B96) with reduced oviposition, and increased resting and web-building time compared to the susceptible B73 line. In contrast, the specialist BGM showed no difference in oviposition, resting and web-building time across all maize inbred lines. Our study suggests that resistance traits in maize, as seen in B75 and B96, appear to affect generalist TSM behavior quite broadly, yet sensitivity to this resistance appears to be reduced as host specialization narrows. Therefore, other mechanisms of plant resistance may be needed for a specialist like BGM.

1. Introduction

Host plant resistance through genetic modification or traditional plant breeding is an ecologically-based pest management tactic, alleviating concerns associated with reliance on pesticide use and pesticide resistance (Pimentel and Burgess, 2014; Schäfer et al., 2007; Sharma and Ortiz, 2002; Smith, 2005). The development of a pest resistant plant is a multifaceted evaluation that includes phenotyping multiple plant lines in a high-throughput screening (Eigenbrode and Trumble, 1994). Once candidate resistant lines are identified, pest behaviors and development can be analyzed on plant tissues through a variety of methods to understand the resistance mechanisms (Ponti 1977). Some of the studies that evaluated resistant plants in cropping systems such as maize, rice, cowpea and soybean showed that plant resistance traits reduced pest behaviors such as feeding (Cook et al. 1987; Mesfin et al. 1992; Bernklau et al. 2010; Ghaffar et al. 2011; Pompon and Pelletier 2012; Chandran et al. 2013) and oviposition (Bynum et al., 2004; Kamali et al., 1989b; Tadmor et al., 1999b), and increased walking as well as resting behaviors (Eigenbrode et al. 1991; Mesfin et al. 1992; Stoner 1997; Mesfin and Perez 1998; Renard et al. 1998; Prasifka et al. 2009; Othim et al. 2018). However, plants encounter diverse herbivorous pests with different host specialization (i.e., generalists, that feed on many plant species and specialists that feed on a single plant family or species), and this specialization may alter the interaction with developed resistance traits (Ali and Agrawal, 2012; Cardoso, 2008; Karley et al., 2016).

Historically, evaluation has focused on either generalist or specialist herbivores. Yet, given how specialists can overcome plant resistance and often generalist herbivores are more sensitive to resistant traits, comparatively few studies have focused on evaluating plant resistance to herbivore groups with varied host specialization (Ali and Agrawal, 2012). For example, a recent study on maize (*Zea mays*) showed that benzoxazinoids (e.g., DIMBOA), a class of plant defense compounds, reduced the population growth of the generalist twospotted spider mite (*Tetranychus urticae*, TSM), while the specialist Banks grass mite (*Oligonychus pratensis*, BGM) was unaffected (Bui et al. 2018). However, the population growth of spider mites depends on host plant acceptance (proportion of female TSMs settling on the host) and the host plant suitability (oviposition within 5 days after introduction to the host plant) (Yano et al., 1998). Host plant acceptance also relates to non-preference or antixenosis (avoidance, behavioral responses of arthropods), while host plant suitability can be determined by antibiosis (adverse effects of plant on arthropod growth, development and fecundity) (Renwick 1983). Antixenosis and antibiosis mechanisms can be quantified by behavioral parameters such as movement (walking and resting), feeding on a host plant, and oviposition, as they have previously reported being impacted by host plant resistance (Cook et al. 1987; Kamali et al. 1989a; Eigenbrode et al. 1991; Mesfin et al. 1992; Stoner 1997; Renard et al. 1998; Mesfin and Perez 1998; Mesfin T. ; Perez 1998; Tadmor et al. 1999b; Bynum et al. 2004a; Prasifka et al. 2009; Bernklau et al. 2010; Ghaffar et al. 2011; Pompon and Pelletier 2012; Chandran et al. 2013; Othim et al. 2018). Spider mites also have a unique behavior in that they engage in web-building or spinning, that they use for oviposition, mate finding, locomotion, dispersal, colonization and assists in protection from natural enemies and acaricides (Hazan et al. 1974, 1975; Saitô 1977; Helle and Sabelis 1985). Gaining a better understanding of changes in these behaviors by considering both generalist and specialist spider mites may enhance our knowledge of spider mite interaction with plants, and the role of host plant resistance.

TSM and BGM are well-documented maize herbivores known to cause severe crop damage and economic losses (Archer and Bynum, 1993; Bacon et al., 1962; Bynum et al., 2015; FAO, 2018; Peairs, 2014; Peairs and Both, 2010; Ruckert et al., 2015). Evaluation of plant resistance to spider mites is of utmost importance for their sustainable management, and of special urgency with species like TSM and BGM that have become resistant to major acaricides (Dermauw et al., 2013; Kwon et al., 2010; Ruckert et al., 2018; Leeuwen et al., 2005; Yang et al., 2001). Maize has been screened and several candidate plants have been identified showing herbivore resistance, in particular toward spider mites (Bynum et al., 2004; Kamali et al., 1989a; Mansour et al., 1993; Tadmor et al., 1999a). B96, for instance, is a maize inbred line that appears to reduce population growth of TSM and carmine mites (*Tetranychus cinnabarinus*) and their feeding (Kamali et al., 1989b; Tadmor et al., 1999a). Moreover, the maize line B75 appears to be moderately resistant to TSM, particularly when compared to B96 (Bui et al., *in prep*). B73, on the other hand, shows susceptibility to TSM and BGM (Bui et al., 2018). As a result, B73 is an important model and control given its genome has been sequenced and annotated, sharing 97% of its genome with at least 50 other maize inbred lines (Bynum et al., 2004; Eichten et al., 2011; Ganal et al., 2011; Lee et al., 2002). Interestingly, both B75 and B96 maize inbreds were previously reported to have higher DIMBOA levels than B73 (Barry et al., 1994; Bing et al., 1990). While population growth of TSM and BGM has been evaluated on B73, B75 and B96 maize inbred lines, little is known about how resistance in B96 and B75 affects the behaviors of the generalist TSM and specialist BGM, or whether behavior is a prominent mechanism of apparent resistance.

Recently, a study on mite susceptible B73 by Gill et al. (2020), showed that while both TSM and BGM outbreak on water-stressed maize plants, the maize responses to water-stress and mite herbivory suggested that the mechanisms for each mite species ability to outbreak may vary. Here, to better understand the mechanisms of resistance in B75 and B96 to spider mites, we investigated the behavioral changes of the generalist TSM and specialist BGM on leaf arenas of B75 and B96 as compared to B73 (control) by using video tracking. This study aimed to better understand and evaluate a variety of mite behaviors not limited to probing, walking, and web-building (unique to spider mites), for each mite species exposed to varied maize resistance.

2. Material and methods

2.1. Maize lines and plant maintenance

Plants were grown at Utah State University's Research Greenhouse and Laboratory, Logan, UT. Three maize inbred lines B73, B75, and B96 were selected based on a screening where B73 was the control, as it is susceptible to both BGM and TSM (Bui et al., 2018; Bynum et al., 2004), while B75 and B96 were moderate and highly resistant to spider mites, respectively (Kamali et al. 1989a; Tadmor et al. 1999a). Specifically, as previously described, B75 and B96 express benzoxazinoids in higher concentrations compared to B73 (Barry et al., 1994; Bing et al., 1990).

Two seeds per pot for each maize inbred line (B73, B75, and B96) were sown in 3.5 L pots filled with soil (Sunshine Mix #3, Sun Gro Horticulture, MA), 8 pots per line, distributed in a complete randomized design. Maize plants were grown under greenhouse-controlled conditions (25±2 °C, 60±5% RH, 16:8 hrs. (L:D) photoperiod) and fertigated at a rate of 4.8 kg/100L of 21N-5P-20K Peters Excel Water Soluble Fertilizer mixture (ICL Specialty Fertilizers, SC, USA) by using drip tape (DIG Corporation, CA, USA; 12.7 mm and 6.35 mm diameter tubing with 3.8 L/hr compensating emitters). At 8 weeks of age, plants were used to evaluate spider mite behavior.

2.2. Video tracking spider mite behavior on maize lines

We conducted a 3 × 2 factorial design experiment using three levels of maize resistance (susceptible B73, and resistant lines B75 and B96) and two levels of mites (TSM and BGM).

A rectangular plastic box (20 × 15 cm^2, Webstaurant Store, PA, USA) was used as an experimental unit and each treatment (3 maize inbred lines × 2 mite species) was replicated six times. A 3 × 3 cm^2 leaf-cutting from the middle section of the 8th leaf up from the bottom of each plant was collected, excluding the leaf midrib. We placed leaf-cuttings for each respective inbred line on a wet cotton pad on a plexiglass sheet fitted within the rectangular plastic box to prevent the leaf arena from desiccating. To ensure the cotton remained moist, the box was filled halfway so the ends of the cotton pad were in the water to wick up moisture. A 2 × 2 cm^2 no-choice arena was created placing Tanglefoot (The Scotts Miracle-Gro Company, OH, USA) non-phytotoxic wax barriers on the edges of each leaf-cutting to keep mites on the feeding site and prevent escape. BGM and TSM colonies used in the study were maintained in lab conditions [28±2 °C, 50±5% RH, 16:8 hr (L:D) photoperiod] on B73 maize. One newly emerged adult female mite, mated and starved overnight, was introduced into the arena of each respective maize inbred line by using a fine paintbrush.

Using a Canon Eos 5D Mark III camera and 65mm MP-E lens, each female mite was video recorded for 50 min following mite introduction to each respective arena. Each video was examined for six behaviors that included the total time that each mite spent 1) walking, 2) probing, 3) feeding, 4) resting, and 5) web-building; and 6) the travel distance (cm) for each mite in an arena. Feeding and walking time, and travel distance were recorded as described. Resting time was represented by mites not moving, probing or feeding. Probing was apparent when a mite stopped its movement, short feeding events occurred in place, and forelegs showed a variety of small tactile movements. Web-building referred to mites swaying their forelegs in a side to side motion connecting threads of silk (Saitô 1977). Each video was analyzed using a behavior tracking software (OpenCV mite tracer, https://github.com/HMKRL/OpenCV-mitetrace). Briefly, videos were uploaded to the software, a tracer was placed on each spider mite, and the software tracked movement in the video and generated a path plot. These data for distance traveled by spider mites in arenas, and time mites moved and stopped were recorded. Detailed visual inspection of each video was used to capture data for specific behaviors (i.e., probing, feeding, resting, and web-building).

Finally, oviposition (number of eggs deposited) was recorded for each replicate 72 hours post mite introduction using a stereomicroscope (Leica S6 D Greenough, NJ, USA).

2.3. Statistical Analysis:

Data from mite oviposition on maize inbred lines were analyzed using a generalized linear model (Proc Glimmix; SAS 9.4 M4 University edition) within two-way ANOVA that included maize resistance (B73, B75, and B96) and mites (TSM and BGM) as fixed factors. Oviposition data were log transformed to conform to the assumptions of normality and heteroscedasticity. Video recordings (50 min each) were analyzed within 10 min intervals. Proportions of time that each mite spent walking, probing, feeding, and resting within a 10 min interval were analyzed by using a generalized linear model (Proc Glimmix; SAS 9.4 M4 University edition) within two-way ANOVA and repeated measures (5 time intervals) with a beta distribution (Stroup 2015). Data for web-building and travel distance were square-root transformed and analyzed using two-way ANOVA (maize inbred lines) with repeated measures (5 time intervals) using Proc Glimmix (SAS 9.4 M4 University edition). Following significant ANOVAs, post hoc tests were performed using Tukey's HSD (Honestly Significant Difference) to separate significant differences among main effects of maize inbred lines or time. For further analysis of significant three-way interactions, we used LSMESTIMATE statement (Proc Glimmix) with Tukey-Kramer adjustment. For instance, when mite walking time revealed a three-way interaction (line × mite × time), each mite species was independently analyzed at each time period comparing maize inbred lines.

3. Results

3.1. Oviposition by TSM and BGM on susceptible and resistant inbred maize lines

Mite oviposition after 72 hours post mite introduction was significantly affected by a maize resistance × mite interaction ($F_{2,27}$ = 4.81, P = 0.01, Fig. 3-1, Table 3-1). To further assess the interaction, we analyzed oviposition for each mite species independently by comparing maize inbred lines. The interaction appeared to be driven by a reduction in oviposition by TSM on B75 ($P < 0.01$, LSMESTIMATE Tukey adjustment) and B96 ($P < 0.01$, LSMESTIMATE Tukey adjustment) representing 0.8 ± 0.58 eggs/female (83 % decrease) and 1.2 ± 0.58 eggs/female (74 % decrease), respectively, compared to 4.66 ± 0.52 eggs/female on the control B73 line (Fig. 3-1). In contrast, BGM oviposition was not significantly different among susceptible and resistant maize lines (Fig. 1).

3.2. Mite probing and feeding time on susceptible and resistant maize lines

Overall, TSM spent more time (6.78 ± 0.87 mins) probing leaves than BGM (3.53 ± 0.59 mins) on all maize inbred lines (mite: $F_{1,26} = 7.88$, $P < 0.01$, Fig. 2, Table 1). For both TSM and BGM, mites probed leaves more in the first 10 min (1.76 ± 0.35 min), then probing was reduced and stayed constant (from 0.84 ± 0.19 mins to 0.85 ± 0.22 mins) for the remaining time (time: $F_{4,104} = 2.65$, $P = 0.03$, Fig. 3-2, Table 3-1).

Mite feeding time was dependent on the maize inbred line they were subjected to (Resistance: $F_{2,26} = 8.73$, $P < 0.01$, Table 3-1). Specifically, mite feeding time over 50 min was reduced on B75 (16 ± 2.22 min) as compared to 26.18 ± 2.12 min on B73 ($P < 0.01$, Tukey) and 24.52 ± 2.34 min on B96 ($P < 0.01$, Tukey), respectively (Fig. 3-3). Surprisingly, no differences were found in mite feeding time on the control B73 and resistant B96 lines ($P = 0.76$, Tukey).

3.3. Mite walking time and travel distance on susceptible and resistant inbred maize lines

Mite walking time was significantly affected by a maize resistance × mite × time interaction, which appeared to be driven by no change in BGM walking time but increased TSM walking time due to maize resistance over 50 mins period ($F_{8,104}$ = 2.40, P = 0.02, Fig. 3-4, Table 3-1). This was confirmed by evaluating each mite species (TSM and BGM) independently, comparing maize inbred lines across time. At 30 and 50 min intervals (P = 0.02 and P = 0.03, respectively, LSMESTIMATE Tukey adjustment), TSM walking time was greater on the resistant line B75 (4.8 ± 1.85 mins and 5.43 ± 2.15 mins) compared to the resistant B96 line (0.27 ± 0.66 mins and 0.41 ± 0.26 mins) (Fig. 3-4). In contrast, BGM walking time appeared to have no significant change on maize inbred lines throughout the experiment (P > 0.05, LSMESTIMATE Tukey adjustment) (Fig. 4).

Travel distance for each mite was significantly affected by maize resistance ($F_{2,26}$ = 7.36, P < 0.01, Table 3-1) and time ($F_{4,104}$ = 20.08, P < 0.01, Table 3-1). Specifically, the travel distance for each mite was greater on the resistant B75 line (92.01 ± 12.66 cm) compared to 28.9 ± 3.35 cm for the control B73 (P < 0.01, Tukey) and 27.95 ± 3.26 cm for the resistant B96 lines (P = 0.01, Tukey), respectively (Fig. 3-5). Further, travel distance by each mite was greater for the first 20 mins, then was reduced and stayed constant for the remainder of the study (Fig. 3-5).

3.4. Mite resting time on susceptible and resistant inbred maize lines

Resting time (i.e., associated with arrested mite movement including no probing or feeding) was significantly affected by resistance × mite ($F_{2,26}$ = 4.91, P < 0.01) and mite × time ($F_{4,104}$ = 2.59, P = 0.04) interactions (Fig. 3-6, Table 3-1). To further assess the resistance × mite interaction, we analyzed mite resting time for each mite species independently by comparing maize inbred lines. The resistance × mite interaction revealed that the resting time increased for TSM on leaves of resistant lines B96 (16.56

± 2.71 mins) ($P < 0.01$, LSMESTIMATE Tukey adjustment) and B75 (10.15 ± 2 mins) ($P < 0.01$, LSMESTIMATE Tukey adjustment), compared to the control B73 (4.04 ± 1.02 mins). As recognized with other behavior traits, no such effect was apparent for BGM (Fig. 3-6, Table 3-1). The mite × time interaction was also further analyzed for each mite species by comparing each time period. BGM's resting time increased from 1.09 ± 0.56 mins at the initial 10 min interval to 3.25 ± 0.67 mins in the final 50 min interval ($P = 0.02$, LSMESTIMATE Tukey adjustment). Alternatively, the resting time for TSM stayed constant at average 1.97 ± 0.27 mins throughout the experiment ($P = 0.99$, LSMESTIMATE Tukey adjustment).

3.5. Mite web-building time on susceptible and resistant inbred maize lines

Web-building time was significantly affected by a resistance × mite interaction ($F_{2,26} = 5.95$, $P < 0.01$, Table 3-1). To further assess the interaction, we analyzed mite web-building time for each mite species independently by comparing maize inbred lines. Here, the time spent web-building for TSM was higher on resistant lines B75 (21.19 ± 4.23 mins) ($P < 0.01$, LSMESTIMATE Tukey adjustment) and B96 (10.22 ± 2.04 mins) ($P < 0.01$, LSMESTIMATE Tukey adjustment), compared to the control B73 (2.86 ± 0.52 mins). Despite differences for TSM, no significant difference was observed for BGM's time spent web-building across all maize inbred lines (Fig. 3-7).

4. Discussion

Our results revealed that resistance in maize inbred lines (B75 and B96) affected the behaviors of spider mites. However, the generalist TSM appeared to be more sensitive to maize resistance as compared to the specialist BGM. In particular, spider mite exposure to resistant B75 resulted in behavioral changes of increased travel distance and reduced feeding, and were common to both mite species. However, resistance in B75 and B96 resulted in additional behavioral changes of reduced oviposition, and increased resting and web-building time, only for TSM as compared to the susceptible maize line (Table 3-1). In contrast, resistant B75 and B96 lines had no impact on oviposition, resting and web-building time of BGM. These results validate our initial screening of three maize inbred lines (B73, B75 and B96) where population growth of TSM was reduced on B75 and B96, while no such impact was noticed for BGM (Bui et al., *in prep*). This suggests that the specialist BGM, seems to be well adapted to maize resistance strategies; probing, resting, web-building and egg-laying were unaffected compared to the differential behaviors exhibited by TSM. Additionally, TSM has other biological differences including a preference for slightly cooler temperatures (optimal 86-90°F/30-32°C), while BGM thrive under hotter weather conditions (optimal 96-99℉/35.5-37°C) (Grbic et al., 2007; Perring et al., 1984a).

Probing and feeding behaviors of herbivores are two of the most important behavioral parameters to evaluate the impacts of resistant hosts (Kozłowski, 1995; Kozłowski and Boczek, 1987). Specifically, increased frequency of probing and decreased feeding by cowpea aphid (*Aphis craccivora* Koch), soybean aphid (*Aphis glycines* Matsumura), and a leafhopper (*Cicadulina storeyi* Naudé) was reportedly due to resistance properties of cowpea (Mesfin et al., 1992), soybean (Chandran et al., 2013) and maize (Mesfin and Bosque Perez, 1998), respectively. In our results, while probing by both mite species was not impacted by maize resistance, feeding was reduced on resistant

B75 as compared to susceptible B73, as found in previous studies (Chandran et al., 2013; Mesfin et al., 1992; Mesfin and Bosque Perez, 1998). However, reduced feeding did not lead to increased mortality, and therefore did not appear to be an antibiosis mechanism (Renwick 1983). Contrastingly, antixenosis, where herbivores continue to feed despite not having a host choice (Renwick 1983), may be the likely mechanism for B75 resistance to both mite species. Surprisingly, feeding by both mite species was not reduced on resistant B96 as compared to susceptible B73, suggesting that B75 and B96 may possess different resistance mechanisms.

