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Investigating Plant Tolerance for the Management of Insect Pests in Rice

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INVESTIGATING PLANT TOLERANCE FOR THE MANAGEMENT OF INSECT PESTS IN RICE

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Entomology

by

James Michael Villegas
B.S., Ateneo de Manila University, 2012
M.S., Louisiana State University, 2017
December 2021

To my wife, Merry

My son, Leon

My daughter, Elisabeth

My mom, Julie

My brothers Jaime and Jaimar

My sisters Dem and Queencel

My dad and grandmother in heaven

This dissertation is dedicated to y'all.

Acknowledgments

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Abstract

The rice water weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), is the most destructive and widespread insect pest of rice (*Oryza sativa* L., Poaceae) in the USA. This insect poses a global threat to rice production, having invaded rice-producing regions of Asia and Europe. Moreover, lepidopteran stemborers, particularly the invasive Mexican rice borer, *Eoreuma loftini* (Dyar) (Lepidoptera: Crambidae), are increasingly becoming problematic in Louisiana rice. Although insecticidal seed treatments have been widely used against weevils and stemborers, alternative management strategies are needed. Plants possess defense-related traits that both reduce injury from herbivores (resistance) and the amount of yield loss per unit injury (tolerance). Tolerance is a type of plant resistance that allows crop plants to maintain yield in spite of injury by herbivores. Both plant resistance and tolerance can be utilized and integrated into pest management programs. Several experiments were conducted from 2016–2020 to (i) examine the susceptibility of rice cultivars to rice water weevil and stemborers and the corresponding impact of these insect pests on yields, (ii) investigate effects of cultural strategies and host plant resistance on weevil and stemborer infestations, and (iii) elucidate effects of chronic feeding by weevil larvae on rice plants. Results from the experiments in this study have shown that the rice cultivar ‘Jupiter’ consistently supported the highest numbers of immature weevils compared to other rice cultivars. Low levels of stemborer injury were observed in ‘Cheniere’ and ‘Jazzman-2’, which suggests that these cultivars express some levels of resistance to stemborers. Plant tolerance was assessed by evaluating differences in yields between insecticide-protected and unprotected plots. Weevil and stemborer infestations negatively affected rice yields, with losses among cultivars ranging from 4–49%. Comparisons of yields between insecticide-protected and unprotected plots indicated that hybrid cultivars exhibited

higher tolerance to rice water weevil infestations than inbred cultivars. Delaying permanent flood application by two weeks reduced weevil densities and stemborer injury. Yield losses were also generally lower in plots subjected to delayed flood compared to normal flood timing. Our data suggest that the combination of cultivar resistance/tolerance and cultural tactics (e.g., delayed flooding) can serve as a valuable component of an integrated pest management program for both rice water weevil and stemborers. Furthermore, results from the experiments conducted in this study demonstrated that feeding by rice water weevil reduced plant growth, yields, and plant nutrient uptake. Rice cultivars expressing tolerance could be used to reduce crop damage in situations where the use of insecticides is not practical, too expensive, or only partially effective.

Chapter 1. Introduction and Literature Review

1.1. Rice Production

Rice (*Oryza sativa* L) is one of the most important crops worldwide and a staple for nearly half of the world's seven billion people (Mohanty, 2013). Rice is a member of the Poaceae family, one of the most important plant families providing vital foods from cereal crops including maize, wheat, barley, and millet. The life cycle of rice plants starts with seed germination and ends with grain formation. During that period, the growth and development of rice plants can be divided into two distinct phases: vegetative and reproductive (Dunand and Saichuk, 2014). Both vegetative and reproductive phases are further subdivided into groups of growth stages. The vegetative growth stage starts with seed emergence and progresses through seedling development, tillering, and internode elongation, while the reproductive growth stage comprises pre-booting, booting, heading, grain filling, and maturity (Dunand and Saichuk, 2014). Rice is a diploid plant composed of 12 chromosomes ($2n=24$) and was the first sequenced crop genome (International Rice Genome Sequencing Project and Sasaki, 2005).

The United States produced approximately 11.5 million tons of rough rice in 2020 which were predominantly grown in four regions: the Arkansas Grand Prairie, Mississippi Delta (parts of Arkansas, Mississippi, Missouri, and Louisiana), Gulf Coast (Texas and Southwest Louisiana), and Sacramento Valley of California (USDA-ERS 2021). About half of the rice produced in the United States is exported to Mexico, Central America, Northeast Asia, the Caribbean, and the Middle East and smaller volumes are exported to Canada, European Union, and Sub-Saharan Africa (USDA-ERS, 2017). Louisiana is the third-largest rice-producing state in the country with more than 425,000 acres of rice planted on 823 farms in 2019. Rice production contributes more than US \$308 million to the state (USA Rice, 2021). Rice

production in Louisiana is concentrated in the southwestern and northeastern parts of the state. Rice is grown annually in flatlands which allows for mechanization and efficient crop management. The majority of rice in Louisiana and the southern U.S. is cultured by drill-seeding in dry soil followed by the establishment of a permanent flood 4–6 weeks after planting (typically when rice plants reach the 5-leaf or early-tillering developmental stage). Water seeding used to be a predominant method of rice seeding in Louisiana, and it is still widely used in some parts of the southwest region of the state with approximately 17% of rice acreage in 2020 were water-seeded. LSU AgCenter recommendations for planting dates are from March 10–April 15 in southwest Louisiana and April 1–May 5 in north Louisiana (Saichuk, 2014). The two primary grain types grown in Louisiana are long and medium grains. Most of the acreage in the state is planted with long-grain rice cultivars. Yields vary among the rice cultivars but typically rice yields in the state range from 8,000–12,000 lbs per acre (Harrell, 2020).

1.2. Insect Pests of Rice

Damage by insect pests is a major limiting factor for rice production globally (Pathak and Khan, 1994). Rice plants are subjected to various pressures by insect pests and diseases throughout their development. There are around 25 insect species in North America that are documented pests of rice. Among these insect pests, the rice water weevil and stemborers can cause serious economic losses.

1.2.1. Rice Water Weevil

The rice water weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), is consistently the most destructive and widespread early-season pest of rice in the U.S. (Aghaee and Godfrey, 2014; Way, 1990). It is found in all rice-producing states including California,

Arkansas, Louisiana, Missouri, Mississippi, and Texas. This insect pest poses a global threat to rice production, having invaded rice-producing regions of Asia and Europe (Saito et al., 2005). Adult rice water weevils are dark-brown to grayish-black beetles with characteristically V-shaped markings on the center of their elytra and are relatively small (approximately 0.32 cm long by 0.16 cm wide). This insect overwinters as adults in various habitats including leaf litter, bunch grasses, grass clumps, and plant debris in and around rice fields (Shang et al., 2004). The emergence of adult weevils from overwintering begins in early spring in southern Louisiana and is highly influenced by temperature (Zou et al., 2004b). Upon emergence, adults move to rice fields to feed on rice leaves, leaving longitudinal scars along the leaf blades. Injury from adult feeding is generally not economically important except under unusually heavy infestations. The establishment of permanent flood in rice fields triggers female weevils to lay eggs (whitish, elongate-shaped) in the submerged part of the leaf sheath in a longitudinal pattern (Stout et al., 2002b). The first instar weevil larvae initially feed on leaf sheath tissue before moving to the soil and continue feeding on or in the roots. The rice water weevil passes through four instars and a pupal stage in roughly 27–30 days depending on temperature (Zou et al., 2004b). Although weevil populations in the southern U.S. are multivoltine, only a single larval peak occurs in a single field during the growing season (Shang et al., 2004). The majority of yield loss is caused by the soil-dwelling, root-feeding larval stage. Root pruning due to larval feeding can cause extensive injury to rice root systems, resulting in reductions in tiller numbers, grain weights, and grains per panicle (Zou et al., 2004a).

Yield losses attributable to injury caused by weevil larvae can exceed 25% particularly if fields are left unmanaged (Stout et al., 2000). Studies conducted by Stout et al. (2002), Zou et al. (2004), and Adams et al. (2016) have reported yield losses ranging from 0.3–4.1% per weevil

larva. Weevil larval densities can easily exceed 25 larvae per plant in southwest Louisiana where weevil populations are typically larger compared to other rice-growing states.

1.2.2. Stemborer Complex

Stemborers are important insect pests worldwide that attack rice plants from the vegetative to the reproductive developmental stages (Akinsola, 1984). A complex of stem-boring lepidopteran pests (Crambidae) attacking rice in the southern United States includes the Mexican rice borer, *Eoreuma loftini* (Dyar), the sugarcane borer, *Diatraea saccharalis* (Fabricius), and the rice stalk borer, *Chilo plejadellus* Zincken (Beuzelin et al., 2016; Way, 2003). Female moths typically lay eggs in clusters of about 2–300 eggs and upon hatching larvae move toward the space between leaf sheaths and plant stems. The stemborer larvae usually feed on the leaf sheath for a few days before boring into the stem. When the boring occurs during the vegetative developmental stage of rice plants, the affected tillers often wither and die, a condition known as a deadheart (Pathak and Khan, 1994). However, when feeding occurs at the reproductive developmental stage of plant development, injury prevents normal panicle development. The rice panicles may emerge but remain straight, are whitish, and do not produce grains, a condition known as a whitehead (Pathak and Khan, 1994). Stemborer activity in the field is generally measured by assessing the density of whiteheads, which is negatively associated with rice yield (Reay-Jones et al., 2007a; Way et al., 2006a). However, the sole use of whiteheads as an indicator of stemborer activity in the field may provide an incomplete picture of the damage caused by larval feeding. Other types of stemborer injury such as deadheart (destruction of the apical part of stalk), partial whiteheads (only a portion of the grains on the panicle are consumed), and unemerged whitehead should also be examined in the field.

Stemborers, particularly the invasive Mexican rice borer, are becoming increasingly problematic in the rice-producing regions of the U.S. especially in southwestern Louisiana and Texas. The Mexican rice borer was first detected in Texas in 1980 on sugarcane in the Lower Rio Grande Valley and has since spread northeast through the rice production area along the Texas Gulf Coast (Johnson and van Leerdaam, 1981; Reay-Jones et al., 2007b). In Louisiana, this insect pest was first detected in Calcasieu Parish in 2008 (Hummel et al., 2010) and was recorded infesting rice in 7 Louisiana parishes by 2013 (Wilson et al., 2015). This invasive Mexican rice borer has become firmly established in Louisiana's rice production area as indicated by continued expansion and high population density in many regions (Wilson et al., 2017). At present, Mexican rice borer is a persistent pest of rice in southwest Louisiana and Texas, where it is responsible for high densities of whiteheads in unprotected rice fields (Way and Pearson, 2019, 2018; Wilson et al., 2015). A recent study reported a loss of 1.7% in yield per whitehead per m² due to Mexican rice borer feeding (Wilson et al., 2021a). The continuous expansion of the Mexican rice borer in Louisiana rice is predicted to cause economic losses exceeding US \$40 million annually if infestations are not managed (Reay-Jones et al., 2008).

1.3. Pest Management Strategies

1.3.1. Chemical Control

Control strategies for rice water weevil and stemborers rely heavily on synthetic insecticides (Johnson et al., 2003; Reay-Jones et al., 2007a; Way, 1990). At present, insecticidal seed treatments are extensively used to control insect pests in rice in the southern USA (Bateman et al., 2020; Wilson et al., 2021b). Seed treatments containing chlorantraniliprole, thiamethoxam, clothianidin, or cyantraniliprole are primarily applied to control the rice water weevil (Hummel et al., 2014; Stout et al., 2011a; Villegas et al., 2019; Wilson et al., 2021b). Insecticidal seed

treatments containing chlorantraniliprole also reduce injury by stemborers in rice (Sidhu et al., 2014; Wilson et al., 2015). Of the available insecticidal seed treatments, chlorantraniliprole provides the best weevil control. Results from field studies demonstrated 72–96% reductions in rice water weevil densities when rice was treated with chlorantraniliprole (Hamm et al., 2014; Hummel et al., 2014; Villegas et al., 2019). Chlorantraniliprole belongs to the anthranilic diamide class of insecticides and is highly selective towards ryanodine receptors that are critical for muscle contraction in insects (Cordova et al., 2006; Lahm et al., 2009, 2007).

Chlorantraniliprole is remarkably safe in mammals due to its high selectivity for the ryanodine receptors of insects over mammals (Lahm et al., 2009, 2007). Moreover, chlorantraniliprole has limited non-target effects on crawfish, *Procambarus* spp. (Decapoda: Cambaridae), which is important because in southwest Louisiana (where the majority of rice is produced in the state) rice and crawfish are typically cultured together or near each other (Barbee et al., 2010).

Similar to rice water weevil, effective control of stemborers in the United States' rice currently relies solely on insecticides. Prior to 2010, management of stemborers in Texas rice was accomplished with foliar applications of the pyrethroid insecticides, ζ -cypermethrin and λ -cyhalothrin (Reay-Jones et al., 2007a). Foliar applications of pyrethroids are generally done during the reproductive and late-boot or early-heading phases of rice development (Reay-Jones et al., 2007a; Way and Espino, 2010). The economic threshold for stemborer control has not been developed, thus application timing is based on producer experience and perceived levels of infestations (Beuzelin et al., 2016). Pyrethroids are not widely used for stemborers in Louisiana because these insecticides can have negative effects on crawfish, which are often produced in rotation with rice in the state (Barbee and Stout, 2009). Currently, stemborer control is

commonly achieved with chlorantraniliprole seed treatments that are applied primarily for rice water weevil (Hummel et al., 2014; Wilson et al., 2019).

1.3.2. Host Plant Resistance

Host-plant resistance is arguably the most sustainable alternative approach for managing insect pests of rice including the rice water weevil. Results from previous studies suggest that varietal resistance has the most potential to complement integrated pest management programs (IPM) for the management of rice water weevil (Stout et al., 2001; Zou et al., 2004b). Growing resistant rice cultivars is an effective strategy because it represents a built-in economically and ecologically friendly tactic for protecting rice from insect pests. Since the 1960s, thousands of rice lines have been screened for resistance to rice water weevil in the U.S. However, none of the rice genotypes evaluated possessed high levels of resistance, and no resistant cultivars are available to growers (Bowling, 1963; Heinrichs and Quisenberry, 1999; N'guessan et al., 1994b, 1994a; N'guessan and Quisenberry, 1992; Smith and Robinson, 1982; Stout et al., 2001). Recently, Vyavhare et al. (2016) reported that there is very little variation in resistance to rice water weevil among rice germplasm and cultivars commercially grown in the southern U.S. Similarly, Saad et al. (2018) found that none of the cultivars (hybrid or inbred) commercially grown in Louisiana showed high levels of resistance to rice water weevil. However, the majority of previous studies have evaluated resistance based on infestation levels alone (i.e., antibiosis or antixenosis/non-preference) without considering impacts on rice yields (tolerance).

Tolerance is a type of resistance that allows plants to compensate for insect pest injury to an extent exceeding that in non-tolerant plants (Painter 1951; Smith 2005), such that tolerant crop genotypes generally suffer lower yield losses than susceptible genotypes when exposed to similar levels of injury. Tolerance encompasses plant traits or physiological processes that

reduce the amount of damage (in terms of plant fitness or yield loss) per unit injury. Tolerance does not affect insect behavior or biology; thus, the use of tolerant genotypes has the advantage of reducing yield losses from insect pests without placing selection pressure on pest populations to overcome plant resistance (Smith, 2005). Studies investigating rice tolerance to rice water weevil are quite sparse. N'guessan et al. (1994a, 1994b) reported two Louisiana breeding lines with moderate levels of tolerance to rice water weevil. These rice lines exhibited similar levels of root injury under high weevil infestations and produced similar grain yields in insecticide-treated and untreated plots, but unfortunately were not released as commercial variety due to unwanted agronomic characteristics. Plant resistance based on tolerance to rice water weevil infestation has not been investigated among currently grown hybrid and inbred rice cultivars in the southern U.S.

In Asia, host-plant resistance is an important component of IPM programs for stemborers in rice. Thousands of rice lines and commercially grown cultivars from the world collection at the International Rice Research Institute (IRRI) have been screened for stemborer resistance. Results from these studies showed that cultivar resistance to stemborers varied from moderate to low levels and that susceptibility of cultivars was positively correlated with oviposition preference of moths (Chaudhary et al., 1984; Pathak, 1971; Pathak and Khan, 1994). Several plant traits such as stem diameter, plant height, length and width of flag leaf, tight leaf sheaths, thick layers of sclerenchymatous or lignified plant tissues, narrow stem lumen, and physiological and biochemical factors influence stemborer resistance (Chaudhary et al., 1984). In the U.S., a study conducted by Way et al. (2006) reported low levels of stemborer injury (mixed infestations by Mexican rice borer and sugarcane borer) in rice cultivar 'Cheniere' and high levels of injury in rice cultivar 'Priscilla' when evaluated under field conditions. In the same study, the authors

reported that hybrid cultivars were less injured and yielded more than conventional inbred rice cultivars. In contrast, high sugarcane borer injury in Cheniere was observed in a field experiment conducted in northeast Louisiana (Sidhu et al., 2013). Moreover, Hamm et al. (2011) reported oviposition preference by sugarcane borer for Cheniere, especially at the tillering stage of development. This suggests that resistance to one stemborer species is not necessarily associated with resistance to another stemborer species. It will be important in the future to conduct studies to differentiate cultivar resistance to different species of stemborers.

1.3.3. Cultural Tactics

Cultural strategies that involve weed control, field draining, delayed flood timing, and early planting have been utilized to manage rice water weevil and stem borers (Hesler et al., 1992; Kendig et al., 2003; Stout et al., 2009; Tindall et al., 2005). Early planting has been suggested as an alternative management strategy for rice water weevil and stemborer control. Planting early relative to the recommended planting dates can reduce exposure of rice plants to these insect pests during the period it is most vulnerable to pests (Stout et al., 2011b; Way et al., 2006a). Weed removal from adjacent areas of the fields can also be a tactic to reduce weevil and stemborers. Non-crop hosts, such as weeds, are important alternative food sources for weevils and stemborers (Aghaee and Godfrey, 2014; Beuzelin et al., 2016). Several studies have documented that manipulation of water management (draining, flood depth, and flood timing) can reduce weevil infestations. It was found that draining of rice fields was comparable to applying insecticide in controlling rice water weevil infestations, however, the tactic is unreliable because of secondary infestations and negative net returns in drained plots (Thompson et al., 1994). The draining of fields has not been studied with modern cultivars and production practices. Previous studies also indicated that delaying the application of permanent flood can

reduce infestations and impacts of rice water weevil (Rice et al., 1999; Stout et al., 2001).