B75 and B96 have higher DIMBOA levels compared to susceptible B73, which was previously shown to provide resistance to TSM but not to BGM by reducing oviposition (Bui et al. 2018). However, it turns out that while DIMBOA can hinder the performance of herbivores by reducing oviposition and fecundity, it may not deter feeding (Bergvinson et al., 1995; Wouters et al., 2016). A possibility is that the decrease in feeding on resistant B75 by both mite species could be due to other factors such as high fiber content and cell wall phenolics as reported for other maize herbivores (Bergvinison et al., 1995; Bergvinson et al., 1995).

As per Renard et al. (1998), a simple walk on a leaf surface allows arthropod herbivores to differentiate host plants. Increased duration of walking and resting was previously shown to be directly proportional to host plant resistance (Mesfin et al., 1992; Mesfin and Bosque Perez, 1998; Renard et al., 1998). Particularly, due to antixenosis resistance in maize, leafhopper (*Cicadulina storeyi*) showed higher walking and resting activities as compared to susceptible varieties (Mesfin and Bosque-Perez 1998). In our results, while average TSM walking time was higher on resistant B75, both mites traveled more distance on resistant B75 as compared to susceptible B73 as well as resistant B96. This suggests that B75 may possess higher antixenosis levels compared to the other lines. Interestingly, while BGM resting time was unaffected by resistance, TSM resting time was higher on resistant B75 and B96 compared to susceptible B73 throughout the experiment. This could be explained by the adverse impacts of resistance traits that often impact generalist herbivores (e.g., mortality and development), while specialists such as BGM have evolved specialized defense mechanisms (e.g., tolerance to plant toxins) to overcome plant resistance traits (Ali and Agrawal, 2012; Ratzka et al., 2002; Wittstock et al., 2004).

The web-spinning capability of spider mites is known to serve many purposes such as protection from natural enemies and acaricides, mate finding, locomotion and dispersal and colonization (Hazan et al., 1975, 1974; Helle and Sabelis, 1985b; Saitô, 1977). The amount of silk produced in the web-spinning behavior of mites depends on temperature, air humidity, smoothness of substrate, plant species and many other unknown factors (Hazan et al., 1975, 1974; Helle and Sabelis, 1985b; Saitô, 1977). In our study, TSM web-building was increased on B75 and B96 as compared to B73 maize inbred. Since temperature and humidity were the same for all treatments, leaf surface properties of B75 and B96 maize inbred lines may have played a role in TSM web-building behavioral changes. Interestingly, one factor that web-building may not depend on is feeding, as starved spider mites produce silk as well (Helle and Sabelis, 1985b). Our study confirms this observation as TSM spent less time feeding on B75 and overnight starved females were still observed spending much time web-building. According to Oku et al. (2009), producing web is costly, and resource allocation by TSM in web-building can result in a decrease in egg-laying. In the present study, while TSM spent more time in web-building on B75 and B96, it also had reduced egg-laying on B75 and B96 as compared to B73. This suggests that reduced egg-laying by TSM on resistant lines may not be solely due to direct negative effects of resistance in B75 and B96, but also indirectly due to the resource allocations in different behaviors.

Concluding remarks

This study evaluated the behavioral changes in generalist TSM and specialist BGM on resistant B75 and B96 maize inbred lines that possess high DIMBOA concentrations as compared to susceptible B73. Exposure of both mite species to a resistant B75 line resulted in two behavioral changes, while the generalist TSM appeared to be sensitive to both resistant B75 and B96 lines as expressed with additional behavioral changes (oviposition, and resting and web-building time). Surprisingly, BGM generally did not show the same sensitivity in behavior when exposed to resistant lines suggesting mechanistic interactions between host and arthropod may be species-specific. Further studies are needed to exploit range of resistance against specialist BGM as well.

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Table 3-1
ANOVA results of spider mite oviposition on susceptible and resistant inbred maize lines

Response	Effect	Num DF	Den DF	F Value	*P*
Oviposition	Resistance	2	27	4.16	0.026
	Mite	1	27	41.05	<.001
	Resistance*Mite	2	27	4.81	0.016
Probing time	Resistance	2	26	0.33	0.721
	Mite	1	26	7.88	0.009
	Mite*Resistance	2	26	2.38	0.112
	Time	4	104	2.65	0.037
	Time*Resistance	8	104	1.01	0.435
	Time*Mite	4	104	0.29	0.882
	Time*Mite*Resistance	8	104	0.46	0.884
Feeding time	Resistance	2	26	8.73	<.001
	Mite	1	26	2.44	0.130
	Mite*Resistance	2	26	2.50	0.101
	Time	4	104	1.69	0.159
	Time*Resistance	8	104	1.33	0.235
	Time*Mite	4	104	1.52	0.201
	Time*Mite*Resistance	8	104	0.91	0.508
Walking time	Resistance	2	26	11.60	<.001
	Mite	1	26	0.68	0.415
	Mite*Resistance	2	26	3.41	0.048
	Time	4	102	0.89	0.472
	Time*Resistance	8	102	0.49	0.858

	Time*Mite	4	102	1.46	0.221
	Time*Mite*Resistance	8	102	2.19	0.033
Resting time	Resistance	2	26	5.22	0.012
	Mite	1	26	0.44	0.511
	Mite*Resistance	2	26	4.91	0.015
	Time	4	104	1.82	0.129
	Time*Resistance	8	104	1.22	0.296
	Time*Mite	4	104	2.59	0.041
	Time*Mite*Resistance	8	104	0.38	0.9316
Web-building time	Resistance	2	26	0.33	0.721
	Mite	1	26	7.88	0.009
	Mite*Resistance	2	26	2.38	0.112
	Time	4	104	2.65	0.037
	Time*Resistance	8	104	1.01	0.435
	Time*Mite	4	104	0.29	0.882
	Time*Mite*Resistance	8	104	0.46	0.884
Travel distance	Resistance	2	26	7.36	0.002
	Mite	1	26	0.02	0.901
	Mite*Resistance	2	26	1.14	0.335
	Time	4	104	2.46	0.050
	Time*Resistance	8	104	1.65	0.119
	Time*Mite	4	104	0.37	0.828
	Time*Mite*Resistance	8	104	1.16	0.332

DF: degrees of freedom; F: F value; P: p-value

Fig. 3-1. Mean (±SE) oviposition by TSM and BGM on susceptible B73 and resistant B75 and B96 maize inbred lines.

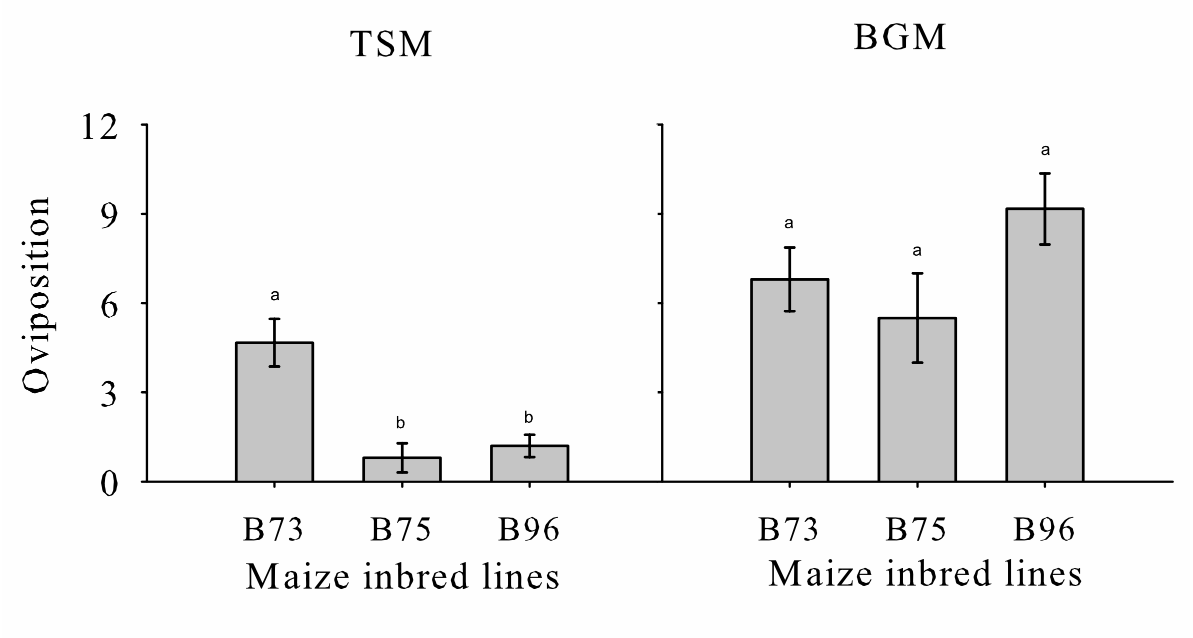


Fig. 3-2. Mean (± SE) time that TSM and BGM spent probing on susceptible B73 and resistant B75 and B96 maize inbred lines.

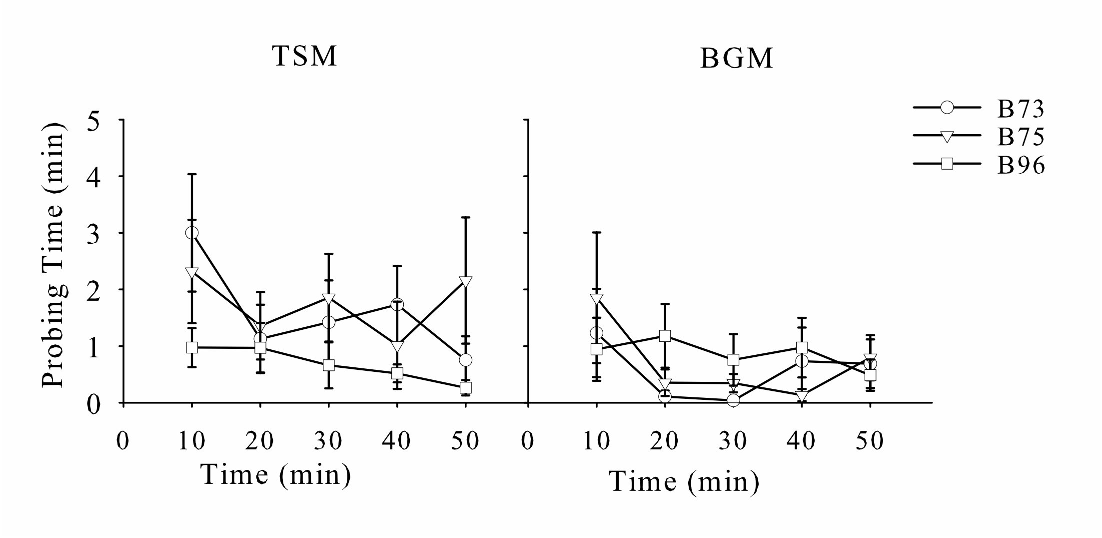


Fig. 3-3. Mean (± SE) time that TSM and BGM spent feeding on susceptible B73 and resistant B75 and B96 maize inbred lines.

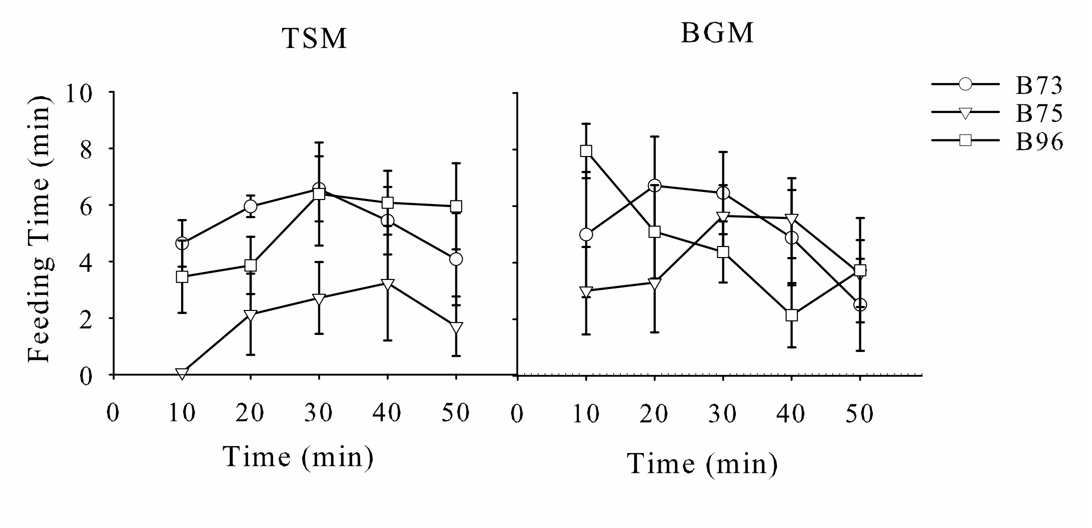


Fig. 3-4. Mean (±SE) time that TSM and BGM spent walking on susceptible B73 and resistant B75 and B96 maize inbred lines.

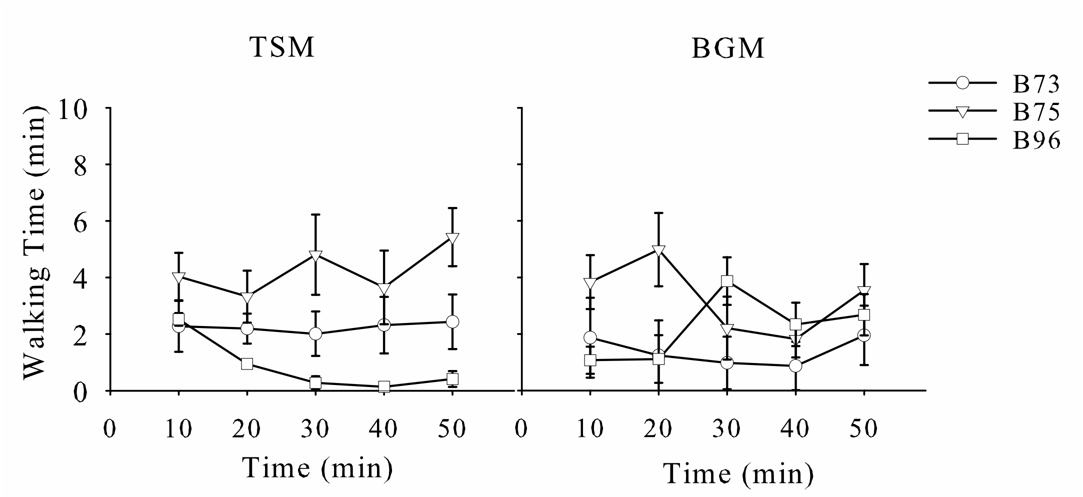


Fig. 3-5. Mean (±SE) travel distance by TSM and BGM on B73, B75 and B96 maize inbred lines

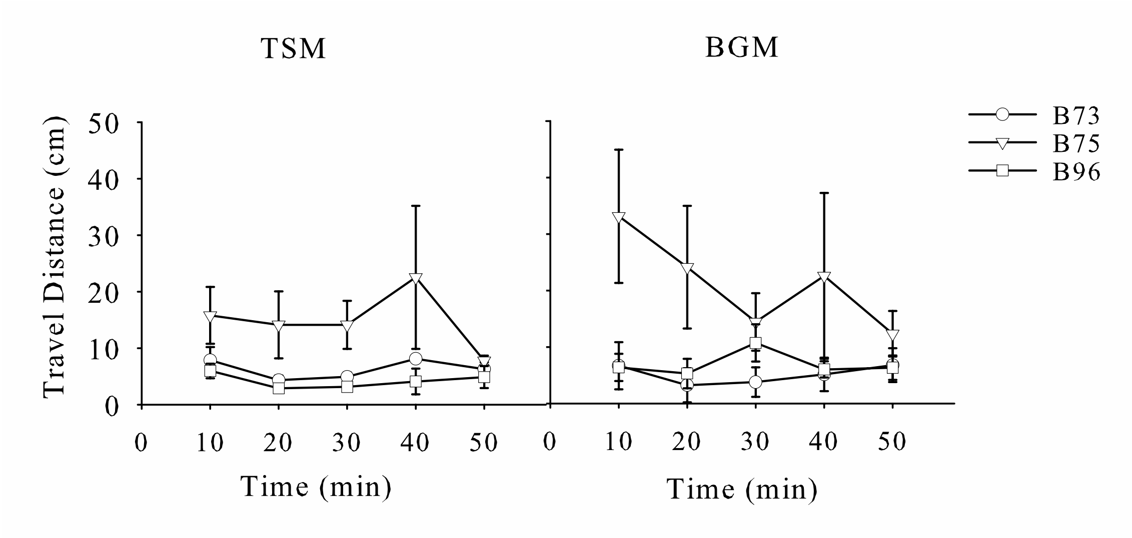


Fig. 3-6. Mean (±SE) Time that TSM and BGM spent resting on susceptible B73 and resistant B75 and B96 maize inbred lines.

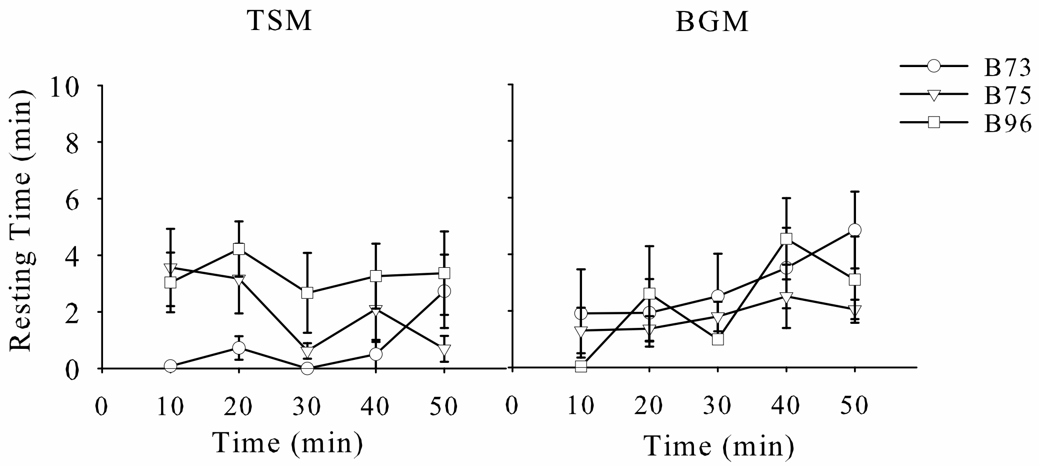


Fig. 3-7. Mean (± SE) time that TSM and BGM spent in web-building on susceptible B73 and resistant B75 and B96 maize inbred lines.

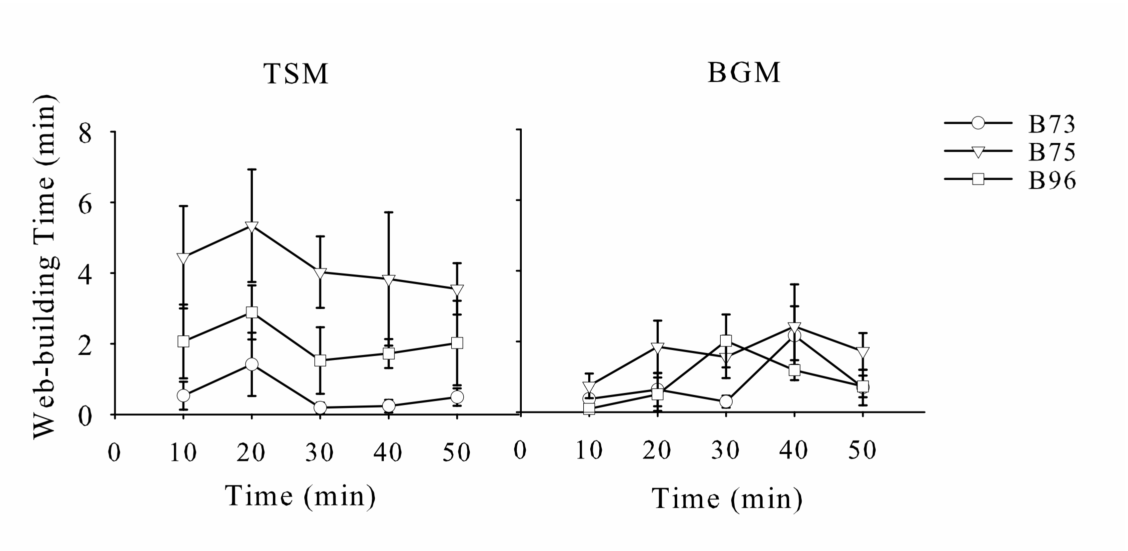


Fig. 3-8. Example of 50 mins tracking map of TSM on a) B73 b) B75 and c) B96 arena. The starting point of video when mite was introduced in the leaf arena is represented by red which followed orange to yellow and to the end point by green.

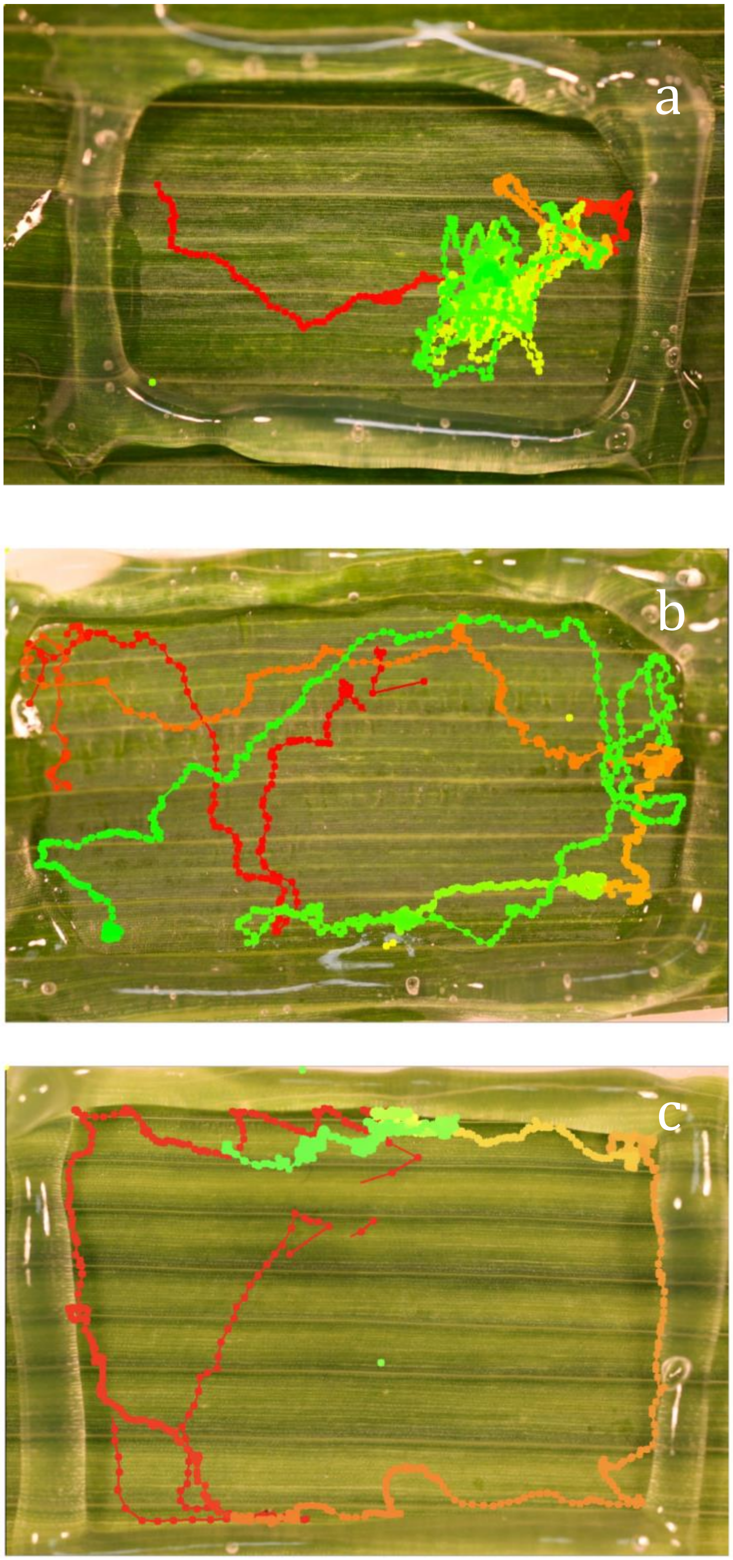
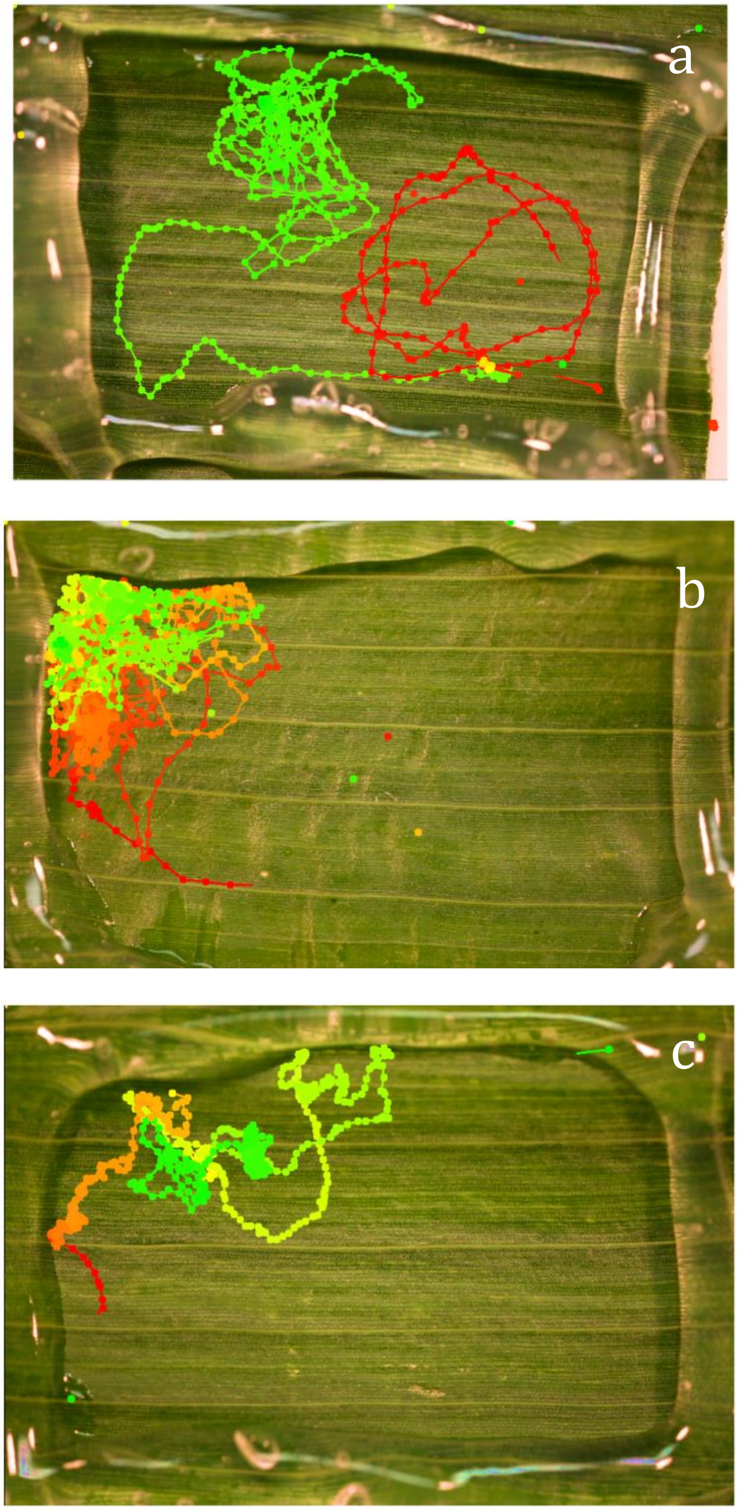


Fig. 3-9. Example of 50 mins tracking map of BGM on a) B73 b) B75 and c) B96 arena. The starting point of video when mite was introduced in the leaf arena is represented by red which followed orange to yellow and to the end point by green.



CHAPTER IV

MAIZE EXPOSED TO WATER-STRESS DOES NOT DISRUPT RESISTANCE TOWARD SPIDER MITES

Abstract: Climate variability has had major implications on agriculture due to the increase in the frequency and intensity of simultaneous abiotic, namely water-stress, and biotic stresses to crops. Plant water-stress alone harms crops but can attract outbreaks of herbivores with varied host specialization, and plants succumb to further yield losses dealing with multiple stressors. Indeed, plants vary in resistance mechanisms to herbivores, acting as the first line of defense against herbivory; when available, plant resistance can be an effective management tool. To understand how plant water-stress interacts with host plant resistance to spider mites that thrive under arid and hot conditions, we conducted parallel greenhouse and field experiments. Here, three maize inbred lines with varied resistance (a susceptible B73, and two resistant lines B75 and B96) to spider mites were subjected to either optimal irrigation or water-stress conditions [50-60% and 5-10% volumetric water content (VWC), and 25-32% and 10-15% VWC, in the greenhouse and field, respectively]. In addition to recording plant physiological responses to water-stress, we measured the population growth of the generalist twospotted spider mite (*Tetranychus urticae,* TSM) and the specialist Banks grass mite (*Oligonychus pratensis,* BGM) on water treatments. We also measured plant defense protein activities (peroxidase, polyphenol oxidase, chitinase and trypsin inhibitor) at 1, 3, and 7 days post mite introduction for each inbred line and water treatment. All maize lines exposed to water-stress had increased leaf temperature, leaf water potential, as well as decreased stomatal conductance and stem height. Under optimal irrigation, resistant lines (B75 and B96) had lower TSM populations compared to the susceptible B73, yet resistance did not appear to affect the population growth of BGM. While water-stressed susceptible plants (B73) led to increased populations of both mite species, water-stressed resistant lines (B75 and B96) maintained their level of resistance for each mite that was observed on optimally irrigated plants. Resistant lines (B75 and B96) had high activity of CHI and TI. Yet, regardless of maize inbred lines, TI activity only increased when TSM was combined with water-stress. In contrast, resistant lines had decreased CHI activity when BGM was combined with water-stress. Collectively, our results suggest that maize resistance to spider mites may be species-specific, and limited when considering host specialization. Despite climate variability, however, management through host plant resistance may be maintained in maize.

1. Introduction

Climatic variability is predicted to have major constraints on global agricultural production due to increase in the frequency and severity of simultaneous abiotic (e.g., water, heat) and biotic (e.g., herbivory, weeds and, pathogens) stresses to crops (Leng and Hall, 2019; Maxmen, 2013; Oerke, 2006; Rosenzweig et al., 2014, 2001). Of particular concern is water-stress, which bring crop losses not only by impairing the growth and development of plants but also by exacerbating herbivorous arthropods that thrive in these conditions (Maxmen, 2013). For example, spider mites, pests of many crops, outbreak in water-stress conditions, and have resulted in severe yield losses as high as 47.2% in maize (Bacon et al., 1962; English-Loeb, 1990; Maxmen, 2013). While overarching success in evaluating plant resistance to pests could serve as a sustainable management tool (Bynum et al., 2004a; Eigenbrode and Trumble, 1994; Gill et al., 2011; Howe and Jander, 2008; Kloth et al., 2015; Mansour et al., 1994; Sedaratian et al., 2009; Singh and Seetharama, 2008; Stoner, 1996; Stout, 2013; Tadmor et al., 1999), our knowledge of the interactions between abiotic factors such as water-stress and pest resistance is limited, particularly for spider mites.

Previous studies based on insects such as aphids, caterpillars, midges and flies in various cropping systems reported that water-stress led to idiosyncratic effects on plant resistance to pests (Grinnan et al., 2013; Ojwang et al., 2010; Sharma et al., 1999; Verdugo et al., 2016, 2015). An evaluation of 29 studies focused on aphids across several cropping systems found that resistance in crops exposed to water-stress was decreased (41.4% of studies), increased (34.5%), showed no change (20.1%), or had conditional effects (3.4%) (Verdugo et al., 2016). Understanding the impacts of water-stress on plant resistance to pests is further complicated as resistance mechanisms can be species-specific and vary based on host specialization considering the ability for herbivores to cope with plant resistance traits (Ali and Agrawal, 2012). Generalist herbivores, that feed on many plant families, may rely on broad detoxification of plant defenses in their diverse hosts (Dermauw et al., 2013a, 2013b; Leeuwen et al., 2011; Szczepaniec et al., 2013). Specialist herbivores, on the other hand, restrict their feeding to a narrow set of plant hosts (e.g., a plant family, genus, or species), evolving ways to sequester, suppress, and manipulate plant defenses of specific hosts (Ratzka et al., 2002; Wheat et al., 2007; Wittstock et al., 2004). Therefore, the next step is not only to understanding how water-stress affects host plant resistance but to consider the breadth of these interactions with regard to herbivore host specialization.

Maize, one of the most important cereal crops, is known to face outbreaks from spider mite herbivores when exposed to water-stress conditions (Archer and Bynum, 1993; Bacon et al., 1962; Bynum et al., 2015; FAO, 2018; Peairs, 2014; Peairs and Both, 2010; Ruckert et al., 2015). Among many spider mite species that attack maize, two that cause major economic damage are the generalist twospotted spider mite (*Tetranychus urticae*, TSM) that feeds on a wide range of plant species (>1100), and specialist Banks grass mite (*Oligonychus pratensis*, BGM) that restricts its feeding to grasses (Poaceae) (Bynum Jr. et al., 2015; Dworak et al., 2016; Grbic et al., 2007; Tadmor et al., 1999a). In hot and dry conditions, especially during the grain filling period, spider mite populations can rapidly increase within weeks and can cause severe yield losses (Archer and Bynum, 1993; Bacon et al., 1962; Bynum et al., 2004; Tadmor et al., 1999). Given that both TSM and BGM are resistant to major acaricides being used for their conventional management (Dermauw et al., 2013; Kwon et al., 2010; Ruckert et al., 2018; Leeuwen et al., 2005; Yang et al., 2001), evaluating plant resistance to TSM and BGM, especially in water-stress conditions is of utmost importance.

A growing volume of the literature demonstrated successes in screening maize inbred lines for spider mite resistance (Bui et al., *in prep*; Bynum et al., 2004; Kamali et al., 1989; Mansour and Karchi, 1990; Tadmor et al., 1999). For example, the B96 maize inbred line was found to be resistant to twospotted spider mite (*Tetranychus urticae,* TSM) and carmine spider mite (*Tetranychus cinnabarinus*) (Kamali et al., 1989b; Tadmor et al., 1999a). Previous screening also reported that B96 and B75 maize inbred lines were resistant to TSM but not to BGM (Bui et al., *in prep*). It is important to note that B73 is a focal maize inbred line whose genome has been sequenced and was reported to be susceptible to TSM and BGM (Bui et al., 2018). B73 shares more than 97% of its genome with more than 50 other maize inbred lines and has served as a model inbred line in the development of commercial maize hybrids (Lee et al. 2002; Bynum et al. 2004a; McMullen et al. 2009; Eichten et al. 2011; Ganal et al. 2011). Recently, Bui et al. (2018), showed that under optimally irrigated conditions, B73 plants respond to TSM and BGM with similar defenses. In another study, B73 responded with increases in protease inhibitors only with combinations of water-stress and herbivory by TSM, an observation not found with BGM (Gill et al., 2020).

Here, via greenhouse and field experiments we investigate the impact of water-stress on maize resistance to TSM and BGM in three maize inbred lines with varied resistance to spider mites (B73 a susceptible line, and two resistant lines, B75 and B96). We also investigate how combined water-stress and mite herbivory impact plant defensive protein responses in each maize inbred line.

2. Materials and methods

2.1. *Experimental design*

2.1.1. Greenhouse TRIAL 1 and TRIAL 2

We conducted a 3 × 2 × 2 factorial design experiment using three levels of mite (Control, TSM, and BGM), two levels of maize resistance (TRIAL 1: susceptible B73 and resistant B75; TRIAL 2: susceptible B73 and resistant B96) and two levels of water (optimal irrigation and water-stress treatments) with repeated measures (1, 3, and 7 days) in the greenhouse. These experiments were performed at Utah State University's Research Greenhouse in Logan, UT.

Experimental units consisted of 18.9 L buckets, filled with potting soil (Sunshine Mix #3, Sun Gro Horticulture, MA) and arranged in a complete randomized design. We planted two maize plants per bucket representing a single line (TRIAL 1: B73 or B75; TRIAL 2: B73 or B96), where each bucket was a replicate and each plant was a subsample. Each treatment (3 levels of mite × 2 levels of maize inbred lines × 2 levels of water) was replicated twelve times. Maize plants were grown in greenhouse-controlled conditions (25±2 °C, 60±5% RH, 16:8 hr (L:D) photoperiod) and fertigated at a rate of 4.8 kg/100L of 21N-5P-20K using Peters Excel Water Soluble Fertilizer mixture (ICL Specialty Fertilizers, SC). We used drip tape (DIG Corporation, CA, 12.7 mm and 6.35 mm diameter tubing with 3.8 L/hr compensating emitters) to irrigate the plants throughout the experiment.

After six weeks, plants were switched from fertigation to irrigation to establish optimal irrigation or water-stress levels. Acclima 315 L soil sensors (Acclima, ID, USA) were used to monitor the volumetric water content (VWC) of soil. All replicates (buckets) were irrigated evenly at the level equivalent to field capacity of potting soil (50-60 % VWC) for seven weeks after sowing. When plants were 8-weeks old, buckets were randomly assigned to either optimal irrigation (by maintaining 50-60 % VWC) at field capacity or water-stress (by reducing irrigation to 5-10 % VWC) which was above permanent wilting point (Fitter and Hay, 2012) (Fig. 4-1). Water-stress or optimal irrigation levels were quantified by measuring stomatal conductance (mmolm$_{-2S-1}$) and leaf temperature (°C) using a leaf porometer (Model SC-1, Meter Group, WA), leaf water potential (bar) using a pressure chamber instrument (Model 615, PMS Instrument Company, OR), and stem height (cm) by using a ruler (Table. 4-1). At an 8-week plant stage, Tanglefoot (Scotts Miracle-Gro Company, OH, USA) non-phytotoxic wax arena was created on the 8th leaf from the bottom of maize plants. Within the arena, twenty adult female mites (mated BGM or TSM) from laboratory colonies sustained on B73 maize (28±2 °C, 50±5% RH, 16:8 hr (L:D) photoperiod) were introduced. Mite transfer to the arena was accomplished by vacuuming twenty mites each into filtered pipette tips attached with a rubber hose to a low power vacuum. The pipette tips were then attached within the leaf arena using tape. This allowed mites to exit the pipette tips within approximately an hour and settle on the undersides of the leaves.

After 1, 3, and 7 days post mite introduction, leaf samples (leaf area inside the Tanglefoot arena) from eight plants of four randomly selected replicates (2 plants/replicate) were collected, flash-frozen using liquid nitrogen and stored in a freezer (-20 °C) until processing. Each sample was processed for counting the number of eggs and all mite stages as well as for performing defense protein bioassays (*see* 2.2. Plant Defense Bioassay section).