Delaying flood application until rice plants are older shortens the period in which rice plants are vulnerable to weevils, thus reducing weevil infestations. The effect of delayed flood timing on stemborer injury in rice is still unknown. Research conducted by Stout et al. (2002b) which examined flood depth as a tactic against rice water weevil showed that fewer weevil larvae were found at 5 cm flood depth compared to 10 cm flood depth. However, flood depth is not sufficient as a tactic alone but is recommended to be a component of an integrated approach in controlling rice water weevil.

1.4. Research Goals

Ideally, management of rice water weevil and stemborers should incorporate combinations of control tactics; however, the current management programs for these pests rely almost exclusively on chemical control. To minimize the impact of insecticides on the environment while maintaining production levels, increased use of alternatives to chemical control is needed. The main goal of this research is to improve the sustainability of current pest management programs by integrating host-plant resistance (with an emphasis on plant tolerance) with other tactics.

Chapter 2 of this dissertation describes the research I conducted to test the hypothesis that hybrid rice cultivars possess greater tolerance to rice water weevil injury than inbred rice cultivars. Densities of rice water weevil larvae and pupae on the roots of rice plants were used as a proxy for injury, while tolerance was assessed by comparing yield responses to infestation among hybrid and inbred cultivars.

Chapter 3 describes the study I conducted to evaluate the influence of inbred rice cultivars commonly grown in Louisiana on infestation by both rice water weevils and stemborers

under field conditions (resistance) and to assess whether yield losses associated with infestations by these pests differed among the rice cultivars (tolerance).

Chapter 4 describes the experiments I conducted to evaluate the influence of rice cultivars and flood timing on the infestations of rice water weevil and stem borers and the corresponding impacts on rice yields.

Lastly, Chapter 5 examines the effects of chronic feeding of rice water weevil on plant growth, nutrient uptake, and phytohormone production between two cultivars (weevil tolerant hybrid cultivar and conventional inbred) under field conditions.

Chapter 2. Tolerance to Rice Water Weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), Infestations among Hybrid and Inbred Rice Cultivars in the Southern U.S.

2.1. Introduction

The rice water weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), is consistently the most damaging insect pest of rice, *Oryza sativa* L., in the United States (Way, 1990; Aghaee and Godfrey, 2014). In addition, this pest has invaded other rice-producing regions in Asia and Europe (Saito et al., 2005; Aghaee and Godfrey, 2014; Lupi et al., 2015). More recently, in 2016, the presence of adult *L. oryzophilus* was detected in the rice field region of Central Macedonia, Greece (Giantsis et al., 2017). Injury caused by *L. oryzophilus* larval feeding on rice roots can result in yield losses exceeding 25% when fields are left untreated (Stout et al., 2000). Yield losses from root injury result from reductions in tiller numbers, grain weights, and grains per panicle (Zou et al., 2004a).

The use of insecticidal seed treatments has been a widely adopted management tactic for insect pests in U.S. rice for the past decade (Wilson et al., 2019). In particular, treatment of seeds with chlorantraniliprole, thiamethoxam, or clothianidin has resulted in effective control of *L. oryzophilus* larvae (Stout et al., 2011; Hummel et al., 2014; Villegas et al., 2019). Despite the effectiveness of insecticidal seed treatments against rice insect pests, alternative management strategies are needed to mitigate the development of insecticide resistance (Graves et al., 1967; Bowling, 1968).

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Reduced reliance on insecticides can be accomplished by the development of an integrated pest management (IPM) program that includes rice cultivars with tolerance/resistance to *L. oryzaophilus*.

Thousands of rice lines have been screened for resistance to *L. oryzaophilus* in the U.S. since the 1960s, but none of the genotypes tested have possessed high levels of resistance, and no resistant cultivars are available to growers (Bowling, 1963; Smith and Robinson, 1982; N'guessan and Quisenberry, 1992; N'guessan et al., 1994a,b; Rice et al., 1994; Heinrichs and Quisenberry, 1999; Stout et al., 2001). Recently, Vyavhare et al. (2016) reported that very little variation in resistance to *L. oryzaophilus* existed among rice germplasm and cultivars commercially grown in southern U.S. Furthermore, Saad et al., (2018) found that none of the inbred or hybrid cultivars widely grown in Louisiana showed high levels of resistance to *L. oryzaophilus*. However, the majority of prior studies have evaluated resistance based on infestation levels alone (i.e., antibiosis or antixenosis) without considering impacts on rice yields (tolerance).

Tolerance is a type of resistance that allows plants to compensate for pest injury to an extent exceeding that found in non-tolerant plants (Painter 1951; Smith 2005), such that tolerant genotypes generally suffer lower yield losses than susceptible genotypes when exposed to similar levels of injury. Unlike other types of host plant resistance, tolerance does not affect insect behavior or biology (Smith 2005); thus, the use of tolerant genotypes has the advantage of reducing yield losses from insect pests without placing selection pressure on pest populations to overcome plant resistance. N'guessan et al. (1994a) reported two Louisiana breeding lines with moderate levels of tolerance to *L. oryzaophilus*. These rice lines exhibited similar levels of root injury under high populations of *L. oryzaophilus* larvae and produced similar grain yields in

insecticide-treated and untreated plots. However, plant resistance based on tolerance to *L. oryzaophilus* infestation has not been investigated among currently grown hybrid and inbred rice cultivars.

Hybrid rice cultivars offer a potential source of tolerance to pests because of their robust growth, high tillering capacity, and improved yields over inbred lines (Yuan 1994; Horgan et al., 2016). Horgan et al. (2016) reported that hybrid lines were more tolerant of injury caused by several stemborer species such as the Asiatic pink stem borer, *Sesamia inferens* Walker, Asiatic rice borer, *Chilo suppressalis* Walker, and yellow stem borer, *Scirpophaga incertulas* Walker. Their study suggests that hybrid tolerance to stemborer damage was governed by some aspects of hybrid physiology other than larger plant size or greater plant growth, e.g. efficiency of nutrient assimilation or partitioning of nutrient resources. Currently, hybrid rice accounts for >60% of the production area in China (Ma and Yuan, 2015) and adoption in Louisiana alone increased from 1.4% in 2004 to 22.4% in 2018 (LSU Agricultural Center). Although hybrid rice has only been commercialized in the U.S since 2000, it accounted for 29% of U.S. rice production by 2013 (McBride et al., 2018). Some of the characteristics of hybrid cultivars include improved tiller production, panicle length, and spikelet number per panicle, resulting in 15–25% yield increases over inbred lines (Zhende, 1988; Li and Yuan, 2000; Bond and Walker, 2011). Hybrid rice is typically planted at a lower seeding rate (28–44 kg ha⁻¹) than inbred rice (56–123 kg ha⁻¹) because of its high tillering capacity (Bond et al., 2005).

This study was conducted to test the hypothesis that hybrid rice cultivars possess greater tolerance to *L. oryzaophilus* injury than inbred rice cultivars. Densities of *L. oryzaophilus* larvae and pupae on the roots of rice plants was used as a proxy for injury, while tolerance was assessed by comparing yield responses to infestation among hybrid and inbred cultivars. Because seeding

rates can affect *L. oryzaophilus* infestations and yield losses (Stout et al., 2009), seeding rates for inbred cultivars in one of the experiments were manipulated to assess possible effects on rice tolerance to *L. oryzaophilus*.

2.2. Materials and Methods

2.2.1. Louisiana Field Experiments 2016–2017

Field experiments were conducted at the LSU AgCenter H. Rouse Caffey Rice Research Station in Crowley, Louisiana in 2016–2017. Rice cultivars used in each experiment were randomly selected from commonly grown hybrid and inbred rice cultivars in the southern U.S. (Table 2.1). Seeds of hybrid cultivars were provided by RiceTec Inc. (Alvin, Texas) with the exception of ‘LAH10’, which was developed and provided by the LSU AgCenter Hybrid Breeding Program (Baton Rouge, Louisiana).

In 2016, two hybrid and two inbred cultivars were selected and drill-planted at a seeding rate of 28 kg ha⁻¹, whereas in 2017, three hybrid and three inbred cultivars were selected and drill-planted at a seeding rate of 28 kg ha⁻¹ for hybrid cultivars and 28 kg ha⁻¹ and 67 kg ha⁻¹ for inbred cultivars (Table 2.2). Seeds were drill-planted in plots measuring 5.5 m in length with seven rows spaced 18 cm apart. The different seeding rates for inbred cultivars in 2017 were employed to control for possible effects of seeding rate on rice tolerance to *L. oryzaophilus* in the field (Stout et al., 2009; Aghaee et al., 2015). *L. oryzaophilus* were suppressed in half of the plots of each cultivar by treating seeds with a standard rate (70 g a.i. ha⁻¹) of an insecticidal seed treatment, chlorantraniliprole (Dermacor® X-100, Corteva Agriscience, Wilmington, Delaware), following the methods of Lanka et al. (2014). Plots were laid out according to a randomized block design with four blocks, each block containing the selected cultivars that were treated (protected) and not treated (unprotected) with chlorantraniliprole seed treatment (8 plots per

block in 2016 and 18 plots per block in 2017) . Protected and unprotected plots of the same cultivar and seeding rate (2017) were planted side-by-side to reduce variation in infestations and yields. After planting, fields were surface irrigated as necessary to facilitate plant emergence and growth. Permanent flood at 5–10 cm in depth was established at five and four weeks after planting in 2016 and 2017, respectively. Field plots were maintained according to recommended production practices for drill-seeded rice in Louisiana (Saichuk, 2014). The soil type at the Crowley locations is a silt loam and fields have been in a two-year rice-fallow rotation for over 30 years.