2.1.2. Field SEASON 1

In the 2018 field season (SEASON 1), we conducted a 3 × 3 × 2 factorial design experiment using three levels of Mite (Control, TSM, and BGM), three levels of maize resistance (susceptible B73, and two resistant lines, B75 and B96) and two levels of water (optimal irrigation and water-stress treatments) with repeated measures (1, 3, and 7 days). This experiment was conducted at the Greenville Research Station at Utah State University, Logan, UT.

Six plants representing each respective maize inbred line (B73, B75, and B96) were grown in a Lumite cage (1.8 m L × 1.8 m W × 1.8 m H) (Lumite, GA, USA), the experimental unit. Cages were arranged in a randomized complete block design (RCBD) within varied water treatments where each treatment (3 levels of mite × 3 levels of maize inbred lines × 2 levels of water) was replicated four times. A total of 72 cages were arranged in 12 rows (6 cages/row), each spaced 4 m apart to establish two irrigation treatments and 2 m apart within rows.

When the plants were 6-week old, water treatments (optimal irrigation and water-stress) were established by maintaining half the number of cages at 25-32% and the other half at 10-15% volumetric water content (VWC). Similar to the greenhouse, stomatal conductance (mmolm$_{-2}$s$_{-1}$), leaf temperature (°C), leaf water potential (bar), and stem height (cm) were measured to assess the impact of water-stress (Table. 4-1).

Mirroring the greenhouse protocol, the 8th leaf from the bottom of 8-week old plants were selected for the establishment of a Tanglefoot arena. Twenty adult female mites, BGM or TSM, were introduced to the leaf arenas for each mite species treatment using the pipette tip method previously described. After 1, 3, and 7 days post mite introduction, leaf samples (leaf area inside the Tanglefoot arena) from two randomly selected plants per treatment were collected, stored and processed as described previously.

2.1.3. Field SEASON 2

In the 2019 field season (SEASON 2), we conducted a 2 × 3 × 2 factorial design experiment using two levels of Mite (Control and TSM), three levels of maize resistance (susceptible B73, and two resistant lines, B75 and B96) and two levels of water (optimal irrigation and water-stress treatments) with repeated measures (1, 3, and 7 days). In SEASON 2, BGM was removed from treatments considering results from SEASON 1 (see *3.3 Results* section). This experiment was conducted at the Greenville Research Station at Utah State University, Logan, UT.

As described for SEASON 1, Lumite cages contained six plants representing a maize line (B73, B75, or B96) arranged in a randomized complete block design (RCBD) within water treatments. Here, each treatment (2 levels of mite × 3 levels of maize inbred lines × 2 levels of water) was replicated five times for a total of 60 cages. Spacing of rows and cages within rows was as previously described.

The procedures for the establishment of water treatments, the Tanglefoot arena, and introduction of mites were the same as described in SEASON 1. After 1, 3, and 7 days post mite introduction, leaf samples from two randomly selected plants per treatment were collected, processed (flash frozen), and evaluated (recording number of eggs, all mite stages, and conducting protein bioassays) as described previously.

2.2 Plant defense bioassays

Leaf samples were processed for analyzing four plant defense proteins: polyphenol oxidase (PPO), trypsin inhibitor (TI), peroxidase (POD), and chitinase (CHI) following methods from Gill et al. (2020). Briefly, each leaf sample (500 mg), pulverized in liquid nitrogen, was mixed with 1 mL of 0.05 M sodium phosphate buffer. Following centrifuging at 12000 RPM for 12 mins, the cell lysate (supernatant), which contained soluble proteins, was obtained. The activities of POD, PPO and CHI were analyzed using a microplate reader (Biotek EPOCH, VT, USA). The activity of TI was analyzed by using radial diffusion techniques. PPO and POD were quantified as ΔAbs_{470nm} $min^{-1}mg$

extract protein^{-1}, CHI was quantified as ΔAbs_{405nm} mg extract protein^{-1}, and TI was quantified as μg TI mg extract protein^{-1}.

2.3 Statistical Analysis:

Data from plant physiological measurements including leaf temperature, stomatal conductance, and stem height from 3 and 7 days were analyzed along with leaf water potential using a generalized linear model (Proc Glimmix; SAS 9.4 M4 University edition). In the greenhouse trials, plant physiological measurements were analyzed using two levels each of water (optimal irrigation and water-stress) and maize inbred line (TRIAL 1: B73 and B75; TRIAL 2: B73 and B96). In the field, measurements were analyzed using two levels of water (optimal irrigation and water-stress) and three levels of maize inbred line (B73, B75, and B96). Square-root transformation was used for plant physiological measurements to conform to the assumption of normality and heteroscedasticity.

Mite (TSM and BGM) population sizes and defense protein activity measurements from greenhouse trials were analyzed using a generalized linear model (Proc Glimmix; SAS 9.4 M4 University edition). Here, analyses consisted of two levels each of mites (TSM and BGM), maize resistance (TRIAL 1: B73 and B75; TRIAL 2: B73 and B96), and water (optimal irrigation and water-stress) with repeated measures (1, 3, and 7 days post mite introduction). However, for defense protein assays, analyses consisted of three levels of mite (Control, TSM and BGM), and two levels for each of maize resistance and water with repeated measures. Square-root transformation was used for both mite population growth and defensive proteins (POD, PPO, CHI and TI) data to conform to the assumption of normality and heteroscedasticity.

When interactions were not significant, differences within significant main effects were determined using Tukey's HSD post hoc test. When multi-factor interactions were significant, the LSMESTIMATE statement (Proc Glimmix) with Tukey-Kramer adjustment was used for further analysis. For instance, when defense protein activity revealed a four-way interaction (water × resistance × mite × time) each mite species was independently analyzed at each time comparing resistance in maize inbred lines and water treatments.

SEASON 1 analyses for mite (TSM and BGM) population sizes and defense protein activity used a generalized linear model as described with greenhouse trials (Proc Glimmix; SAS 9.4 M4 University edition). Here, three levels of maize resistance (B73, B75 and, B96) along with each respective level of water, mite and repeated measures described for greenhouse trials was analyzed. Data transformations as well as additional analyses for interactions were performed as described previously.

For SEASON 2, BGM was removed from treatments considering results from SEASON 1 (see *3.3 Results* section). Therefore, analyses consisted of only TSM, and the three levels of maize resistance and two levels of water within repeated measures as previously described. Additionally, defense protein assays were analyzed instead with two levels of mite (Control and TSM), and the same levels described for each factor (i.e., resistance and water) within repeated measures. Data transformations as well as further analyses of significant interactions were performed as described previously.

3. Results

3.1. *Greenhouse TRIAL 1 (susceptible B73 and resistant line B75) and TRIAL 2 (susceptible B73 and resistant line B96)*

3.1.1. Effect of water-stress on plant physiological measures

In greenhouse TRIAL 1, plant physiological measurements such as leaf water potential and leaf temperature significantly increased due to water-stress, and these effects were similar between the maize lines (susceptible B73 and resistant line B75) (Table 4-1). Specifically, water-stressed plants increased leaf water potential and leaf temperature by 3.87 ± 0.85 bar and 1.32 ± 0.34 °C compared to optimally irrigated plants (Table 4-1). Water-stress also significantly reduced stomatal conductance and stem height of plants by as much as 59.17 ± 8.38 mmolm$_{-2}$s$_{-1}$ and 17.22 ± 2.81 cm compared to optimally irrigated plants (Table 4-1). Further, regardless of maize inbred line, stem height increased by 11.23 ± 4.62 cm, leaf temperature increased by 0.24 ± 0.44 °C, and stomatal conductance decreased by 43 ± 11.63 mmolm$_{-2}$s$_{-1}$ when comparing a significant effect of time from 3 to 7 days post mite introduction (Table 4-1).

TRIAL 2 plants (susceptible B73 and resistant line B96) exposed to water-stress conditions similarly increased leaf water potential by 3.87 ± 0.85 bar, and decreased stomatal conductance and stem height by 128.28 ± 18.11 mmolm$_{-2}$s$_{-1}$ and 17.07 ± 1.51 cm compared to optimally irrigated plants (Table 4-1). However, in TRIAL 2, the effect of water-stress on leaf temperature was only marginally significant ($P = 0.06$, Table 4-1). Further, significant main effect of time from 3 days to 7 days revealed that regardless of maize inbred lines (B73 and B96), stem height increased by 7.5 ± 2.01 cm, leaf temperature increased by 4.11 ± 0.63 °C, stomatal conductance decreased by 51.58 ±

25.83 mmolm$_{-2S-1}$ (Table 4-1).

3.1.2. Effect of water-stress on mite population growth

For TRIAL 1, mite population growth appeared to be significantly affected by the interactions of water × resistance × time ($P < 0.01$, Table 4-2, Fig. 4-2) and mite × resistance × time ($P = 0.05$, Table 4-2, Fig. 4-2). The water × resistance × time interaction appeared to be driven by a lack of mite population change on resistant plants (B75) exposed to water-stress over the 7 day period compared to optimally irrigated plants. To further assess the water × resistance × time interaction, we analyzed mite population growth on individual maize inbred lines by comparing water treatments (optimal irrigation and water-stress) in time. We found that water-stressed susceptible plants (B73) had increased mite population growth ($P < 0.05$, LSMESTIMATE Tukey adjustment), while resistant plants (B75) exposed to water-stress did not differ in mite populations ($P > 0.05$, LSMESTIMATE Tukey adjustment) compared to optimally irrigated plants. Further, a significant mite × resistance × time interaction appeared to be driven by specialist BGM not being impacted by maize resistance over the 7 day period compared to TSM. To further understand this interaction, we analyzed population growth for TSM and BGM independently, comparing maize inbred lines, at each time. Here, TSM population growth was decreased on resistant B75 plants compared to susceptible B73 plants at 7 days post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment). Yet, BGM populations grew equally well on both B73 and B75 throughout the experiment ($P > 0.05$, LSMESTIMATE Tukey adjustment, Fig. 4-2).

For TRIAL 2, mite population growth was also significantly affected by the interactions of water × resistance × time ($P < 0.01$, Table 4-4, Fig. 4-2) and mite × resistance × time (TRIAL 2: $P = 0.01$, Table 4-4, Fig. 4-2). Similar to TRIAL 1, the water × resistance × time interaction was driven by mite populations remaining low on resistant plants (B96) exposed to water-stress after 7 days compared to control plants. As in TRIAL 1, we evaluated each maize line (B73 and B96) to compare water treatments across time. Again, water-stress increased mite populations in B73 at 7 days post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment). Yet, B96, the resistant line in TRIAL 2, was not affected by water stress as mite populations remained low over 7 days ($P > 0.05$, LSMESTIMATE Tukey adjustment). Furthermore, as in TRIAL 1, the mite × resistance × time interaction appeared to be driven by an unresponsive BGM to resistant plants (B96) while resistance traits appeared to decrease TSM through the experiment. To confirm, each mite was analyzed independently, to compare B73 and B96 across time. At 3 and 7 days post mite introduction, TSM populations were decreased on resistant B96 plants compared to susceptible B73 plants ($P < 0.05$, LSMESTIMATE Tukey adjustment). In contrast, BGM population growth was similar on B73 and B96 throughout the experiment ($P > 0.05$, LSMESTIMATE Tukey adjustment, Fig. 4-2).

3.1.3. Effect of water-stress and mite herbivory on the activity of plant defense proteins in the greenhouse TRIAL 1

POD activity was significantly affected by a complex water × mite × resistance × time interaction ($P < 0.01$, Table 4-3, Fig. 4-3). To understand the interaction, we analyzed plant responses to TSM and BGM herbivory independently, comparing water treatments on maize lines across time. TSM herbivory appeared to have no impact on

POD activity in susceptible B73 and resistant B75 with or without water-stress ($P > 0.05$, LSMESTIMATE Tukey adjustment). BGM combined with water-stress resulted in a 6.45-fold increase in POD activity compared to optimally irrigated susceptible plants (B73) at 3 days post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment). Regardless of water-stress exposure, BGM herbivory did not change POD activity in resistance B75 plants.

PPO activity was also significantly affected by a water × mite × resistance × time interaction ($P = 0.01$, Table 4-3, Fig. 4-3). To better understand the interaction we evaluated as described for POD, for each mite independently. While TSM herbivory did not change PPO activity in B75, TSM herbivory combined with water-stress in susceptible B73 increased PPO activity by 6.58-fold compared to optimally irrigated plants with TSM at 1 day post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment). Similarly, BGM herbivory combined with water-stress in susceptible B73 also increased PPO activity by 11.11-fold compared to optimally irrigated plants with BGM at 1 day post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment). Like POD, regardless of water-stress exposure, BGM herbivory did not change PPO activity in resistant B75 plants throughout the experiment ($P > 0.05$, LSMESTIMATE Tukey adjustment).

The significant water × mite × resistance × time interaction for CHI activity ($P < 0.01$, Table 4-3, Fig. 4-3), similar to previous proteins was reanalyzed for TSM and BGM independently. Here, CHI activity in B73 and B75 did not respond to TSM herbivory, water-stress, or combinations of abiotic and biotic stress for the 7 days of the experiment ($P > 0.05$, LSMESTIMATE Tukey adjustment). However, the combination of water-stress and BGM herbivory modestly decreased CHI activity by 0.23-fold after 3 days post mite introduction in resistant B75 plants compared to plants exposed to BGM herbivory alone (no water stress) ($P < 0.05$, LSMESTIMATE Tukey adjustment). Yet, B73 response to BGM herbivory, water stress, or combinations of abiotic and biotic stress was not significantly different ($P > 0.05$, LSMESTIMATE Tukey adjustment).

Like POD, PPO and CHI, TI activity also had a significant interaction of water × mite × resistance × time ($P = 0.02$, Table 4-3, Fig. 4-3), to which TSM and BGM were analyzed independently. TSM herbivory combined with water-stress in susceptible B73 plants increased TI activity by 2.28-fold compared to herbivory alone at 1 day post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment). Interestingly, BGM herbivory, regardless of maize resistance and water-stress, had no impact on TI activity over 7 days.

3.1.4. Effect of water-stress and mite herbivory on the activity of plant defense proteins in the greenhouse TRIAL 2

POD, PPO and CHI activity appeared to be significantly affected by a water × resistance × time interaction ($P < 0.05$, Table 4-5, Fig. 4-4). The interaction appeared to be driven by resistant plants (B96) having increased POD, PPO and CHI activity over 7 days compared to B73. We analyzing each maize line (B73 and B96) independently to compare water treatments across time. While no significant impact of water-stress was observed for susceptible B73 throughout the experiment ($P > 0.05$, LSMESTIMATE Tukey adjustment), resistant B96 plants exposed to water-stress resulted in a 1.52-fold (at 3 days), 5-fold (at 7 days), and 1.48-fold (at 3 days) increase in POD, PPO, CHI activity, respectively, compared to optimally irrigated plants at each respective time ($P < 0.05$, LSMESTIMATE Tukey adjustment).

With the exception of PPO, POD and CHI also had a significant mite × resistance × time interaction ($P < 0.05$, Table 4-5, Fig. 4-4). For POD, the interaction was driven by an increase in POD activity by TSM herbivory but not by BGM herbivory in resistant plants (B96) over 7 days. To confirm, each mite (TSM and BGM) was independently analyzed to compare maize inbred lines across time. While TSM herbivory did not impact POD activity in susceptible plants (B73), TSM increased POD activity in resistant plants (B96) by 2.11-fold compared to control (no mite) plants at 7 days post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment). In contrast, BGM herbivory did not impact POD activity of either maize line (B73 and B96) over 7 days ($P > 0.05$, LSMESTIMATE Tukey adjustment).

For CHI, the mite × resistance × time interaction appeared to be driven by BGM increasing CHI in B73 more than in B96 at 7 days compared to TSM not impacting CHI ($P < 0.05$, Table 4-5, Fig. 4-4). TSM and BGM were independently analyzed to compare maize inbred lines across time. CHI activity was not affected by TSM herbivory on either line over 7 days ($P > 0.05$, LSMESTIMATE Tukey adjustment). Rather, susceptible plants (B73) exposed to BGM had 2-fold higher CHI activity compared to resistant plants (B96) at 7 days post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment).

For TI activity, the mite × resistance × time ($P < 0.01$), water × mite × resistance ($P = 0.01$) and water × mite × time ($P = 0.04$) interactions were significant (Table 4-5, Fig. 4-4). The mite × resistance × time interaction appeared to be driven by an increase in TI activity in resistant B96 plants by TSM herbivory compared to BGM over time. This was confirmed by evaluating each mite (TSM and BGM) independently to compare maize inbred lines across time. TI activity was 7.47-fold higher when resistant (B96) plants were exposed to TSM as compared to susceptible (B73) plants at 7 days post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment). The interaction of water × mite × resistance also appeared to be driven by an increase in TI activity when optimally irrigated resistant B96 plants were exposed to TSM herbivory compared to optimally irrigated susceptible plants (B73). This was confirmed by analyzing individual mite species (TSM and BGM) by comparing maize inbred lines exposed to water treatments (optimal irrigation and water-stress). We found that optimally irrigated B96 plants exposed to TSM treatments had 6.35-fold higher TI activity compared to optimally irrigated B73 plants exposed to TSM ($P < 0.05$, LSMESTIMATE Tukey adjustment). Highlighting the effect of water (no herbivory), resistant B96 plants exposed to water-stress had a modest 0.27-fold lower TI activity compared to optimally irrigated plants ($P < 0.05$, LSMESTIMATE Tukey adjustment). Further, a significant water × mite × time interaction appeared to be driven by an increase in TI due to TSM herbivory and the lack of change in activity due to BGM herbivory over the duration of experiment ($P < 0.05$, Table 4-5, Fig. 4-5). This was confirmed by evaluating TSM and BGM independently to compare water treatments across time. Combined water-stress and TSM herbivory increased TI activity by 2.31-fold compared to optimally irrigated plants with TSM herbivory at 1 day post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment). As indicated previously, BGM herbivory did not affect TI activity ($P > 0.05$, LSMESTIMATE Tukey adjustment).

3.2. *Field SEASON 1 and SEASON 2*

3.2.1. Effect of water-stress on plant physiological measures

In SEASON 1, a significant interaction of water × resistance revealed that leaf water potential was significantly lower for optimally irrigated resistant B96 plants (2.57 ± 0.25 bar) compared to optimally irrigated susceptible B73 plants (3.33 ± 0.37 bar) ($P < 0.05$, LSMESTIMATE Tukey adjustment). Also, water-stress increased leaf water potential in susceptible B73 as well as in resistant B75, and resistant B96 by 3.8 ± 0.45 bar, 2.93 ± 0.46 bar and 5.62 ± 0.47, respectively ($P < 0.05$, LSMESTIMATE Tukey adjustment). For stomatal conductance, a significant interaction between resistance × time revealed that resistant B75 and resistant B96 plants had modest 0.66-fold and 0.54-fold lower stomatal conductance compared to susceptible B73 plants, respectively ($P < 0.01$, Table 4-1). The significant main effect of water-stress in plants also reduced stomatal conductance by 68.29 ± 16.85 mmolm$_{-2}$s$_{-1}$, increased leaf temperature by 0.9 ± 0.25 °C, and reduced stem height by 11.09 ± 2.24 cm compared to optimally irrigated plants (water: $P < 0.01$, Table 4-1). Also, the main effect of resistance was significant for stem height which showed that susceptible B73 (82.41 ± 2.43 cm) and resistant B75 (82.60 ± 1.97 cm) plants had higher stem height compared to resistant B96 (52.38 ± 2 cm) in the field (resistance: $P < 0.01$, Table 4-1). Further, a significant main effect of time from 3 days to 7 days revealed that regardless of maize inbred lines, stem height increased by 6.6 ± 1.99 cm (Time: $P < 0.01$, Table 4-1).

Similar to SEASON 1, a significant effect of water-stress in SEASON 2 also increased leaf water potential and leaf temperature by 8.48 ± 0.5 bar and 1.55 ± 0.39 °C, respectively, compared to optimally irrigated plants (Table 4-1). Water-stressed plants significantly decreased stem height and stomatal conductance by 14.66 ± 2.96 cm and 146.82 ± 24.17 mmolm$_{-2}$S$_{-1}$ compared to optimally irrigated plants (Table 4-1). Further, a significant main effect of time from 3 days to 7 days revealed that regardless of maize inbred lines, stem height increased by 14.14 ± 3.2 cm, leaf temperature decreased by 1.79 ± 0.56 °C, and stomatal conductance decreased by 86.67 ± 34.34 mmolm$_{-2}$S$_{-1}$ (Table 4-1).

3.2.2. Effect of water-stress on mite population growth

In SEASON 1, mite × resistance × time and water × time interactions significantly affected mite population growth ($P < 0.01$, Table 4-5, Fig. 4-6). The mite × resistance × time appeared to be driven by lower populations of TSM throughout the experiment than BGM populations that were lower only at 7 days on resistant plants (B75 and B96) compared to susceptible B73 plants over 7 days. This was confirmed by evaluating each mite species (TSM and BGM) to compare maize inbred lines across time. The resistant B75 and B96 plants had lower TSM populations compared to susceptible B73 plants throughout the experiment ($P < 0.05$, LSMESTIMATE Tukey adjustment). Lower BGM populations were found on resistant B75 (at 1 and 7 days) and B96 (at 7 days) compared to susceptible B73 plants (Table 4-6, Fig. 4-6). Interestingly, resistant B96 plants also had lower BGM mite populations compared to resistant B75 at 3 days post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment). Further, a water × time interaction revealed that water-stress increased both mite populations in plants (B73, B75 and B96) at 7 days post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment).

In SEASON 2, a significant resistance × time interaction ($P < 0.01$) revealed lower TSM population on resistant B75 (at 7 days) and resistant B96 (at 3 and 7 days) compared to susceptible B73 plants (Table 4-8, Fig. 4-5). Also, resistant B96 plants had lower TSM populations than resistant B75 plants at 7 days post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment).

3.2.3. Effect of water-stress and spider mite herbivory on plant defense protein activity in the field SEASON 1

For POD activity, the significant interaction of mite × resistance × time ($P < 0.01$, Table 4-7, Fig. 4-6) appeared to be driven by increased POD activity in B73 and B75 plants exposed to BGM herbivory compared to B96 plants at 7 days post mite introduction. This was confirmed by evaluating TSM and BGM individually to compare maize inbred lines across time. TSM herbivory, regardless of water-stress, appeared to cause no change in POD activity in any lines (B73, B75 and B96). In contrast, B73 and B75 exposed to BGM herbivory had 8-fold and 5.83-fold higher POD activity compared to B96, respectively at 7 days post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment).

For PPO activity, a complex water × mite × resistance × time interaction was significant ($P < 0.01$, Table 4-7, Fig. 4-6). To understand the interaction, we analyzed plant responses to TSM and BGM herbivory independently, comparing water treatments on maize lines across time. Combined water-stress and TSM herbivory in resistant B96 resulted in an increase of PPO activity by 2.05-fold at 3 days post mite introduction ($P = 0.05$, LSMESTIMATE Tukey adjustment). However, TSM herbivory appeared to cause no change in PPO activity in susceptible (B73) plants ($P > 0.05$, LSMESTIMATE Tukey adjustment). Also, BGM herbivory, regardless of maize inbred line and water treatment, did not change PPO activity throughout the experiment ($P > 0.05$, LSMESTIMATE Tukey adjustment).

For CHI activity, a significant main effect of maize resistance ($P = 0.03$, Table 4-7, Fig. 4-6) showed that resistant B75 had 1.54-fold higher CHI activity compared to resistant B96 ($P < 0.05$, Tukey's HSD post hoc). However, we found no significant difference in CHI activity for susceptible B73 compared to resistant B75 ($P > 0.05$, Tukey's HSD post hoc) and B96 ($P > 0.05$, Tukey's HSD post hoc).

TI activity was significantly impacted by a water × mite × time ($P < 0.01$) and water × mite × resistance ($P = 0.01$) interaction (Table 4-7, Fig. 4-6). The water × mite × time interaction was driven by an increase in TI activity due to TSM herbivory and opposite effect due to BGM on water-stressed plants over 7 days. This was confirmed by evaluating each mite species (TSM and BGM) to compare water treatments across time. Plants exposed to a combination of TSM and water-stress increased TI activity by 4.55-fold compared to TSM herbivory alone at 1 day post mite introduction ($P < 0.05$, LSMESTIMATE Tukey adjustment). In contrast, plants exposed to a combination of BGM and water-stress decreased TI activity by a modest 0.42-fold compared to BGM herbivory alone at 7 days ($P < 0.05$, LSMESTIMATE Tukey adjustment). The significant water × mite × resistance interaction appeared to be driven by an increase in TI activity by TSM herbivory on water-stressed susceptible (B73) plants, where BGM did not affect TI activity on either maize inbred line. Here, we evaluated each mite species (TSM and BGM) to compare water treatments and maize resistant lines. TSM herbivory combined with water-stress in susceptible B73 increased TI activity by 1.74-fold compared to TSM herbivory alone on B73 ($P < 0.01$, LSMESTIMATE Tukey adjustment) (Fig. 4-7, Table 4-7) As indicated previously, BGM herbivory did not change TI activity in maize inbred lines ($P > 0.01$, LSMESTIMATE Tukey adjustment).

3.2.4. Effect of water-stress and spider mite herbivory on plant defense protein activity in the field SEASON 2

Although water-stress did not impact CHI and TI activity, the interaction of mite × time and the main effect of maize resistance were significant (Table 4-9, Fig. 4-7). The mite × time interaction revealed that BGM herbivory did not impact CHI or TI activity; however compared to control (no mite) plants, TSM herbivory had 0.65-fold lower CHI activity and 1.64-fold higher TI activity at 3 ($P < 0.01$, LSMESTIMATE Tukey adjustment) and 7 ($P < 0.01$, LSMESTIMATE Tukey adjustment) days, respectively. A significant effect of maize resistance showed that resistant B96 plants had 1.4-fold higher CHI ($P < 0.01$, LSMESTIMATE Tukey adjustment) and 3.11-fold higher TI activity ($P < 0.01$, LSMESTIMATE Tukey adjustment) compared to susceptible B73 plants. Further, TI activity appeared to be 2.81-fold higher in resistant B96 compared to resistant B75 plants ($P < 0.01$, LSMESTIMATE Tukey adjustment).

4. Discussion

In both the greenhouse and field experiments, we found that water-stress reduced stem height, increased leaf water potential, decreased stomatal conductance, and elevated leaf temperatures in plants of all maize inbred lines. These responses validate the induction of water-stress in plants (Bradford and Hsiao, 1982; Kramer, 1983; Niu et al., 2006; Ruckert et al., 2018; Shahenshah and Isoda, 2010), which is essential for studying spider mite interactions, as their outbreaks are known to be associated with water-stressed plants. Under optimal irrigation, resistant lines (B75 and B96) had lower TSM populations compared to the susceptible B73 line, yet resistance did not appear to affect the population growth of BGM. While water-stressed susceptible plants (B73) led to an increase in populations of both mite species, water-stressed resistant lines (B75 and B96) maintained their level of resistance to each respective mite as when lines were optimally irrigated. Our results suggest that although resistance varied for generalist and specialist mite herbivory, B75 and B96 maize inbred lines maintained their resistance levels in water-stress conditions. Therefore, in the face of changing climate (i.e., increased frequency of plant water-stress) the stability of pest resistance within breeding programs may be conserved in maize.

Our findings were consistent with 20.1% of studies reviewed by Verdugo et al., (2016) that showed no-change in resistance to aphids due to abiotic stress in wheat (Fluegel and Johnson, 2020), barley (*Hordeum vulgare* L.) (Aslam et al., 2013; Brewer and Webster, 2001; Oswald and Brewer, 1997), *Arabidopsis thaliana* (Mewis et al., 2012) and canola (*Brassica napus* L.) (King et al., 2006) systems. In these systems increased abiotic stressors such as water-stress and suboptimal soil nitrogen levels, surprisingly did not alter host plant resistance of each respective crop to aphid feeding. However, one of the limitations of these studies was that the effect of water-stress on plant resistance was tested for a single plant genotype or cultivar. In our study, three maize inbred lines (resistant B75 and B96, susceptible B73) were compared to elucidate the performance of mites among lines with varied resistance. Further, our results were consistent with Willmot *et al.*, (2009), where five resistant maize genotypes to European corn borer (*Ostrinia nubilalis* Hubner) remained consistent across eleven different environments. Although we cannot ignore the fact that abiotic stresses involved in different environments did not highlight water-stress independently, it is important to note that maize plants maintained resistance to herbivory across a wide range of conditions. Indeed, evidence exists in other systems such as soybean (*Glycine max* L.), Lucerne (*Medicago sativa* L.) and sweet potato (*Ipomoea batatas* L.), where water-stress had idiosyncratic impacts on plant resistance of different genotypes to herbivores (Grinnan et al., 2013; Johnson et al., 2014; Mao et al., 2004). Overall, abiotic stress interactions with plant resistance to herbivores depend on several factors including plant species and herbivore type.

As per Brewer and Webster (2001), herbivore performance on a plant may depend on a number of factors including plant defenses, feeding strategies of herbivores, plant responses to stress, and the severity and type of stress. Plant physiological responses such as increased leaf temperature resulting from water-stress, and an effect we saw in susceptible (B73) as well as in resistant (B75 and B96) plants, have been previously shown to promote mite performance (Perring et al., 1984). Interestingly, TSM and BGM population growth only increased on susceptible plants (B73) exposed to water-stress as would be predicted. The addition of abiotic stress did not alter the resistant qualities of B75 and B96 toward each mite species. B75 and B96 have higher DIMBOA levels (Barry et al., 1994; Bing et al., 1990), and although DIMBOA levels were not evaluated in our study, they appeared to have a strong effect on TSM performance as population growth was decreased. Despite resistant plants being exposed to water-stress, TSM population growth was not different from optimally irrigated plants, and resistance was maintained. This effect, however, was species-specific given that resistant plants (B75 and B96) did not impact BGM population growth compared to susceptible plants (B73). Instead, BGM populations continued to increase despite plants being resistant or not. Indeed, evidence exists showing that plants may not induce DIMBOA for some herbivores (Pereira et al., 2017; Shavit et al., 2018). For example, DIMBOA and DIMBOA-glucoside in wheat (*Triticum turgidum* ssp. Durum) was induced by *Rhopalosiphum Padi* L. and *Sitobion avenae* Fabricius but not by *Schizaphis graminum* Rondani (Shavit et al., 2018). Given that specialist herbivores can manipulate or suppress plant defenses (Ali and Agrawal, 2012), it is likely that BGM has evolved specialized defense mechanisms to overcome a major class of defense compounds like DIMBOA in maize plants. Considering that several studies might suggest water-stress would decrease resistance (41.4% of studies in Verdugo et al., (2016)), here resistant plants (B75 and B96) exposed to water-stress did not alter the population growth of BGM. While DIMBOA may be a major contributor for host plant resistance in maize, several plant defense responses which are broadly conserved across the plant phylogeny may also be involved in these interactions.

The plant defense proteins (POD, PPO, CHI and TI) evaluated in this study can negatively affect herbivores (Arnaiz et al., 2018; Broadway and Duffey, 1986; Cipollini et al., 2004; English-Loeb et al., 1997; Fürstenberg-Hägg et al., 2013; Thipyapong et al., 2004). CHI, for instance, degrades exoskeleton and peritrophic membrane of herbivores, while TI, a protease inhibitor, disrupts their digestion and amino acid acquisition (Arnaiz et al., 2018; Broadway and Duffey, 1988, 1986; Cipollini et al., 2004; Duffey and Felton, 1991; Duffey and Stout, 1996; Fürstenberg-Hägg et al., 2013). Here, resistant plants (B75 and B96) had elevated CHI and TI activity compared to susceptible plants (B73). In addition to DIMBOA, it appears higher levels of CHI and TI may contribute to maize resistance. Further, resistant (B96) plants induced TI activity in response to herbivory by TSM and BGM beyond initial elevated levels, and the magnitude of increase was higher for TSM. In one experimental setting, resistant plants (B96) also appeared to have lower CHI activity in response to BGM compare to susceptible B73 plants. Previous work on susceptible plants (B73) also demonstrated that TSM and BGM herbivory induced similar transcriptomic levels for genes encoding chitinases and protease inhibitors (Bui et al. 2018). Although they did not assay CHI and TI protein activities directly, however, it appears that resistant plants may have different abilities to respond to TSM versus BGM compared to susceptible plants.

Plant defense responses can amplify with combined stress from mite herbivory and water-stress than by individual respective stresses (Santamaria et al., 2018). In barley (*Hordeum vulgare* L.), up-regulation of defensive genes were reported for combined water-stress and TSM compared to individual stresses alone (Santamaria et al., 2018). Sabzi et al. (2019), found that a combination of water-stress and TSM herbivory in common bean (*Phaseolus vulgaris* L.) induced defensive genes in susceptible as well as resistant genotypes. Plant responses in our study appeared to be most sensitive when combining water-stress and mite herbivory. TI activity, for example, increased when combining water-stress and TSM herbivory for all maize inbred lines at 1 day (in most experimental settings) and at 3 days (in SEASON 2). Interestingly, the elevated TI activities at the 1 day time point were transient and returned to levels observed for all other treatments (resistance, mite and water) after 3 days. Yet, plants exposed to combinations of water-stress and BGM resulted in either decreased TI activity or no change. These unique responses in correspondence with each species were also observed in Gill et al. (2020), where water-stressed maize (B73) plants had elevated CHI and TI defenses when combined with TSM, but the responses were not induced when combined with BGM. Indeed, in *Arabidopsis thaliana*, induction of protease inhibitors, such as TI, by TSM resulted in negative impacts for mite performance (Arnaiz et al., 2018). In our study, however, the induction of TI activity in all maize inbred lines, did not alleviate TSM populations as they still increased on susceptible plants (B73) exposed to water-stress. Similar results were reported by Santamaria et al., (2018), where TSM populations enhanced despite elevated plant defensive responses. As per Leeuwen et al., (2011), the TSM genome shows the expansion of gene families involved in xenobiotic detoxification, which provides a possible explanation for TSMs ability to cope with elevated plant defenses. Indeed, we cannot rule out other possible mechanisms such as increased leaf temperature, and increased leaf proteins that have been previously reported to enhance mite populations (Dworak et al., 2016; Perring et al., 1984b; Rott and Ponsonby, 2000). Interestingly, herbivory by the specialist BGM combined with water-stress either decreased or did not change CHI and TI activities, and the performance of BGM on water-stress plants increased. Ruckert et al., (2018) also reported a decrease in CHI and TI activities when maize plants were exposed to combined water-stress and BGM. This response had also been reported in other systems such as tomato, where herbivory from the specialist mite *Aculops lycopersici* Massee combined with water-stress antagonized tomato defenses and increased plant nutrition to benefit the performance of this mite

(Ximénez-Embún et al., 2017b). This suggests that specialist mites are capable of coping with plant defenses of B75 and B96 plants, and the development of resistant plants to BGM may require further evaluation of effective traits.

POD and PPO, broadly conserved proteins across plant phylogeny, are known to be induced by herbivory, water-stress as well as mechanical wounding (Constabel et al., 2000; English-Loeb et al., 1997; Han et al., 2009; Lee et al., 2007; Liang et al., 2017; Mahanil et al., 2008; Minibayeva et al., 2015; Shoorooei et al., 2013; Suzuki et al., 2012; Thipyapong et al., 2004). In our study, POD and PPO increased in response to herbivory, water stress or combinations of both, albeit sporadically. This variation resulted in these proteins not being evaluated in SEASON 2. Despite the variation, POD and PPO activity appeared to be a general response to stress by water and mite herbivory rather than an obvious pattern for resistance as previously reported by Cao et al., (2015).

Concluding remarks

Previous work that examined maize resistance to spider mites reported that B75 and B96 maize inbred lines were resistant to TSM but not to BGM, and B73 is susceptible to both mite species (Bui et al., *in prep*). In this study, we extended this work to test how water-stress may impact the resistance levels of B75 and B96, as both TSM and BGM outbreaks are known to associate with water-stress. Our results validate the findings of previous studies and showed that B75 and B96 maintained resistance to spider mites in water-stress conditions. We also found that resistant lines, especially B96, had increased levels of defensive proteins (e.g., TI) which further increased with TSM herbivory in particular when combined with water-stress. However, combinations of water-stress with BGM herbivory resulted in either a decrease or no impact on defensive proteins (CHI and TI). Our results suggest that maize resistance varies for generalist and specialist mite herbivores, and that resistant B75 and B96 maize inbred lines that are capable of maintaining resistance under multiple stresses (water-stress and mite herbivory) could provide new maize cultivars suitable for future climatic conditions.

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Table 4-1
Effect of water treatments (optimal irrigation and water-stress) on height, leaf temperature, stomatal conductance and leaf water potential in the greenhouse and field experiments.

Experiment	**Variable**	**Optimal-irrigation (mean ±_SE)**	**Water-stress (mean ± SE)**	**DF**	**F**	***P***
Greenhouse TRIAL 1	Leaf temp (°C)	23.85 ± 0.32	25.17 ± 0.35	1,29	7.33	0.01
	Leaf water potential (bar)	9.12 ± 0.82	12.99 ± 0.88	1,29	8.40	<0.01
	Stomatal conductance (mmolm$_{-2}$S$_{-1}$)	131.95 ± 10.47	72.78 ± 6.38	1,29	24.31	<0.01
	Stem height (cm)	102.02 ± 3.2	84.80 ± 2.42	1,29	14.71	<0.01
Greenhouse TRIAL 2	Leaf temp (°C)	27.80 ± 0.49	29.67 ± 0.54	1,28	3.66	0.06
	Leaf water potential (bar)	8.34 ± 0.35	19.81 ± 0.72	1,28	229.72	<0.01
	Stomatal conductance (mmolm$_{-2}$S$_{-1}$)	259.04 ± 24.09	130.76 ± 11.99	1,28	24.40	<0.01
	Stem height (cm)	96.95 ± 1.56	79.87 ± 1.45	1,28	57.47	<0.01
Field SEASON 1	Leaf temp (°C)	25.07 ± 0.22	25.97 ± 0.27	1,30	4.88	0.03

	Leaf water potential (bar)	3.5 ± 0.24	7.62 ± 0.31	1,30	124.77	<0.01
	Stomatal conductance (mmolm$_{-2}$s$_{-1}$)	424.74 ± 17.72	356.45 ± 15.98	1,30	8.54	<0.01
	Stem height (cm)	78.21 ± 2.85	67.12 ± 1.62	1,30	14.64	<0.01
Field SEASON 2	Leaf temp (°C)	31.88 ± 0.42	33.43 ± 0.36	1,26	4.61	0.04
	Leaf water potential (bar)	5.85 ± 0.41	14.33 ± 0.59	1,23	94.17	<0.01
	Stomatal conductance (mmolm$_{-2}$s$_{-1}$)	419.29 ± 26.89	272.46 ± 21.4	1,26	16.76	<0.01
	Stem height (cm)	69.37 ± 2.84	54.71 ± 3.08	1,26	13.38	<0.01

SE: standard error of the mean; DF: degrees of freedom; T: T value; *P*: p-value

Table 4-2
ANOVA results of the effect of water treatments (optimal irrigation and water-stress) on population growth of mites (TSM and BGM) on B73 and B75 maize inbred lines at time (1, 3 and 7 days post mite introduction) in the greenhouse TRIAL 1.