Table 2.1. List of rice cultivars used in this study (2016–2018).

Reference No.	Plant-type	Cultivar	Origin	Hectarage ^a
1	Hybrid	CL XL745	RiceTec	41,953
2	Hybrid Line	LAH10	LSU AgCenter	-
3	Hybrid	Gemini214 CL	RiceTec	15, 311
4	Hybrid	RT7311 CL	RiceTec	5, 138
5	Hybrid	XP760	RiceTec	576
6	Inbred	CL111	LSU AgCenter	61, 102
7	Inbred	CL153	LSU AgCenter	84, 503
8	Inbred	CL261	LSU AgCenter	-
9	Inbred	Presidio	Texas A&M	-
10	Inbred	Jupiter	LSU AgCenter	25, 326
11	Inbred	Mermentau	LSU AgCenter	45, 517

^a Numbers of hectares planted in 2018 in Louisiana for each cultivar (Harrell, 2019)

Densities of *L. oryophilus* immatures (larvae and pupae) were evaluated 3–4 weeks after establishment of permanent flood according to established procedures (N’guessan and Quisenberry, 1992; Stout et al., 2001). Root-soil core samples were taken from each plot using a metal corer with a diameter of 9.2 cm and a depth of 7.6 cm. Each core sample contained a minimum of one rice plant with intact roots. In 2016, core sampling was conducted at one time

point (two per plot, 96 samples total) while in 2017, core sampling was conducted twice (three per plot, 216 total per time point). Core samples were processed by washing the soil and larvae from roots under moderate water pressure in 40-mesh screen sieve buckets that were then placed in basins containing salt water. *L. oryzaophilus* larvae were counted as they floated to the surface. Pupae were counted by inspecting bottoms of sieve buckets after all larvae had been counted. The numbers of larvae and pupae in the two or three core samples from each plot were averaged to obtain an estimate of *L. oryzaophilus* density in each plot prior to data analysis.

Entire plots were harvested with a small-plot combine at grain maturity. The weights of rough rice yields from each plot were adjusted to 12% moisture and converted to kg ha⁻¹.

Percentage yield losses were calculated for each cultivar in each block using the formula:

$$\% \text{ Yield Losses} = \frac{\text{Yield}_{\text{Protected}} - \text{Yield}_{\text{Unprotected}}}{\text{Yield}_{\text{Protected}}} \times 100$$

where “protected” yields were yields from plots treated with label rate of chlorantraniliprole and “unprotected” yields were yields from plots not treated with chlorantraniliprole.

Table 2.2. Field activities and corresponding dates.

	Louisiana 2016–2017		Multiple Location 2018		
	2016	2017	Louisiana	Texas	Mississippi
Variety (Ref. No.)*	2, 5, 6, 11	1, 3, 4, 8, 10, 11	1, 4, 5, 7, 10, 11	2, 4, 5, 7, 9, 11	1, 4, 7, 11
Planting date	25-Jun	9-Apr	19-Apr	3-May	7-May
Permanent flood	1-Aug	9-May	25-May	1-Jun	30-May
1 st core sampling	1-Sep	1-Jun	19-Jun	26-Jun	19-Jun
2 nd core sampling	-	8-Jun	26-Jun	3-Jul	28-Jun
Harvest	18-Oct	10-Aug	20-Sep	29-Aug	11-Oct

2.2.2. Multiple Location Field Experiment

In 2018, field experiments were conducted at the Texas A&M AgriLife Research and Extension Center in Beaumont, TX, the Mississippi State University Delta Research and Extension Center in Stoneville, MS, and the LSU AgCenter H. Rouse Caffey Rice Research Station in Crowley, LA to examine yield response to *L. oryzaephilus* infestations under variable growing conditions. The soil types at each location were League clay soil (fine, montmorillonitic, Entic Pelludert) in Texas, Tunica clay (clayey over loamy, mixed, superactive, nonacid, thermic, Vertic Epiaquert) in Mississippi, and Crowley silt loam (fine, smectitic, thermic Typic Albaquaf) in Louisiana. Three hybrid and three inbred cultivars were evaluated in Texas and Louisiana, while two hybrid and two inbred cultivars were evaluated in Mississippi (Table 2.2). At all locations, seeds were drill-planted at standard seeding rates of 28 kg ha⁻¹ for hybrid cultivars and 67 kg ha⁻¹ for inbred cultivars. Plots were 5.5 m in length with seven rows spaced 18 cm apart in Texas and Louisiana, whereas plots in Mississippi were 4.6 m in length with eight rows spaced 20 cm apart. Chlorantraniliprole seed treatment was used on half of the plots of each cultivar to suppress populations of *L. oryzaephilus* following the methods of Lanka et al. (2014). For all locations, plots were laid out in a randomized block design with four blocks and one replicate per block (12 plots per block in Louisiana and Texas and 8 plots per block in Mississippi). Protected and unprotected plots of the same cultivar were placed side-by-side.

L. oryzaephilus densities were evaluated at 3–4 weeks after permanent flood (5–10 cm in depth). Three core samples were taken from each plot (144 total in Texas and Louisiana, and 96 total in Mississippi per time point) twice, with the two samplings spaced 7–9 days apart. Each core sample was processed as previously described. The numbers of immature *L. oryzaephilus* in three core samples from each plot were averaged prior to data analysis. At grain maturity, entire

plots were harvested with a small plot combine and grain yields were adjusted to 12% moisture and converted to kg ha⁻¹. Percentage yield losses were calculated as previously described.

2.2.3. Statistical Analyses

All analyses were performed in SAS version 9.4 (SAS Institute, Cary, NC). Insect data were analyzed separately by year and location because cultivars varied among field experiments. *L. oryzaophilus* densities in 2016 were analyzed using generalized linear mixed-models (PROC GLIMMIX) with plant-type (hybrid or inbred), cultivar, seed treatment (protected and unprotected), and their interactions as fixed effects and block as a random effect. Whereas, *L. oryzaophilus* data from 2017 and the multiple location experiment in 2018 were analyzed using repeated-measures generalized linear-mixed models (PROC GLIMMIX) with plant-type, cultivar, seed treatment, seeding rate (2017 experiment only), and their interactions as fixed effects, sampling time as repeated-measures, and block and plot as random effects. The analyses of *L. oryzaophilus* data were modelled using Poisson distributions (Stroup 2014) and means were separated using Tukey's HSD ($\alpha = 0.05$).

Yield loss data were initially analyzed separately by year and location to evaluate variation in yield losses among cultivars. Percentage yield loss data from 2016 and the multiple location experiment were analyzed using generalized linear-mixed models (PROC GLIMMIX) with plant-type (hybrid or inbred) and cultivar as fixed effects. Whereas, yield loss data from 2017 were analyzed with plant-type, cultivar, seeding rate, and their interactions as fixed effects. Block was set as a random effect in both models. Data residuals were examined after each analysis (PROC UNIVARIATE) to ensure normality and homogeneity of variances. Yield loss data from Mississippi were arcsine transformed prior to analysis but untransformed means and

standard errors are presented. The analyses of yield loss data were modelled using Gaussian distributions. Means were separated using Tukey's HSD ($\alpha = 0.05$).

Finally, yield data across years and locations were pooled to analyze overall effects of plant-type (hybrid or inbred) and *L. oryzaophilus* densities on rice yields using analysis of covariance (PROC GLM). Linear relationships between *L. oryzaophilus* density and yield for each plant-type was analyzed using PROC REG.

2.3. Results

2.3.1. Rice Water Weevil Infestations

Treatment of seeds with chlorantraniliprole reduced densities of *L. oryzaophilus* relative to unprotected plots by 92.3% in 2016 (seed treatment effect: $F_{1, 21} = 41.90$; $P < 0.001$) (Fig. 2.1C) and by 74.8% in 2017 ($F_{1, 128} = 205.05$; $P < 0.001$) (Fig. 2.1F). No differences in *L. oryzaophilus* densities between plant-types or among cultivars were observed in 2016 and 2017 (plant-type or cultivar effects: $P > 0.05$) (Fig. 2.1A, B, D, E). Seeding rate did not affect *L. oryzaophilus* densities in 2017 (seeding rate effect: $P > 0.05$). Significant interactions between cultivar and seed treatment ($F_{4, 128} = 4.35$; $P = 0.003$) and between plant-type and seed treatment ($F_{1, 128} = 5.76$; $P = 0.018$) were observed in 2017 (Fig. 2.2C, D). There were no other significant interactions detected.