Effect	**Num DF**	**Den DF**	**F Value**	***P***
Water	1	58	0.09	0.7605
Mite	1	58	90.13	<.0001
Water × Mite	1	58	1.67	0.2015
Resistance	1	58	23.14	<.0001
Water × Resistance	1	58	1.53	0.2205
Mite × Resistance	1	58	28.38	<.0001
Water × Mite × Resistance	1	58	1.26	0.2667
Time	2	104	90.36	<.0001
Water × Time	2	104	0.37	0.6943
Mite × Time	2	104	1.20	0.3057
Water × Mite × Time	2	104	0.30	0.7431
Resistance × Time	2	104	9.94	0.0001
Water × Resistance × Time	2	104	7.92	0.0006
Mite × Resistance × Time	2	104	2.98	0.0552
Water × Mite × Resistance × Time	2	104	2.11	0.1264

DF: degrees of freedom; F: F value; *P*: p-value

Table 4-3
ANOVA results of the effect of water treatments (optimal irrigation and water-stress) and mite (TSM and BGM) herbivory on the activity of B73 and B75 inbred line plant defense proteins at time (1, 3 and 7 days post mite introduction) in the greenhouse TRIAL 1.

	Effect	**Num DF**	**Den DF**	**F Value**	***P***
POD	Water	1	36	3.36	0.0749
	Mite	2	36	1.61	0.2131
	Water × Mite	2	36	0.07	0.9343
	Resistance	1	36	64.29	<.0001
	Water × Resistance	1	36	1.41	0.2429
	Mite × Resistance	2	36	1.12	0.3373
	Water × Mite × Resistance	2	36	7.86	0.0015
	Time	2	70	10.46	0.0001
	Water × Time	2	70	0.13	0.8816
	Mite × Time	4	70	1.86	0.1266
	Water × Mite × Time	4	70	6.62	0.0001
	Resistance × Time	2	70	0.35	0.7056
	Water × Resistance × Time	2	70	2.35	0.1027
	Mite × Resistance × Time	4	70	2.14	0.0850
	Water × Mite × Resistance × Time	4	70	4.03	0.0054
PPO	Water	1	36	0.12	0.7321
	Mite	2	36	13.85	<.0001
	Water × Mite	2	36	21.32	<.0001
	Resistance	1	36	7.90	0.0080
	Water × Resistance	1	36	1.78	0.1906
	Mite × Resistance	2	36	0.30	0.7462
	Water × Mite × Resistance	2	36	12.61	<.0001
	Time	2	72	80.85	<.0001
	Water × Time	2	72	4.65	0.0126
	Mite × Time	4	72	18.73	<.0001
	Water × Mite × Time	4	72	12.28	<.0001
	Resistance × Time	2	72	11.27	<.0001
	Water × Resistance × Time	2	72	8.53	0.0005
	Mite × Resistance × Time	4	72	4.70	0.0020
	Water × Mite × Resistance × Time	4	72	3.40	0.0133
CHI	Water	1	36	13.51	0.0008
	Mite	2	36	8.73	0.0008
	Water × Mite	2	36	2.34	0.1105
	Resistance	1	36	1.10	0.3010
	Water × Resistance	1	36	1.28	0.2650
	Mite × Resistance	2	36	0.77	0.4704

	Water × Mite × Resistance	2	36	8.33	0.0011
	Time	2	72	65.26	<.0001
	Water × Time	2	72	0.83	0.4384
	Mite × Time	4	72	6.78	0.0001
	Water × Mite × Time	4	72	0.33	0.8582
	Resistance × Time	2	72	0.55	0.5795
	Water × Resistance × Time	2	72	2.81	0.0670
	Mite × Resistance × Time	4	72	7.39	<.0001
	Water × Mite × Resistance × Time	4	72	4.08	0.0049
TI	Water	1	36	0.48	0.4948
	Mite	2	36	1.76	0.1863
	Water × Mite	2	36	5.33	0.0094
	Resistance	1	36	21.86	<.0001
	Water × Resistance	1	36	2.62	0.1145
	Mite × Resistance	2	36	0.34	0.7136
	Water × Mite × Resistance	2	36	6.21	0.0048
	Time	2	70	70.81	<.0001
	Water × Time	2	70	3.75	0.0283
	Mite × Time	4	70	12.57	<.0001
	Water × Mite × Time	4	70	6.73	0.0001
	Resistance × Time	2	70	1.30	0.2783
	Water × Resistance × Time	2	70	2.72	0.0729
	Mite × Resistance × Time	4	70	2.04	0.0982
	Water × Mite × Resistance × Time	4	70	2.96	0.0256

DF: degrees of freedom; F: F value; *P*: p-value

Table 4-4
ANOVA results of the effect of water treatments (optimal irrigation and water-stress) on population growth of mites (TSM and BGM) at time (1, 3 and 7 days post mite introduction) on B73 and B96 maize inbred lines in the greenhouse TRIAL 2.

Effect	**Num DF**	**Den DF**	**F Value**	***P***
Water	1	71	0.00	0.9473
Mite	1	71	27.28	<.0001
Water × Mite	1	71	0.44	0.5095
Resistance	1	71	252.60	<.0001
Water × Resistance	1	71	4.66	0.0343
Mite × Resistance	1	71	31.32	<.0001
Water × Mite × Resistance	1	71	0.02	0.8898
Time	2	89	106.80	<.0001
Water × Time	2	89	0.25	0.7759
Mite × Time	2	89	13.22	<.0001
Water × Mite × Time	2	89	0.80	0.4539
Resistance × Time	2	89	5.66	0.0048
Water × Resistance × Time	2	89	4.54	0.0132
Mite × Resistance × Time	2	89	16.59	<.0001
Water × Mite × Resistance × Time	2	89	1.73	0.1833

DF: degrees of freedom; F: F value; *P*: p-value

Table 4-5
ANOVA results of the effect of water treatments (optimal irrigation and water-stress) and mite (TSM and BGM) herbivory on the activity of B73 and B96 plant defense proteins at time (1, 3 and 7 days post mite introduction) in the greenhouse TRIAL 2.

	Effect	**Num DF**	**Den DF**	**F Value**	***P***
POD	Water	1	36	0.06	0.8064
	Mite	2	36	10.29	0.0003
	Water × Mite	2	36	1.90	0.1645
	Resistance	1	36	63.67	<.0001
	Water × Resistance	1	36	4.18	0.0483
	Mite × Resistance	2	36	0.83	0.4423
	Water × Mite × Resistance	2	36	0.54	0.5868
	Time	2	196	30.06	<.0001
	Water × Time	2	196	1.36	0.2601
	Mite × Time	4	196	2.04	0.0901
	Water × Mite × Time	4	196	0.62	0.6469
	Resistance × Time	2	196	0.73	0.4816
	Water × Resistance × Time	2	196	3.41	0.0350
	Mite × Resistance × Time	4	196	2.56	0.0398
	Water × Mite × Resistance × Time	4	196	2.27	0.0630
PPO	Water	1	36	2.19	0.1480
	Mite	2	36	0.99	0.3818
	Water × Mite	2	36	0.50	0.6127
	Resistance	1	36	2.12	0.1541
	Water × Resistance	1	36	2.47	0.1248
	Mite × Resistance	2	36	1.79	0.1821
	Water × Mite × Resistance	2	36	0.89	0.4204
	Time	2	201	4.99	0.0077
	Water × Time	2	201	0.16	0.8516
	Mite × Time	4	201	0.71	0.5846
	Water × Mite × Time	4	201	0.93	0.4476
	Resistance × Time	2	201	1.47	0.2327
	Water × Resistance × Time	2	201	3.64	0.0280
	Mite × Resistance × Time	4	201	1.95	0.1041

	Water × Mite × Resistance × Time	4	201	0.63	0.6451
CHI	Water	1	36	4.64	0.0379
	Mite	2	36	0.55	0.5811
	Water × Mite	2	36	0.87	0.4272
	Resistance	1	36	2.54	0.1196
	Water × Resistance	1	36	2.45	0.1263
	Mite × Resistance	2	36	1.83	0.1746
	Water × Mite × Resistance	2	36	2.96	0.0643
	Time	2	196	6.80	0.0014
	Water × Time	2	196	4.42	0.0133
	Mite × Time	4	196	0.71	0.5871
	Water × Mite × Time	4	196	1.58	0.1817
	Resistance × Time	2	196	5.00	0.0076
	Water × Resistance × Time	2	196	3.06	0.0493
	Mite × Resistance × Time	4	196	4.60	0.0014
	Water × Mite × Resistance × Time	4	196	2.18	0.0731
TI	Water	1	36	1.49	0.2301
	Mite	2	36	4.87	0.0134
	Water × Mite	2	36	1.32	0.2809
	Resistance	1	36	26.23	<.0001
	Water × Resistance	1	36	9.23	0.0044
	Mite × Resistance	2	36	1.07	0.3539
	Water × Mite × Resistance	2	36	5.16	0.0107
	Time	2	201	5.29	0.0058
	Water × Time	2	201	2.06	0.1296
	Mite × Time	4	201	5.01	0.0007
	Water × Mite × Time	4	201	2.52	0.0422
	Resistance × Time	2	201	5.15	0.0066
	Water × Resistance × Time	2	201	2.60	0.0770
	Mite × Resistance × Time	4	201	5.46	0.0003
	Water × Mite × Resistance × Time	4	201	1.37	0.2455

DF: degrees of freedom; F: F value; *P*: p-value

Table 4-6
ANOVA results of the effect of water treatments (optimal irrigation and water-stress) on population growth of mites (TSM and BGM) at time (1, 3 and 7 days post mite introduction) on B73, B75 and B96 maize inbred lines in the field SEASON 1.

Effect	**Num DF**	**Den DF**	**F Value**	***P***
Water	1	35	1.96	0.1708
Mite	1	35	16.67	0.0002
Water × Mite	1	35	2.17	0.1501
Resistance	2	35	31.59	<.0001
Water × Resistance	2	35	0.30	0.7417
Mite × Resistance	2	35	5.02	0.0122
Water × Mite × Resistance	2	35	0.81	0.4511
Time	2	56	38.95	<.0001
Water × Time	2	56	4.74	0.0125
Mite × Time	2	56	4.74	0.0125
Water × Mite × Time	2	56	1.53	0.2249
Resistance × Time	4	56	3.76	0.0089
Water × Resistance × Time	4	56	1.37	0.2545
Mite × Resistance × Time	4	56	3.57	0.0116
Water × Mite × Resistance × Time	4	56	1.49	0.2182

DF: degrees of freedom; F: F value; *P*: p-value

Table 4-7
ANOVA results of the effect of water treatments (optimal irrigation and water-stress) and mite (TSM and BGM) herbivory on the activity of B73, B75 and B96 plant defense proteins at time (1, 3 and 7 days post mite introduction) in the field SEASON 1.

	Effect	**Num DF**	**Den DF**	**F Value**	***P***
POD	Water	1	53	0.16	0.6864
	Mite	2	53	9.27	0.0004
	Water × Mite	2	53	1.70	0.1924
	Resistance	2	53	38.43	<.0001
	Water × Resistance	2	53	1.78	0.1788
	Mite × Resistance	4	53	4.60	0.0029
	Water × Mite × Resistance	4	53	1.32	0.2755
	Time	2	95	48.32	<.0001
	Water × Time	2	95	1.40	0.2512
	Mite × Time	4	95	4.62	0.0019
	Water × Mite × Time	4	95	0.48	0.7478
	Resistance × Time	4	95	0.70	0.5945
	Water × Resistance × Time	4	95	0.59	0.6698
	Mite × Resistance × Time	8	95	3.39	0.0018
	Water × Mite × Resistance × Time	8	95	0.73	0.6684
PPO	Water	1	53	1.32	0.2550
	Mite	2	53	0.74	0.4838
	Water × Mite	2	53	2.21	0.1194
	Resistance	2	53	15.87	<.0001
	Water × Resistance	2	53	0.64	0.5308
	Mite × Resistance	4	53	1.17	0.3365
	Water × Mite × Resistance	4	53	3.41	0.0148
	Time	2	95	10.71	<.0001
	Water × Time	2	95	0.96	0.3861
	Mite × Time	4	95	4.53	0.0022
	Water × Mite × Time	4	95	0.74	0.5646
	Resistance × Time	4	95	2.41	0.0544
	Water × Resistance × Time	4	95	0.56	0.6892
	Mite × Resistance × Time	8	95	1.84	0.0789
	Water × Mite × Resistance × Time	8	95	2.81	0.0077
CHI	Water	1	53	0.02	0.8800
	Mite	2	53	1.86	0.1659
	Water × Mite	2	53	0.60	0.5541
	Resistance	2	53	3.65	0.0327
	Water × Resistance	2	53	0.66	0.5213
	Mite × Resistance	4	53	0.75	0.5597

	Water × Mite × Resistance	4	53	2.42	0.0599
	Time	2	95	3.00	0.0543
	Water × Time	2	95	0.80	0.4532
	Mite × Time	4	95	1.69	0.1584
	Water × Mite × Time	4	95	2.31	0.0634
	Resistance × Time	4	95	1.13	0.3454
	Water × Resistance × Time	4	95	0.43	0.7895
	Mite × Resistance × Time	8	95	0.67	0.7183
	Water × Mite × Resistance × Time	8	95	0.73	0.6650
TI	Water	1	53	0.31	0.5797
	Mite	2	53	1.93	0.1549
	Water × Mite	2	53	4.49	0.0158
	Resistance	2	53	51.37	<.0001
	Water × Resistance	2	53	5.31	0.0079
	Resistance × Mite	4	53	1.26	0.2961
	Water × Resistance × Mite	4	53	3.44	0.0143
	Time	2	95	11.22	<.0001
	Water × Time	2	95	7.04	0.0014
	Mite × Time	4	95	1.73	0.1493
	Water × Mite × Time	4	95	4.17	0.0037
	Resistance × Time	4	95	12.47	<.0001
	Water × Resistance × Time	4	95	1.73	0.1494
	Resistance × Mite × Time	8	95	1.29	0.2578
	Water × Resistance × Mite × Time	8	95	0.35	0.9415

DF: degrees of freedom; F: F value; *P*: p-value

Table 4-8
ANOVA results of the effect of water treatments (optimal irrigation and water-stress) on population growth of mites (TSM) at time (1, 3 and 7 days post mite introduction) on B73, B75 and B96 maize inbred lines in the field SEASON 2.

Effect	**Num DF**	**Den DF**	**F Value**	***P***
Water	1	24	3.84	0.0616
Resistance	2	24	26.08	<.0001
Water × Resistance	2	24	0.19	0.8285
Time	2	129	30.21	<.0001
Water × Time	2	129	2.51	0.0850
Resistance × Time	4	129	11.69	<.0001
Water × Resistance × Time	4	129	2.39	0.0539

DF: degrees of freedom; F: F value; *P*: p-value

Table 4-9
ANOVA results of the effect of water treatments (optimal irrigation and water-stress) and mite (TSM) herbivory on the activity of B73, B75 and B96 plant defense proteins at time (1, 3 and 7 days post mite introduction) in the field SEASON 2.

	Effect	**Num DF**	**Den DF**	**F Value**	***P***
CHI	Mite	1	50	2.02	0.1610
	Water × Mite	1	50	0.00	0.9564
	Resistance	2	50	3.30	0.0451
	Water × Resistance	2	50	0.46	0.6355
	Mite × Resistance	2	50	0.79	0.4603
	Water × Mite × Resistance	2	50	0.22	0.8040
	Time	2	90	8.08	0.0006
	Water × Time	2	90	0.63	0.5344
	Mite × Time	2	90	4.22	0.0177
	Water × Mite × Time	2	90	0.46	0.6348
	Resistance × Time	4	90	1.21	0.3116
	Water × Resistance × Time	4	90	0.20	0.9359
	Mite × Resistance × Time	4	90	0.34	0.8535
	Water × Mite × Resistance × Time	4	90	1.10	0.3634
TI	Water	1	50	1.50	0.2263
	Mite	1	50	0.06	0.8008
	Water × Mite	1	50	2.00	0.1632
	Resistance	2	50	16.21	<.0001
	Water × Resistance	2	50	0.04	0.9631
	Mite × Resistance	2	50	0.60	0.5553
	Water × Mite × Resistance	2	50	1.14	0.3293
	Time	2	89	0.54	0.5836
	Water × Time	2	89	0.33	0.7169
	Mite × Time	2	89	6.44	0.0024
	Water × Mite × Time	2	89	0.17	0.8477
	Resistance × Time	4	89	1.30	0.2760
	Water × Resistance × Time	4	89	1.02	0.3994
	Mite × Resistance × Time	4	89	0.82	0.5176
	Water × Mite × Resistance × Time	4	89	0.12	0.9738

DF: degrees of freedom; F: F value; *P*: p-value

Fig. 4-1. Volumetric soil water content for water treatments in the greenhouse and the field experiments. The solid line represents optimal irrigation and the dashed line represents water-stress conditions.

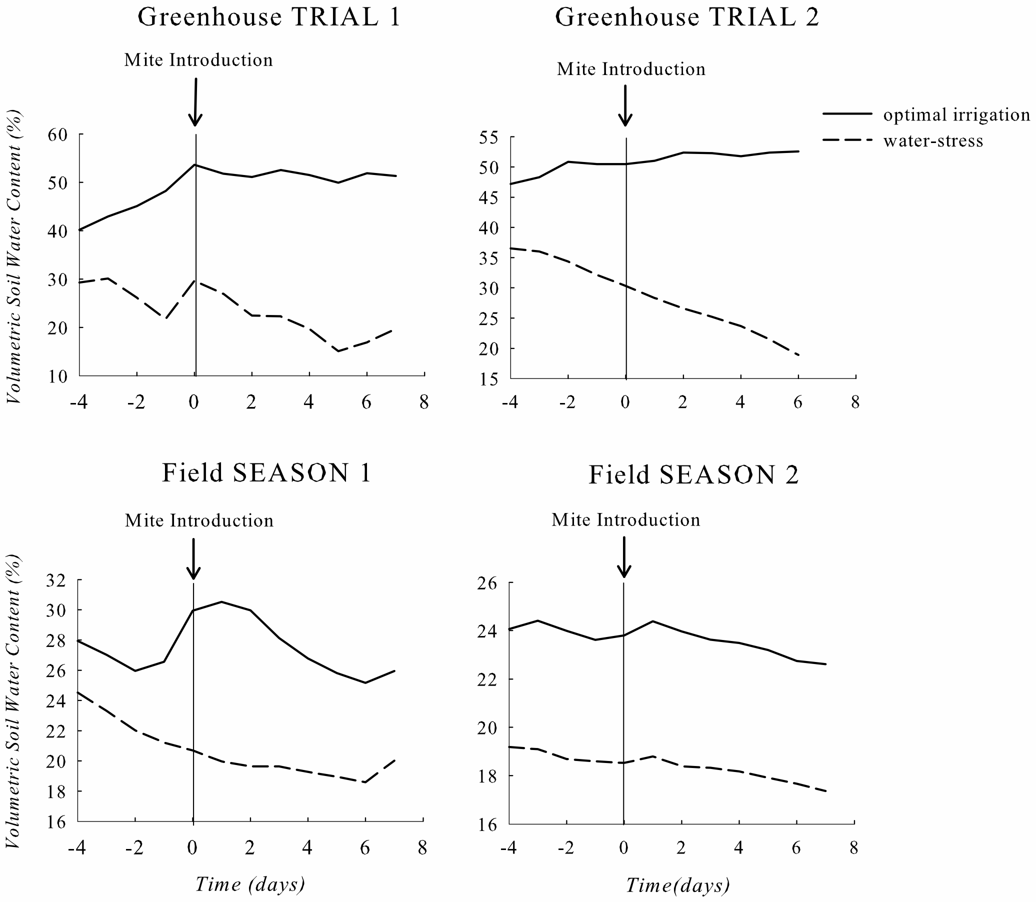


Fig. 4-2. Effect of water treatments (optimal irrigation and water-stress) on population growth of mites (TSM and BGM) on B73 and B75 maize inbred lines at time (1, 3 and 7 days post mite introduction) in the greenhouse TRIAL 1 (upper two panels) and TRIAL 2 (lower two panels).