In the 2018 multiple location experiment, densities of *L. oryzaophilus* were reduced by 76.7, 75.8, and 52.1% in protected plots compared to unprotected plots in Louisiana (seed treatment effect: $F_{1, 80} = 257.72$; $P < 0.001$) (Fig. 2.3C), Texas ($F_{1, 81} = 119.75$; $P < 0.001$) (Fig. 2.3F), and Mississippi ($F_{1, 53} = 105.55$; $P < 0.001$) (Fig. 2.3I), respectively. No differences in *L. oryzaophilus* densities were observed between plant-types or among cultivars in Louisiana and Mississippi (cultivar or plant-type effects: $P > 0.05$) (Fig. 2.3A, B, G, H). In Texas, densities of

L. oryzaophilus were 1.8-fold greater in hybrid compared to inbred cultivars (plant-type effect: $F_{1, 81} = 51.85$; $P < 0.001$) (Fig. 2.3E). Interactions were observed between plant-type and seed treatment in Louisiana ($F_{1, 80} = 6.44$; $P = 0.013$) (Fig. 2.4B) and Texas ($F_{1, 81} = 26.82$; $P < 0.001$) (Fig. 2.4D), and between cultivar and seed treatment in Mississippi ($F_{2, 53} = 3.34$; $P = 0.043$) (Fig. 2.4E).

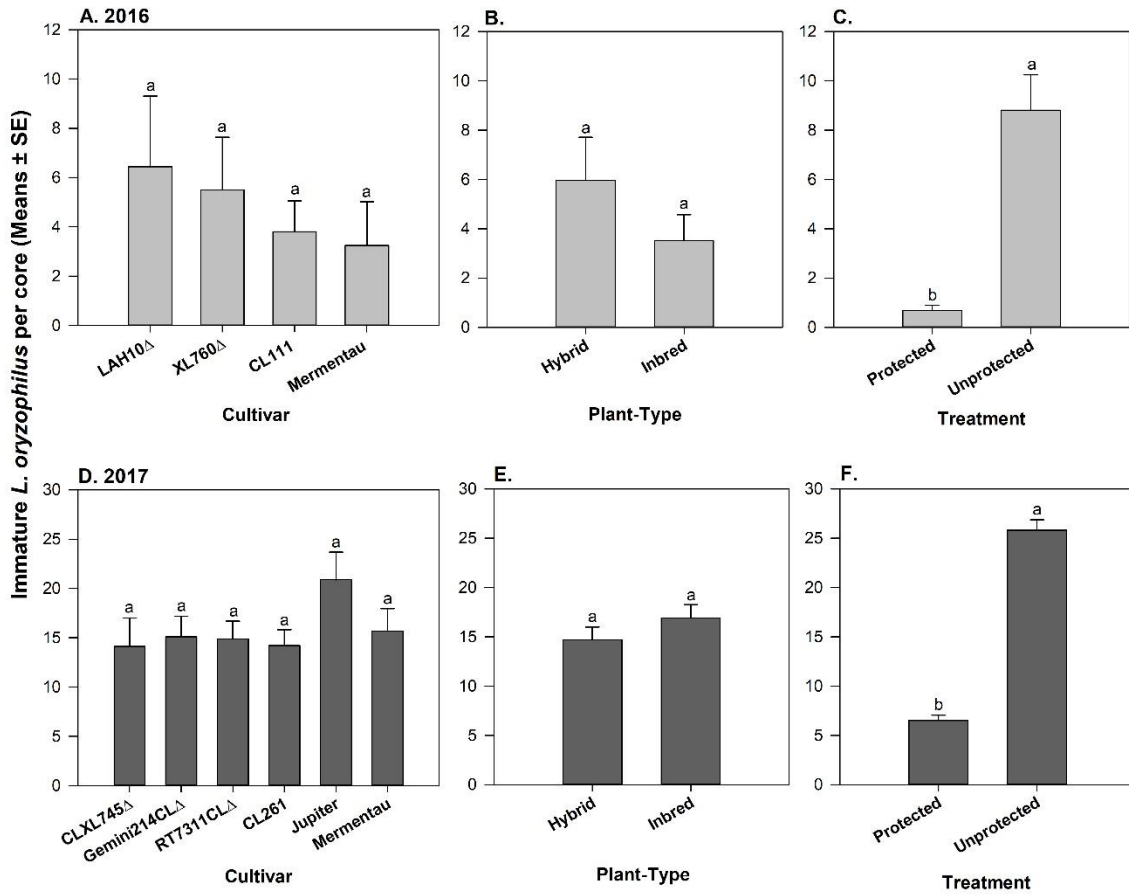


Figure 2.1. Densities of immature *L. oryzaophilus* as affected by cultivar (A, D), plant-type (B, E), and seed treatment (C, F), Louisiana field experiments 2016–2017. Bars within each graph accompanied by the same letter indicate means that do not differ significantly ($P > 0.05$, Tukey's HSD). The Δ symbol following a cultivar name designates a hybrid cultivar.

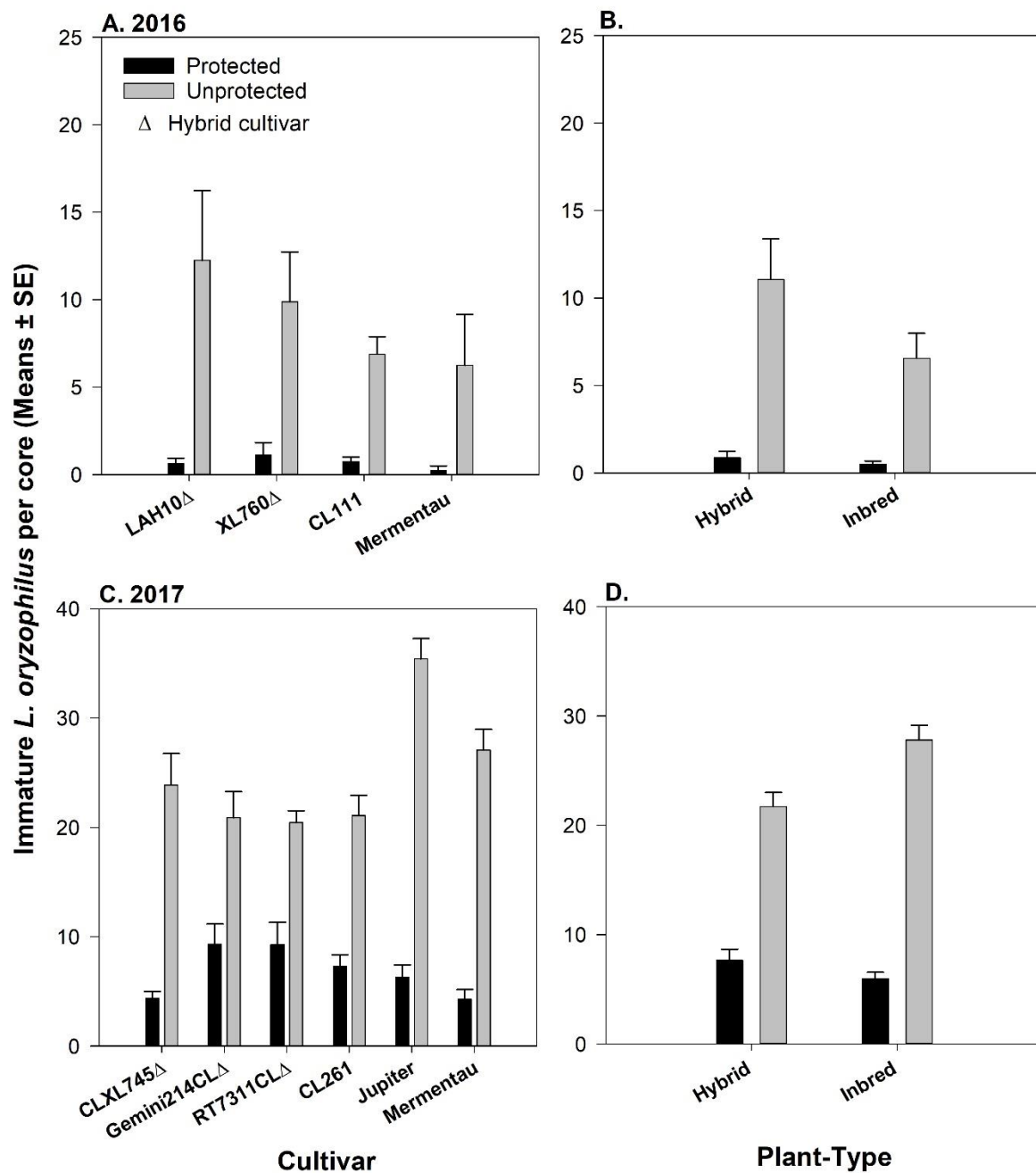


Figure 2.2. Densities of immature *L. oryzaephilus* as affected by cultivar × seed treatment (A, C) and plant-type × seed treatment (B, D), Louisiana field experiments 2016–2017. The Δ symbol following a cultivar name designates a hybrid cultivar.

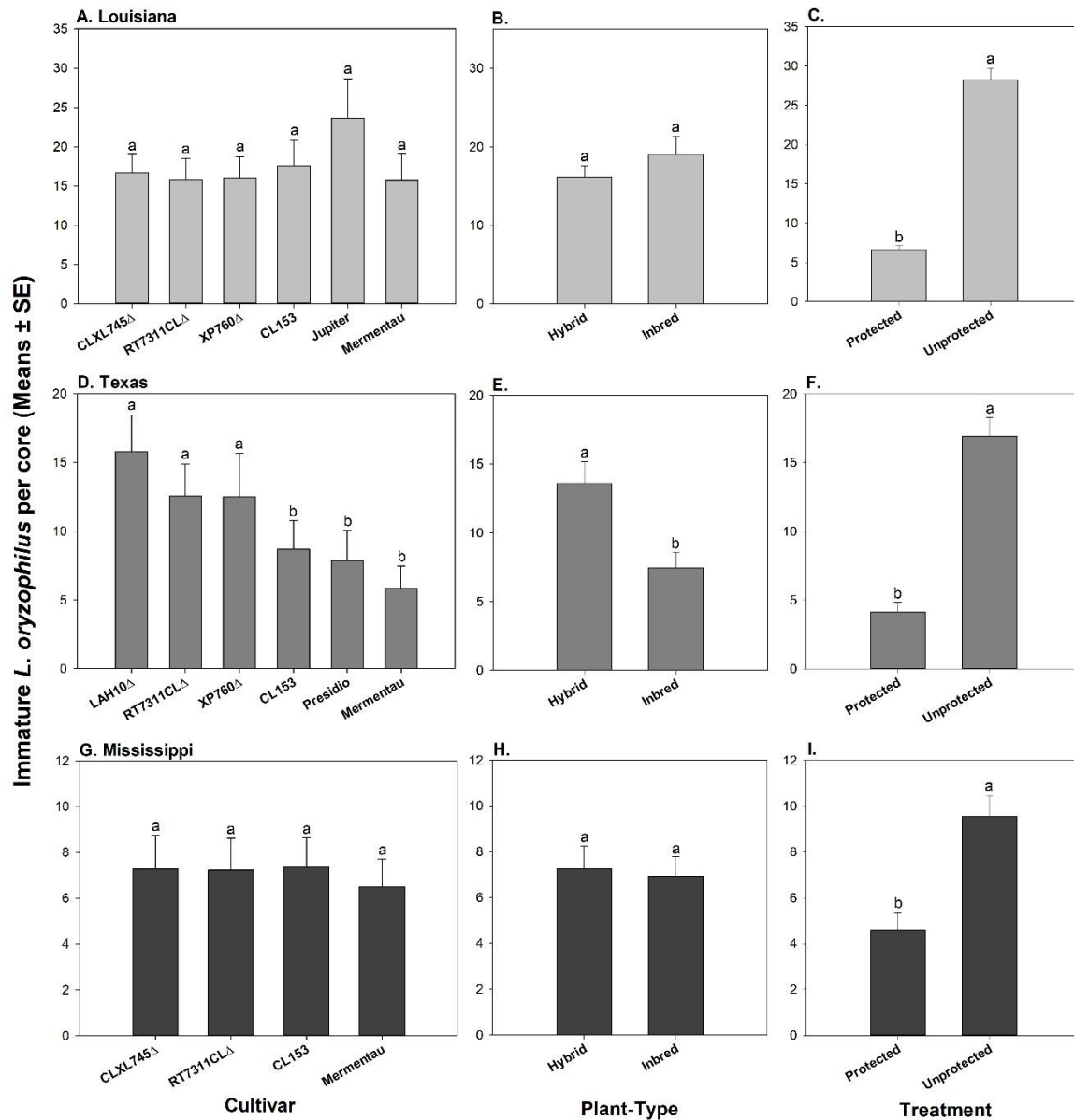


Figure 2.3. Densities of immature *L. oryzaephilus* as affected by cultivar (A, D, G), plant-type (B, E, H), and seed treatment (C, F, I), multiple location field experiment, 2018. Bars within each graph accompanied by the same letter indicate means that do not differ significantly ($P > 0.05$, Tukey's HSD). The Δ symbol following a cultivar name designates a hybrid cultivar.

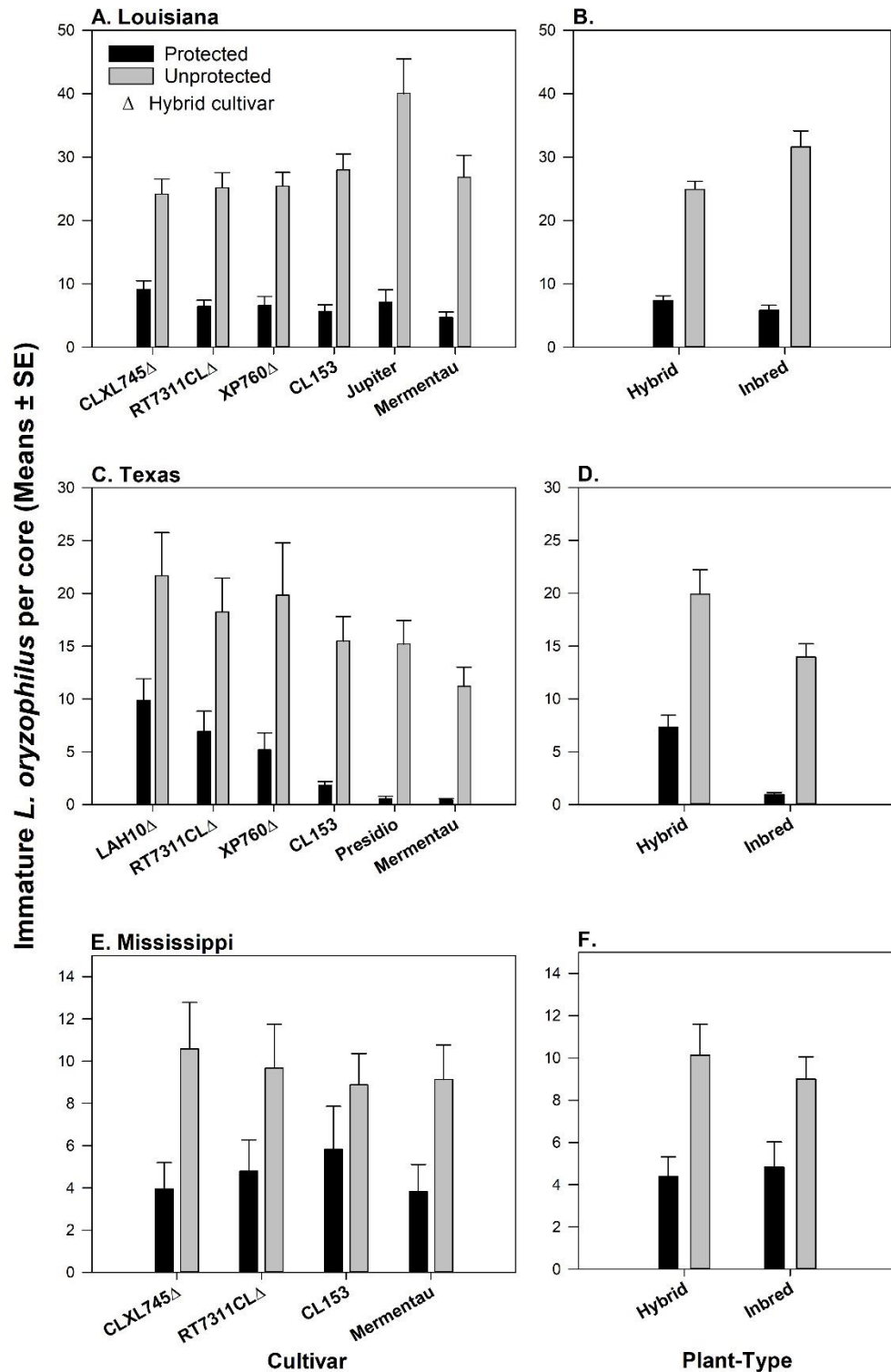


Figure 2.4. Densities of immature *L. oryzaephilus* as affected by cultivar \times seed treatment (A, C, E) and plant-type \times seed treatment (B, D, F), multiple location field experiment, 2018. The Δ symbol following a cultivar name designates a hybrid cultivar.

2.3.2. Yield Responses

Yield losses due to *L. oryzaophilus* infestations ranged from 16.4–48.0% in 2016 and 4.2–29.2% in 2017 across cultivars. Inbreds exhibited 1.9-fold greater yield losses compared to hybrids in 2016 (plant-type effect: $F_{1,9} = 12.48$; $P = 0.006$) and 4.1-fold greater yield losses in 2017 ($F_{1,19} = 10.19$; $P < 0.001$) (Fig. 2.5B, D). In 2016, yield losses from the inbred cultivar ‘CL111’ was 3-fold greater than from the hybrid cultivar ‘LAH10’ (cultivar effect: $F_{2,9} = 4.76$; $P = 0.039$) (Fig. 2.5A). Moreover, inbred cultivars ‘Jupiter’ and ‘Mermentau’ had 5.2- and 4.6-fold greater yield losses, respectively, compared to hybrid cultivars in 2017 (cultivar effect: $F_{5,26} = 3.48$; $P = 0.025$) (Fig. 2.5C). Seeding rate did not affect yield losses in 2017 (seeding rate effect: $P > 0.05$). Also, no significant interactions were detected in 2017. Yield losses based on a per-insect basis among cultivars ranged from 1.9–9.1% in 2016 and 0.3–1.2% in 2017.

In the 2018 multiple location experiment, yield losses were 4.1–29.7, 7.7–17.2, and 4.5–12.2% across cultivars in Louisiana, Texas, and Mississippi, respectively (Fig. 2.6A, C, E). In Texas, yield losses from inbred cultivars were 1.4-fold greater compared to hybrid cultivars (plant-type effect: $F_{1,15} = 6.20$; $P = 0.025$) (Fig. 2.6D). When individual cultivars were considered, the hybrid cultivars ‘RT7311CL’ and ‘XP760’ suffered the highest and lowest yield losses, respectively (cultivar effect: $F_{4,15} = 3.42$; $P = 0.035$) (Fig. 2.6C). There were no differences in yield losses between plant-types or among cultivars in Louisiana and Mississippi (plant-type or cultivar effects: $P > 0.05$). Yield losses on a per-insect basis across cultivars ranged from 0.1–1.2% in Louisiana, 0.7–1.6% in Texas, and 1.2–2.9% in Mississippi.