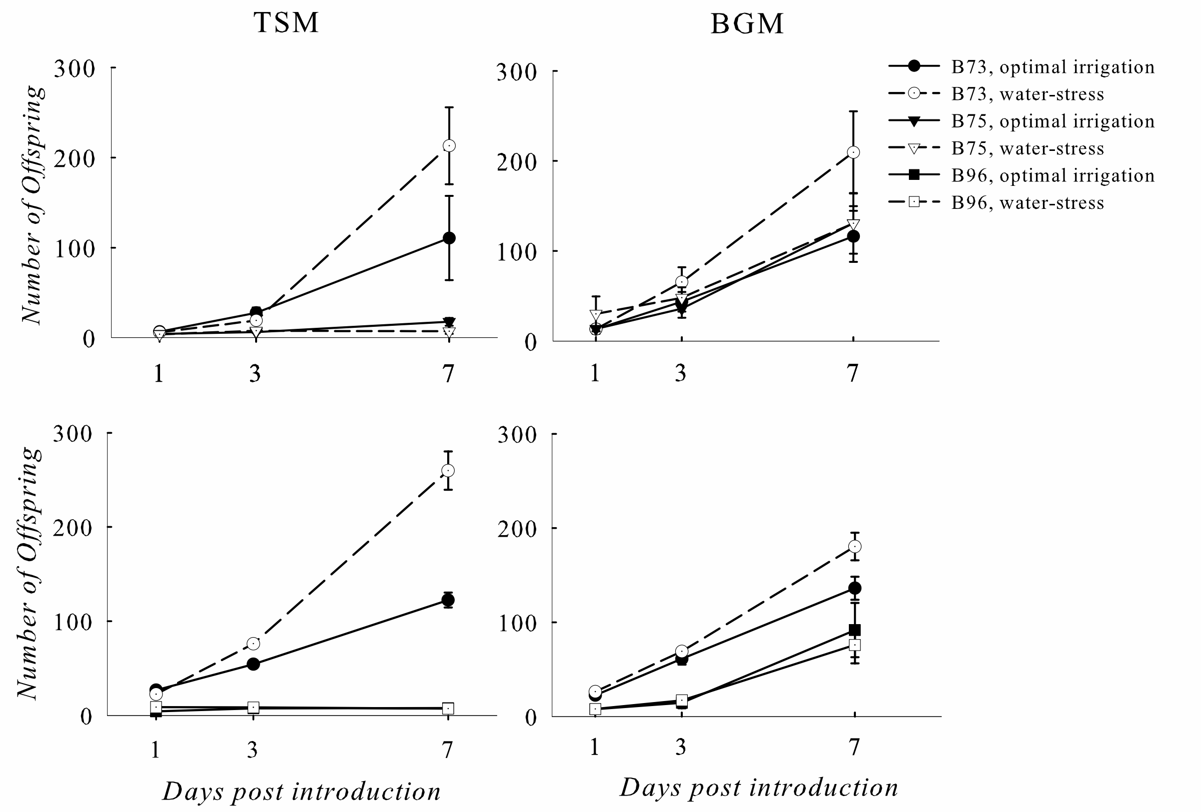


Fig. 4-3. Effect of water treatments (optimal irrigation and water-stress) and mite (TSM and BGM) herbivory on the activity of B73 and B75 plant defense proteins at time (1, 3 and 7 days post mite introduction) in the greenhouse TRIAL 1.

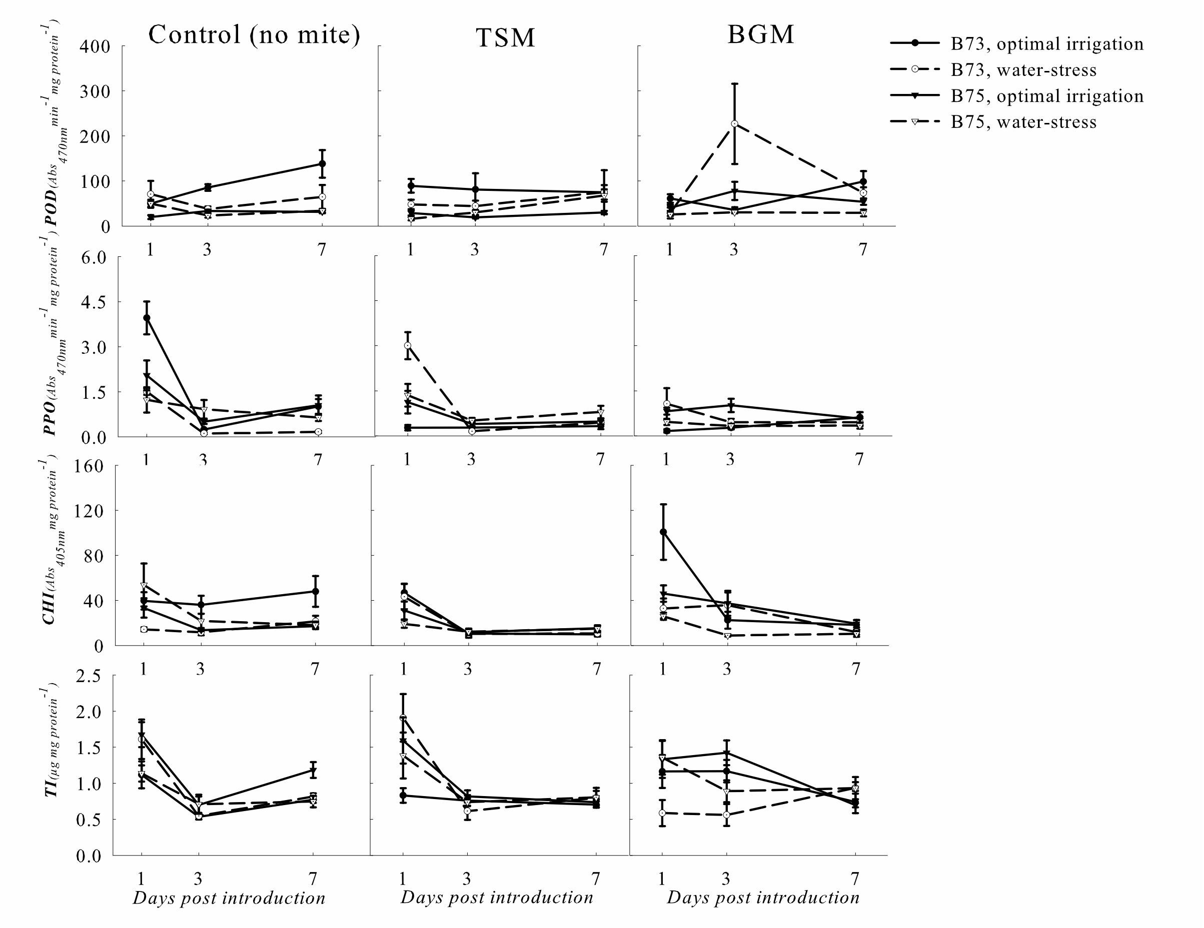


Fig. 4-4. Effect of water treatments (optimal irrigation and water-stress) and mite (TSM and BGM) herbivory on the activity of B73 and B96 plant defense proteins at time (1, 3 and 7 days post mite introduction) in the greenhouse TRIAL 2.

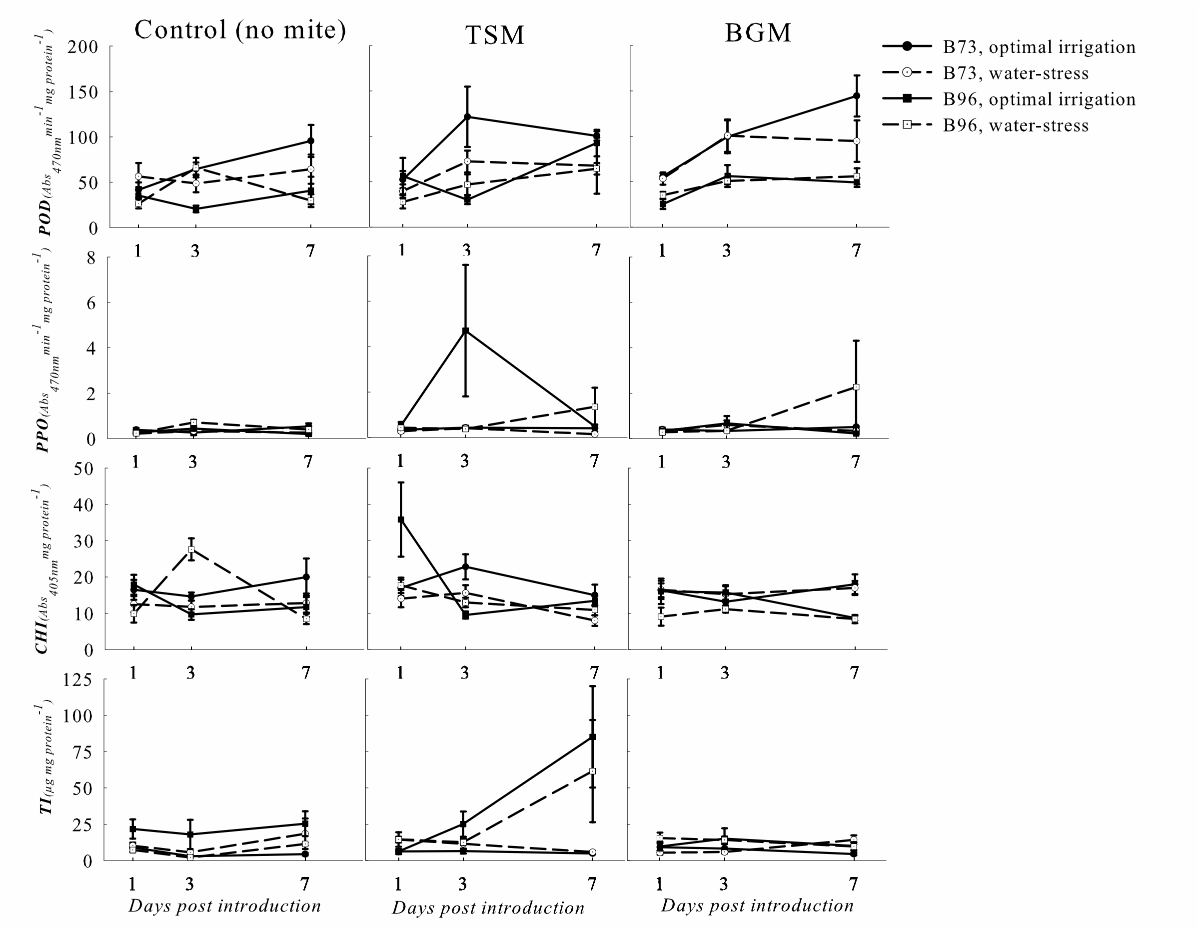


Fig. 4-5. Effect of water treatments (optimal irrigation and water-stress) on population growth of mites (TSM and BGM) on B73, B75 and B96 maize inbred lines at time (1, 3 and 7 days post mite introduction) in the field SEASON 1 (upper two panels) and SEASON 2 (lower panel).

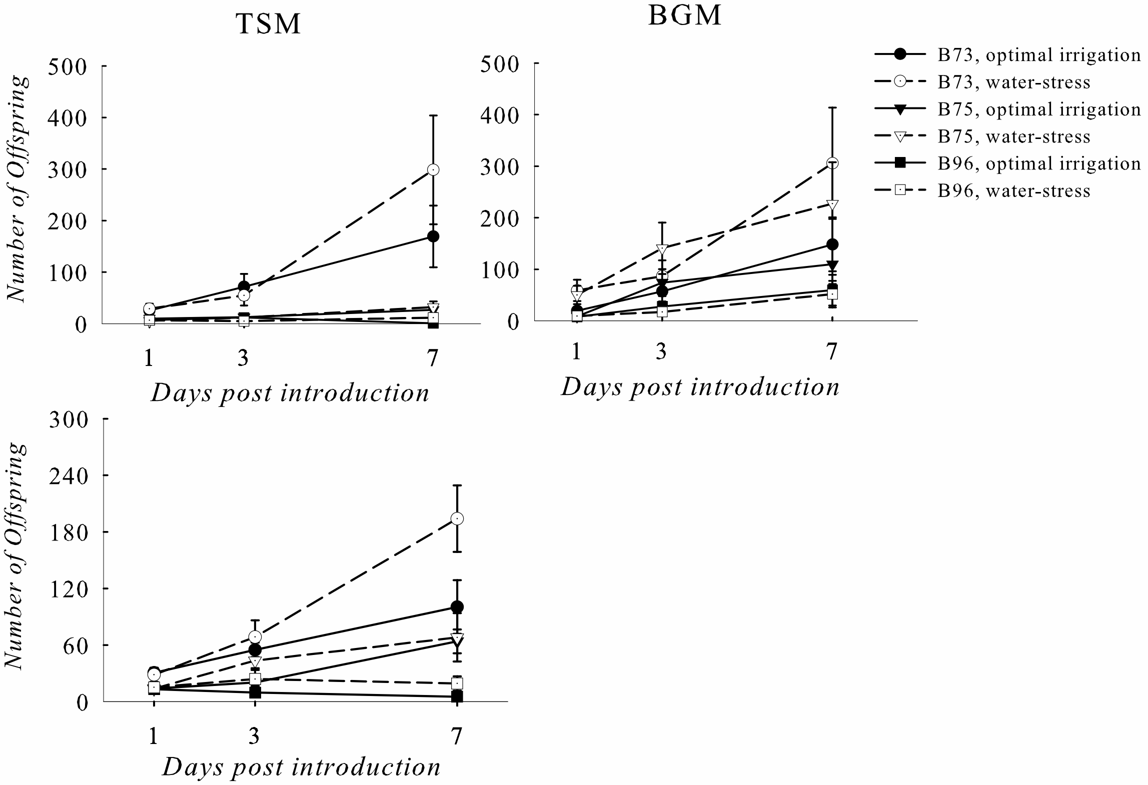


Fig. 4-6. Effect of water treatments (optimal irrigation and water-stress) and mite (TSM and BGM) herbivory on the activity of B73, B75 and B96 plant defense proteins at time (1, 3 and 7 days post mite introduction) in the field SEASON 1.

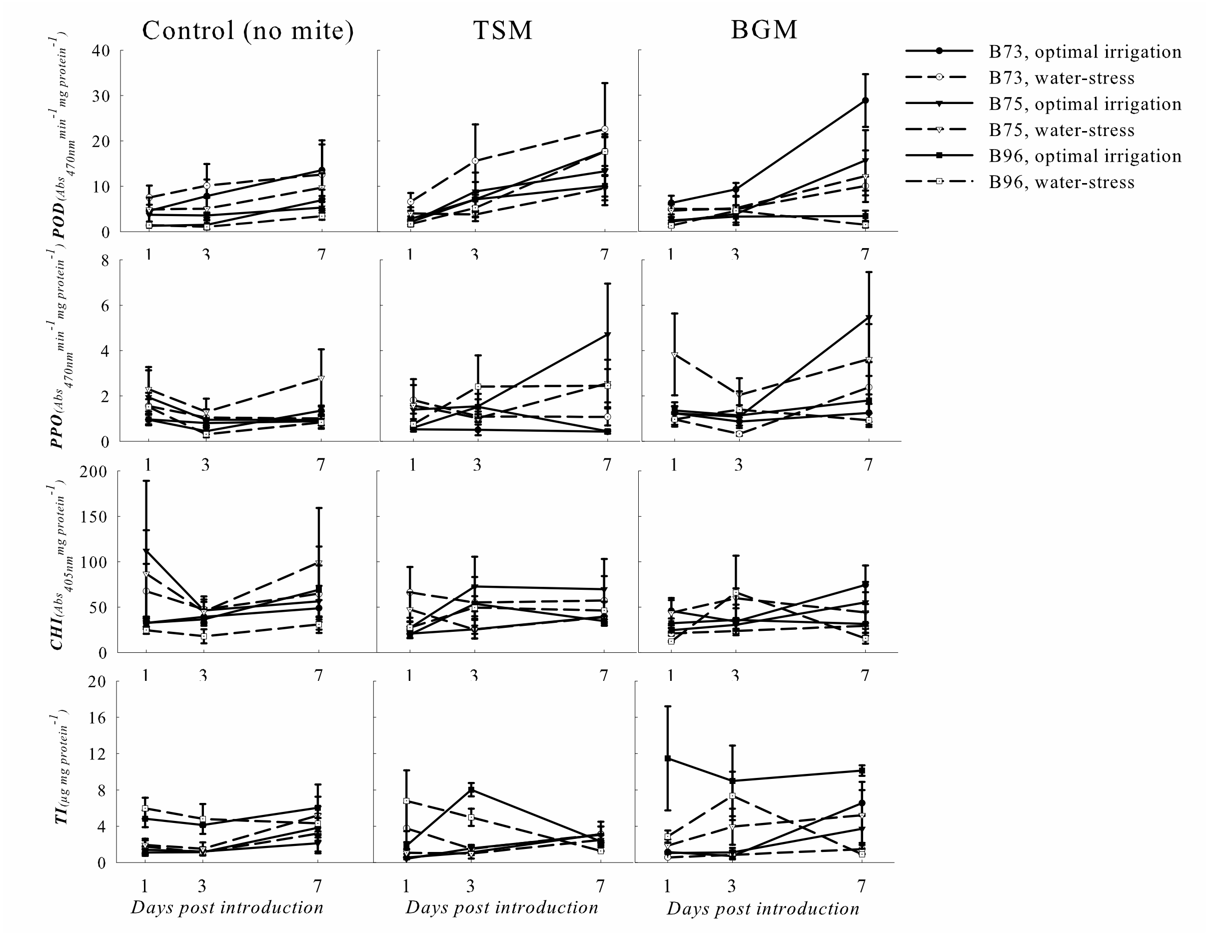
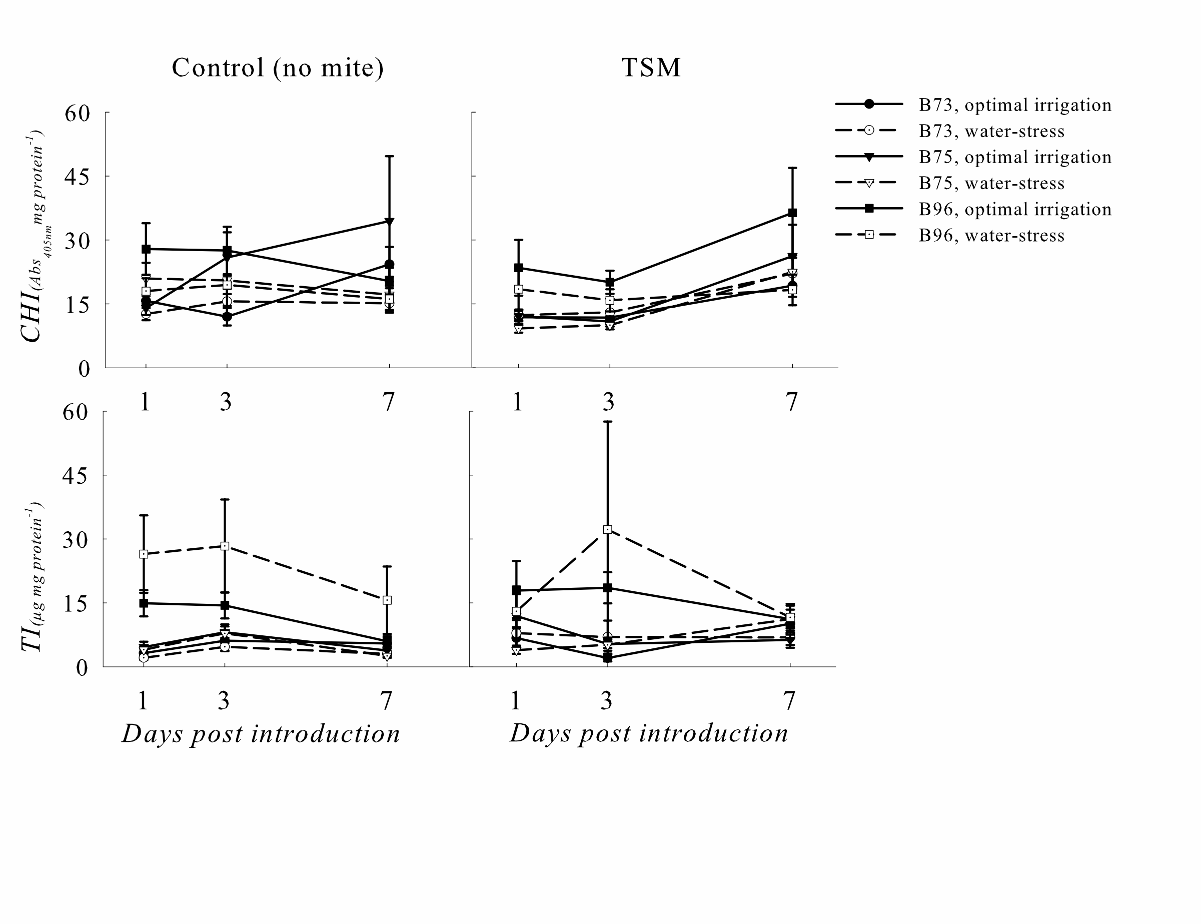


Fig. 4-7. Effect of water treatments (optimal irrigation and water-stress) and mite (TSM and BGM) herbivory on the activity of B73, B75 and B96 plant defense proteins at time (1, 3 and 7 days post mite introduction) in the field SEASON 2.



General summary

Extreme fluctuations in temperature and rainfall due to climate change is predicted to increase the frequency and severity of abiotic (e.g., water-stress) and biotic (e.g., herbivory) stresses which could have major implications on global agricultural production. While abiotic stresses such as water-stress can reduce crop yields by harming plant growth and development, it can also promote outbreaks of herbivorous pests including spider mites, leading to additional yield losses. Maize resistance to spider mites could serve as a possible management tool to mitigate population outbreaks; however, maize resistance can vary for diverse herbivores, and our understanding of interactions between water-stress and maize resistance to spider mites is limited.

In my first study, I investigated how water-stress in a maize inbred line (B73) affected the population of two spider mite species (TSM and BGM) and resulting plant herbivore-related defenses. I found that water-stressed B73 plants increased populations of TSM and BGM. Also, combined water-stress and TSM herbivory increased the activity of defensive proteins such as chitinase (CHI) and trypsin inhibitor (TI). However, a combination of water-stress and BGM appeared to not affect plant defensive proteins.

In my second study, I evaluated the behaviors of TSM and BGM on three maize inbred lines (a susceptible line B73, and two resistant lines B75 and B96) that were previously shown to vary for spider mite resistance. I found that TSM was more sensitive to maize resistance compared to BGM. Specifically, I found that maize resistance decreased feeding and oviposition and increased probing, walking, travel distance, web-building, and resting. Contrastingly, except for increased walking and travel distance and decreased feeding in BGM, other behaviors such as probing, web-building, resting, and oviposition were not impacted by maize resistance.

In my third study, I tested whether water-stress impacted maize resistance to spider mites by evaluating the same three maize inbred lines in the previously described study (a susceptible line B73, and two resistant lines B75 and B96). I found that maize resistance varied for TSM and BGM, in particular that BGM was not affected by resistant lines. Further, B75 and B96 maize inbred lines maintained their resistance levels in water-stressed conditions.

Conclusions

The data collected in this study represents an important step in the understanding of interactions between water-stress and maize resistance to spider mites. My research is innovative because first, it examined the combined effect of abiotic and biotic stresses and second because I considered both generalist and specialist herbivory. Studies have often focused on either abiotic or biotic stress based on either generalist or specialist herbivory.

From my work, it was clear that water-stress in plants led to spider mite outbreaks and growers should plan their management accordingly. For instance, commercially available drought tolerant hybrids are available and may help alleviate the issues related to abiotc stress, such as water stress. However, while this has not been evaluated in corn, in other systems, drought resistant plant hybrids have alleviated pest pressure. Continuous monitoring of plants every 10 days, and when plants are near tasselling, monitoring every 2-3 days is very important to implement control measure actions. My research also reported that maize resistance to spider mite exists; however, it is limited to some spider mite species (only generalist TSM). Therefore, further work is needed to evaluate broad-range resistance to multiple mite species (e.g., specialist pests like BGM). Nevertheless, the resistant plants (B75 and B96 maize inbred lines) that were screened maintained spider mite resistance under water-stress conditions, and therefore, could provide new cultivars suited for spider mite management in changing climatic conditions. Overall, my research provides a strong contribution to the study of interactions of abiotic stress (water-stress) with maize resistance to arthropods. Furthermore, my research offers information for screening resistance and sustainable spider mite management in maize.

APPENDICES

APPENDIX A

AUTHORSHIP AND CITATION OF PUBLISHED CHAPTERS

Chapter II:

This is a pre-copyedited, author-produced version of an article published in the *Journal of Environmental and Experimental Botany* following peer review. The version of record **Gill, G.S., Bui, H., Clark, R.M., Ramirez, R.A., 2020**. Varying responses to combined water-stress and herbivory in maize for spider mite species that differ in host specialization. Environmental and Experimental Botany 177, 104131. is available online at: https://doi.org/10.1016/j.envexpbot.2020.104131.

APPENDIX B

LETTERS OF PERMISION

MONTANA
STATE UNIVERSITY
NORM ASBJORNSON
College of
ENGINEERING

June 22, 2020

To Whom It May Concern:

I, Huyen Bui, hereby grant my permission for use of the chapter “Varying responses to combined water-stress and herbivory in maize for spider mite species that differ in host specialization", of which I am a coauthor, in the dissertation of Gunbharpur S. Gill.

Sincerely,

Huyen Bui
Research Scientist
Center for Biofilm Engineering
Montana State University
Bozeman, Montana
huyen.bui@montana.edu

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366 Barnard Hall
P.O. Box 173980
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Mountains & Minds

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257 South 1400 East, Rm 201 Salt Lake City, Utah 84112-0840
Phone (801) 581-6517 Fax (801) 581-4668 www.biology.utah.edu

June 22, 2020

To Whom It May Concern:

I, Richard M. Clark, hereby grant my permission for use of the chapter “Varying responses to combined water-stress and herbivory in maize for spider mite species that differ in host specialization", of which I am a coauthor, in the dissertation of Gunbharpur S. Gill.

Sincerely,

Richard M. Clark
Professor
School of Biological Sciences
University of Utah
Salt Lake City, Utah
(801) 585-9722; richard.m.clark@utah.edu

CURRICULUM VITAE

Gunbharpur S. Gill

EDUCATION

2020 **Ph.D. Entomology, Utah State University (USU)**, Logan, UT
Dissertation: Interactions between water-stress and maize resistance to spider mites with varied host specialization.
Committee: Dr. Ricardo Ramirez (academic advisor), Dr. Diane Alston, Dr. Noelle Beckman, Dr. Neil Allen, Dr. Juan Villalba

2016 **M.S. Integrative Genomics, Black Hills State University (BHSU)**, Spearfish, SD
Thesis: Effect of drought on herbivore-induced plant gene expression: Population comparison for range limit inferences. https://www.mdpi.com/2223-7747/5/1/13
Committee: Dr. David Siemens (academic advisor), Dr. Cynthia Anderson, Dr. Justin Ramsey

2014 **B.S. Agriculture (Honors), Punjab Agricultural University (PAU)**, PB, India
Specialization: Crop protection (Entomology and plant pathology)

PUBLICATIONS

Scientific Journals (Refereed and peer-reviewed)

2020 **Gill, G*.**, Bui, H., Clark, R., Ramirez, R. Varying responses to combined water-stress and herbivory in maize for spider mite species that differ in host specialization. *Environmental and Experimental Botany* [Impact Factor: 3.7, CiteScore: 4.45] **Corresponding Author*
https://doi.org/10.1016/j.envexpbot.2020.104131

2019 Olsen, J., **Gill G.**, Haugen R., Matzner S., Alsdurf J., Siemens D. Evolutionary constraint on low elevation range expansion: Defense abiotic stress tolerance trade-off in crosses of the ecological model *Boechera stricta*. *Ecology and Evolution* [Impact Factor: 2.34, CiteScore: 2.67]
https://doi.org/10.1002/ece3.5499

2018 Bui, H., Greenhalgh, R., Ruckert, A., **Gill, G.**, Lee, S., Ramirez, R., Clark, R. Generalist and specialist mite herbivores induce similar defense responses in maize and barley but differ in susceptibility to benzoxazinoids. *Frontiers in Plant Science* [Impact Factor: 4.29, CiteScore: 4.47]
https://www.frontiersin.org/articles/400569

2016 **Gill, G.**, Haugen, R., Matzner, S., Barakat, A., Siemens, D. Effect of drought on herbivore-induced plant gene expression: population comparison for range limit inferences. *Plants* [Impact Factor: 2.63, CiteScore: 4.06]
https://www.mdpi.com/2223-7747/5/1/13

Book Chapters

2016 **Gill, G.**, Haugen, R., Larson, J., Olsen, J., Siemens, D. Plant evolution in response to abiotic and biotic stressors at "rear-edge" range boundaries. *Abiotic and Biotic Stress in Plants - Recent Advances and Future Perspectives* https://doi.org/10.5772/61976

In pipeline

- **Gill, G.**, Lu, H., Price, S., Bui, H., Clark, R., Ramirez, R. Behavioral responses of a generalist and specialist spider mite to maize with varied host plant resistance. *Animal Behavior* [Impact Factor: 2.67, CiteScore: 2.73]
- **Gill, G.**, Bui, H., Clark, R., Ramirez, R. Maize resistance to spider mites is not disrupted with water-stress. *Environmental and Experimental Botany* [Impact Factor: 3.7, CiteScore: 4.45]
- **Gill, G.**, Bui, H., Clark, R., Ramirez, R. Interactions between water-stress and maize resistance to spider mites with varied host specialization. *New Phytologist* [Impact Factor: 7.43, CiteScore: 11.24]

PROFESSIONAL EXPERIENCE

Department of Biology, Utah State University, Logan, UT
Jun 2016-May 2020 ***Graduate Research Assistant***

- Hired, trained, and supervised the 13 undergrad research technicians (part-time and full-time)
- Led student teams to achieve research project objectives in the laboratory, greenhouse, and field settings
- Maintained maize (*Zea mays*) plants and spider mite (TSM and BGM) colonies
- Conducted plant defensive protein assays; polyphenol oxidase (PPO), peroxidase (POD), chitinase (CHI), trypsin inhibitor (TI) and total protein concentration
- Plant and soil measurements; leaf temperature, plant height, stomatal conductance, leaf water potential, and volumetric soil water content
- Data analysis utilizing SAS, R, and Microsoft Excel

Collaborative Research Projects:

1) **Evaluate the basis of maize responses to twospotted spider mite (TSM, *Tetranichus urticae*) and the Banks grass mite (BGM, *Oligonychus pratensis*) in the greenhouse settings**
Collaborators: Dr. Huyen Bui (Montana State University (MSU), Bozeman, MT), Robert Greenhalgh (University of Utah (U of U), Salt Lake City, UT), Dr. Alice Axtell (Scotts Miracle-Gro, Marysville, OH), Sarah Lee (U of U, Salt Lake City, UT), Dr. Ricardo Ramirez (USU, Logan, UT) and Dr. Richard Clark (U of U, Salt Lake City, UT).
Progress to date: Project completed and published.
https://www.frontiersin.org/articles/400569

2) **Examine the effect of water-stress on population growth of TSM and BGM, and on plant defense responses to conspecifics**
Collaborators: Dr. Huyen Bui (MSU, Bozeman, MT), Dr. Ricardo Ramirez (USU, Logan, UT) and Dr. Richard Clark (U of U, Salt Lake City, UT).
Progress to date: Project completed and published.
https://doi.org/10.1016/j.envexpbot.2020.104131T

3) **Screen 30 maize inbred lines for resistance to TSM and BGM, and evaluate the impacts of water-stress on the resistance of selected maize inbred lines**
   Collaborators: Dr. Huyen Bui (MSU, Bozeman, MT), Dr. Ricardo Ramirez (USU, Logan, UT) and Dr. Richard Clark (U of U, Salt Lake City, UT).
   Progress to date: Project completed, and the publication is in pipeline.

4) **Investigate the behavioral changes of TSM and BGM on resistant and susceptible maize inbred lines using video tracking software**
   Collaborators: Hsuan Lu (National Chung Hsing University, Taiwan), Steven Price (USU Carbon County Extension, UT), Dr. Huyen Bui (MSU, Bozeman, MT), Dr. Ricardo Ramirez (USU, Logan, UT) and Dr. Richard Clark (U of U, Salt Lake City, UT).
   Progress to date: Project completed and publication is in pipeline.

School of Natural Sciences, Black Hills State University, Spearfish, SD
Aug 2014-May 2016
Graduate Research Assistant

- Maintained *Boechera stricta* plants and reared beet armyworm (*Spodoptera exigua*) on artificial diet in the lab
- Performed DNA extraction and RNAseq analysis
- Measured plant phenotypic responses; rosette width, betacyanin content, carbon isotope ratio and glucosinolates concentration
- Data analysis utilizing bioinformatics tools, SYSTAT, and Microsoft Excel

Collaborative Research Project:

1) **Evaluate the effect of water-stress on herbivore (*Spodoptera exigua*) induced plant (*Boechera stricta*) gene expression, and gene expression analysis by using RNAseq technique**
   Collaborators: Dr. David Siemens (BHSU, Spearfish, SD), Dr. Steven Matzner (Augustana University, Sioux Falls, SD), Dr. Abdelali Barakat (University of South Dakota, Vermillion, SD), Riston Haugen (BHSU, Spearfish, SD) and Jason Olsen (BHSU, Spearfish, SD).
   Progress to date: Project completed and produced three publications.
   https://www.mdpi.com/2223-7747/5/1/13, https://doi.org/10.5772/61976, https://doi.org/10.1002/ece3.5499

Graduate Teaching Assistant

Courses: BIOL 101 and BIOL 103

- Delivered lectures on cells, photosynthesis, cell respiration, mitosis and meiosis, genetic diversity and evolution, plant diversity, population biology, ecology and plant morphology
- Guided students in the use of microscopy, laboratory safety, and scientific methods
- Demonstrated DNA extraction from living cells and taught its use in paternity testing
- Collaborated on curriculum and examination development with the supervisor to improve the teaching process

- Graded all written work, weekly quizzes, final exam papers and discussed the graded quizzes with the students for their better understanding of concepts

Department of Entomology, Punjab Agricultural University, PB, India
Jun 2010-Jun 2014
Researcher

- Monitored field crops at the regular intervals for the pest and utilized IPM techniques
- Identification of insects and damage symptoms on the field and horticultural crops
- Prepared and applied *Trichogramma* (endoparasitoid) cards for bio-control of rice stem borer (*Chilo suppressalis*) in the field settings
- Reared cotton bollworm (*Helicoverpa armigera*) and beet armyworm on artificial diet in the lab
- Isolation of DNA from whitefly (*Bemisia tabaci*), PCR analysis, and tissue culture
- Cultivated pigeon pea (*Cajanus cajan*), toria (*Brassica* spp.) and wheat (*Triticum aestivum*) crops in the field during Practical Crop Production (PCP) training (Grade 93/100)
- Demonstrated the use of Tensiometer to the farmers at farmer's festival, PAU, India
- Collaborated with various extension organizations engaged in the dissemination of newer technologies from the research labs to the farmers' fields during the Rural Agriculture Work Experience (RAWE)

RESEARCH PRESENTATIONS

2019 **Gill, G.**, Lu, H., Price, S., Bui, H., Clark, R., Ramirez, R. Generalist spider mites behave on resistant maize while specialists do not, talk, **Entomological Society of America (ESA)**, MO

2019 **Gill, G.**, Bui, H., Clark, R., Ramirez, R. Understanding how water-stress affects spider mite resistance in maize, talk, **Pacific Branch ESA**, CA

2018 **Gill, G.**, Bui, H., Clark, R., Ramirez, R. Understanding how water-stress affects spider mite resistance in maize, talk, Joint Annual Meeting with ESA, **Entomological Society of Canada and Entomological Society of British Columbia meeting**, BC, Canada

2018 **Gill, G.**, Bui, H., Clark, R., Ramirez, R. Effects of water-stress on plant defense responses toward twospotted spider mite in maize, talk, **Pacific Branch ESA**, NV

2017 **Gill, G.**, Bui, H., Clark, R., Ramirez, R. Effects of water-stress on plant defense responses toward twospotted spider mite in maize, talk, **ESA**, CO

2017 **Gill, G.**, Ruckert, A., Bui, H., Clark, R., Ramirez, R. Plant defense responses to generalist and specialist spider mites in maize, poster, **Pacific Branch ESA**, OR

2017 Bui, H., Greenhalgh, R., Ruckert, A., Lee, S., **Gill, G.**, Ramirez, R., Clark, R. Differential impact of benzoxazinoids on generalist and grass-specialist spider mite herbivores, poster by Bui, H., **Gordon Research Conference on Plant-Herbivore Interactions (GRC PHI)**, CA

2016 **Gill, G.**, Haugen, R., Matzner, S., Barakat, A., and Siemens, D. Effect of drought on herbivore-induced plant gene expression: population comparison for range limit inferences, talk, **Annual Research Symposium**, BHSU, SD

2016 **Gill, G.**, Haugen, R., Matzner, S., Barakat, A., and Siemens, D. Effect of drought on herbivore-induced plant gene expression: population comparison for range limit inferences, talk, **American Society of Plant Biologists**, SD

2016 **Gill, G.**, Haugen, R., Matzner, S., Barakat, A., Siemens, D. Effect of drought on herbivore-induced plant gene expression: population comparison for range limit inferences, poster, **Annual Research Symposium**, BHSU, SD

2016 **Gill, G.**, Haugen, R., Matzner, S., Barakat, A., Siemens, D. Effect of drought on herbivore-induced plant gene expression: population comparison for range limit inferences, poster, **American Society of Plant Biologists (ASPB)**, SD

2016 **Gill, G.**, Haugen, R., Matzner, S., Barakat, A., Siemens, D. Effect of drought on herbivore-induced plant gene expression: Population comparison for range limit inferences. poster, **Ecological Genomics Symposium**, KS

2015 **Gill, G.**, Siemens, D. Chemical defense response to drought and herbivory: Relevance to plant range limits, talk, **Annual Research Symposium**, BHSU, SD

2014 **Gill, G.**, Haugen, R., Siemens, D. Chemical defense response to drought and herbivory: Relevance to plant range limits, poster, **Ecological Genomics Symposium**, MO

EXTENSION PRESENTATIONS

2019 **Gill, G.**, Spider mite management in corn, talk, **Utah Association of County Agricultural Agent summer meeting**, Salt Lake County, UT

2019 **Gill, G.**, Spider mite management, talk, **Box Elder County Crop Management School**, UT

2017 **Gill, G.**, Identification, life cycle and management of the twospotted spider mite (*Tetranychus urticae*) and the banks grass mite (*Oligonychus pratensis*), talk, **Hay Symposium**, UT

MEDIA

2019 Aggie Impact: Defending Utah's Crops. https://www.youtube.com/watch?v=SBMGcsG1gC4&feature=share