In the overall analysis across years and locations, *L. oryzaophilus* negatively affected rice yields ($F_{1,229} = 4.69$; $P = 0.031$) (Fig. 2.7). Yields were lower in inbred cultivars planted at a rate of 28 kg ha⁻¹ compared to hybrid cultivars or inbred cultivars planted at a rate of 67 kg ha⁻¹ (F_2 ,

$_{228} = 26.66$; $P < 0.001$). Differences in slopes for the relationships between densities of *L. oryzaophilus* and yields were observed between inbred cultivars planted at 67 kg ha⁻¹ and hybrid cultivars ($F_{1, 189} = 3.76$; $P = 0.054$) and between inbred cultivars planted at 28 and 67 kg ha⁻¹ ($F_{1, 125} = 6.01$; $P = 0.016$), but no differences in slopes were detected between hybrid cultivars and inbred cultivars planted at 28 kg ha⁻¹ ($F_{1, 142} = 0.03$; $P = 0.859$) (Fig. 2.7). Yield reductions associated with every immature *L. oryzaophilus* were 70.9 ± 13.4 (SE) kg and 6.8 ± 19.1 kg in inbred cultivars planted at 67 and 28 kg ha⁻¹, respectively, and 7.5 ± 33.6 kg in hybrid cultivars.

2.4. Discussion

This study provides the first in-depth examination of tolerance as a type of plant resistance to *L. oryzaophilus* among hybrid and inbred rice cultivars. Tolerance in this study was determined by comparing yields from plots of the same cultivar that were protected and not protected from *L. oryzaophilus* infestations. Our findings from three out of five field experiments that yield losses from hybrid cultivars were lower than yield losses from inbred cultivars under similar *L. oryzaophilus* densities supports the hypothesis that hybrid cultivars are more tolerant. Furthermore, regression analyses using pooled data from all experiments showed that yield reductions per immature *L. oryzaophilus* were greater in inbred cultivars planted at 67 kg ha⁻¹ than for hybrid cultivars. Although yield reductions per insect were no higher for inbred cultivars planted at 28 kg ha⁻¹ than for hybrid cultivars at the same seeding rate, yields in the inbred plots at this sub-optimal seeding rate were overall very low, and this may have obscured the ability to discern density-yield relationships.

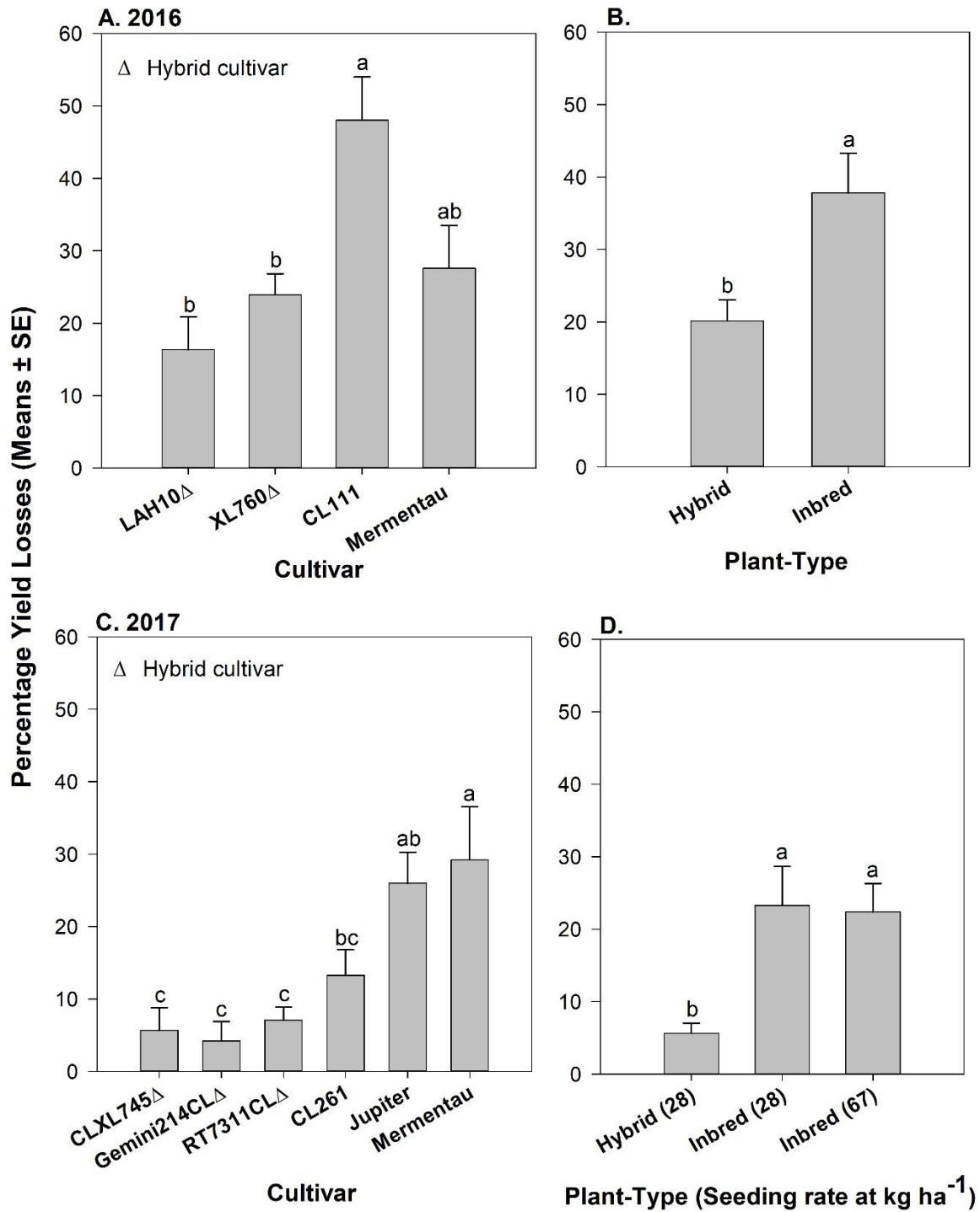


Figure 2.5. Percentage yield losses due to *L. oryzoephilus* infestations as affected by cultivar (A, C), plant-type (B), and plant-type and seeding rate (D), Louisiana field experiments 2016–2017. Bars within each graph accompanied by the same letter indicate means that do not differ significantly ($P>0.05$, Tukey's HSD). The Δ symbol following a cultivar name designates a hybrid cultivar.

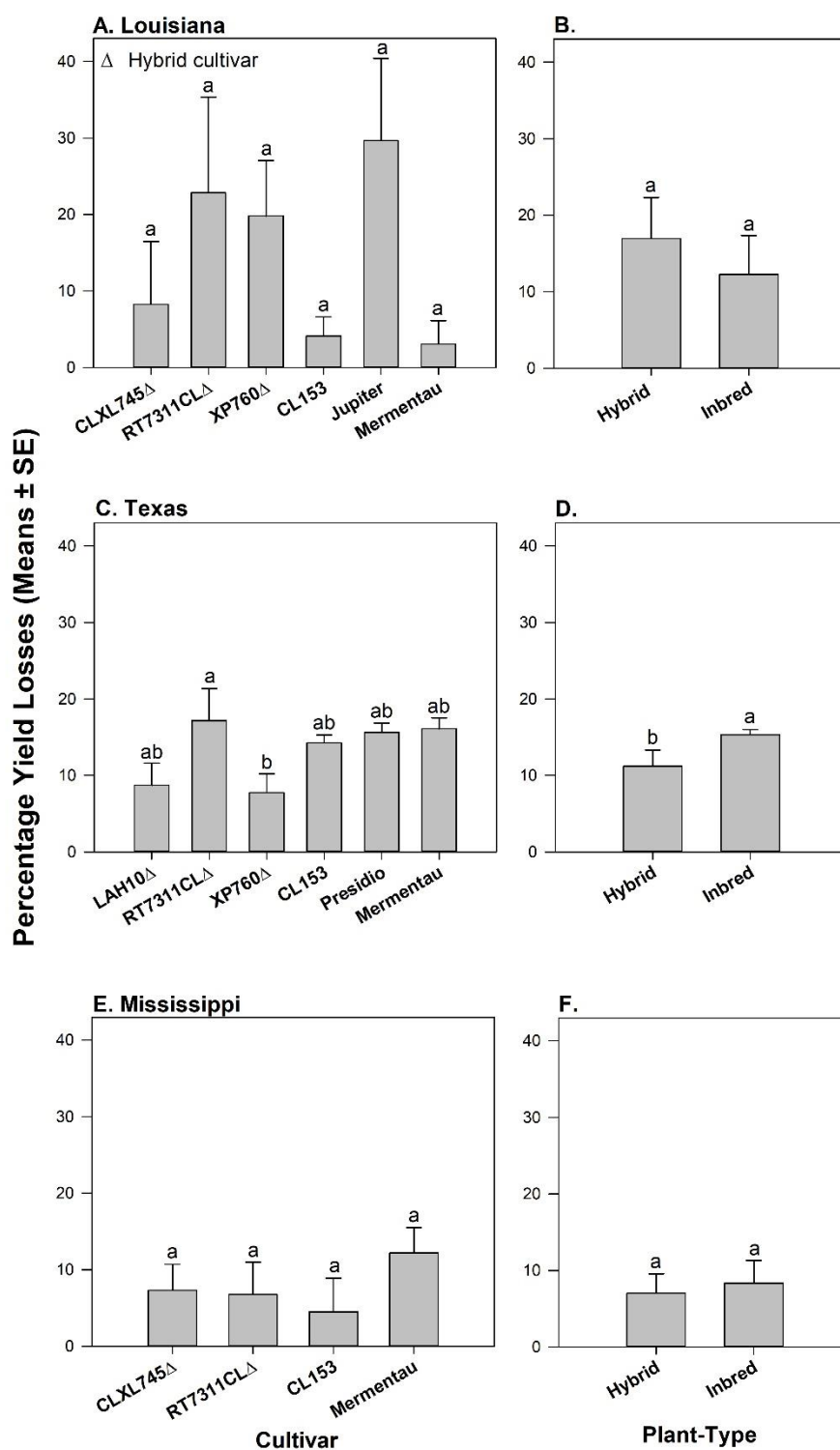


Figure 2.6. Percentage yield losses due to *L. oryzophilus* infestations as affected by cultivar (A, C, E) and plant-type (B, D, F), multiple location field experiment, 2018. Bars within each graph accompanied by the same letter indicate means that do not differ significantly ($P > 0.05$, Tukey's HSD). The Δ symbol following a cultivar name designates a hybrid cultivar.

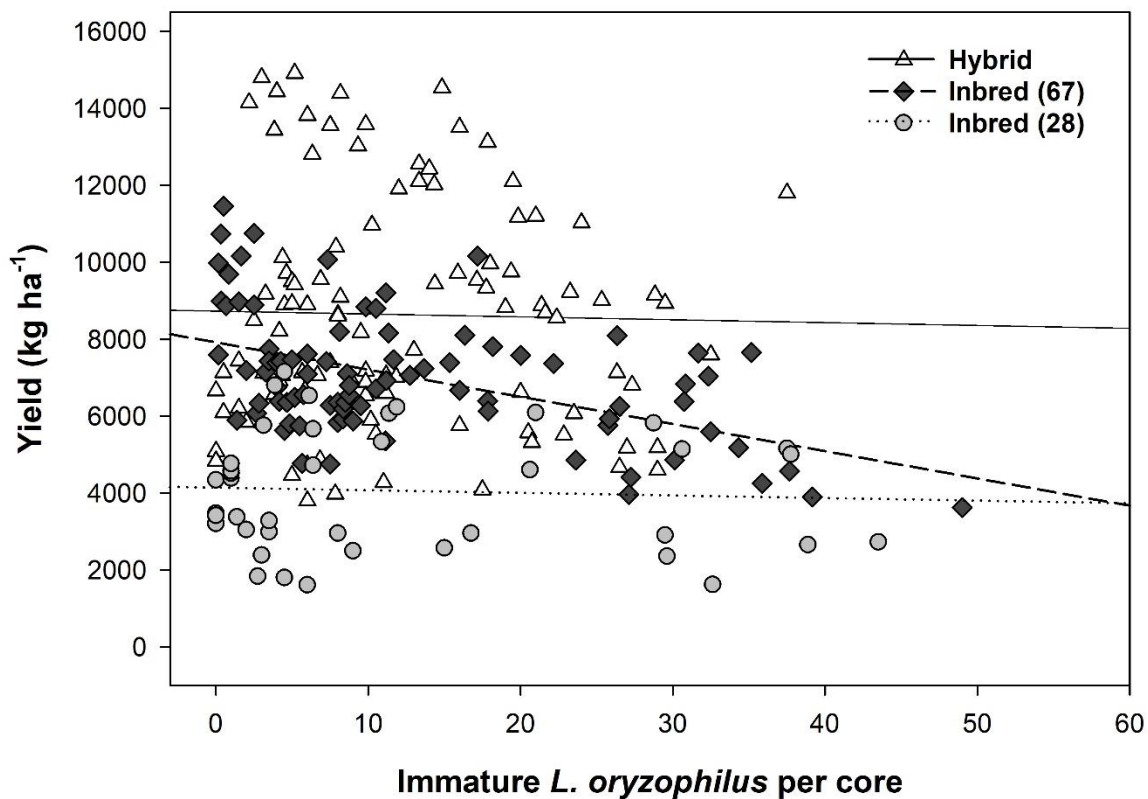


Figure 2.7. Relationships among rice yields and densities of immature *L. oryzaephilus* as affected by plant-type and seeding rate, 2016–2018. The slope of the relationship is significantly lower for inbred cultivars planted at 67 kg ha⁻¹ than for hybrid cultivars.

The finding of lower per-insect yield losses in hybrid cultivars is consistent with those of Zou et al. (2004), who reported that a hybrid cultivar, XP1003, possessed tolerance to *L. oryzaephilus*, and our data suggest further that this may apply generally across hybrids. However, it is important to realize that we did not control for phenotypic differences among cultivars related to their parentage, because the parental lines of hybrid cultivars could not be acquired (patent protection). Thus, hybrid cultivars were not compared to inbred cultivars possessing similar genetics.

Direct root injury (loss in root biomass) caused by *L. oryzaephilus* larval feeding was not evaluated in the study. This is because entire, intact root systems are very difficult to obtain from

field plots of rice grown under realistic conditions (i.e., at commercial seeding rates and under flooded conditions), and the number of plots employed in this study made direct measurements of injury cost- and labor-prohibitive. Rather, densities of immature *L. oryzaephilus* present on the roots of rice plants were used as a proxy for injury. A previous study conducted by Zou et al. (2004a) in Louisiana showed that the effects of *L. oryzaephilus* feeding on root biomass (injury) were correlated with densities of immature larvae and that the relationship between infestation and injury were similar among inbred cultivars and a hybrid cultivar.

The lack of consistency in tolerance of hybrid cultivars observed across years and locations suggests that tolerance to *L. oryzaephilus* is also influenced by environmental and other factors. Notably, chlorantraniliprole seed treatment, which effectively managed *L. oryzaephilus* infestations in protected plots, is also effective against stemborers (Sidhu et al., 2014; Wilson et al., 2015; Villegas et al., 2019). Unprotected plots were left vulnerable to stemborers in Louisiana and Texas where stemborers are established pests of rice, and differences in stemborer infestations among cultivars and among treated and untreated plots may have confounded the ability to detect differences in tolerance to *L. oryzaephilus* among hybrid and inbred cultivars.

Our results corroborate the findings of Horgan et al. (2016) with other rice pests. These authors concluded that hybrid lines were generally more tolerant of insect feeding than inbred lines (see also review by Horgan and Crisol 2013). They reported that hybrid rice lines were more tolerant of stemborer feeding as indicated by lower stemborer damage in hybrids when evaluated under field conditions. Several studies have similarly demonstrated that hybrid cultivars appear to be more tolerant to stemborers and other lepidopterans compared to inbred cultivars (Tan et al., 1983; Pang, 1987; Xu et al., 2007). Moreover, Horgan et al. (2016) reported that tolerance was generally higher in the hybrid lines and was, in part, a result of compensation

by redirection of resources away from shoots and towards grains and roots when hybrid lines were attacked by stemborers. Although traits associated with tolerance such as biomass, root-regrowth (compensation), nutrient allocation, and other parameters were not evaluated in our study, hybrids have physiological advantages over conventional inbreds due to heterosis (also known as hybrid vigor) which can be manifested across several traits such as increases in stature, growth rate, biomass accumulation, and yield potential (Yuan, 1994; Birchler et al., 2006; Horgan and Crisol, 2013). These traits may contribute to faster recovery from root injury in hybrid cultivars, thereby increasing tolerance to *L. oryzaephilus* infestations. Future studies should compare changes in plant physiology that occur in hybrid and inbred cultivars during *L. oryzaephilus* feeding to identify potential tolerance mechanisms.

N'guessan et al. (1994a, 1994b) found four experimental Louisiana rice lines that had moderate levels of tolerance to *L. oryzaephilus*; however, none of those experimental lines were released as commercial rice cultivars because of undesirable agronomic characteristics (i.e. susceptibility to lodging and extra short grain type). Nonetheless, their study showed that tolerance in the experimental lines may have resulted from increased root regrowth after heavy pruning by *L. oryzaephilus* larvae and better yield potential in tolerant lines compared to susceptible cultivars. Stout et al. (2001) and Zou et al. (2004a) also reported the presence of tolerance to *L. oryzaephilus* among some of the commercially available inbred rice cultivars in Louisiana. These studies all reported differences among cultivars in yield responses to insecticidal treatment, but their studies did not examine relationships with *L. oryzaephilus* densities. Our study has demonstrated differences among rice cultivars in yield responses on a per-insect basis, a critical component of tolerance (Painter 1951). In Japan, some rice cultivars were reported to be highly tolerant of *L. oryzaephilus* after screening around 150 rice varieties of

Japanese and foreign origin (Matsui, 1987). Similarly, a few rice cultivars were found to have some level of tolerance against *L. oryzaophilus* in China and Italy (Chen et al., 2005; Lupi et al., 2012).

Our results confirm the severity of *L. oryzaophilus* as a pest of rice in the southern U.S., where yield losses exceeding 25% due to feeding of *L. oryzaophilus* on rice roots have been previously reported (Stout et al., 2000). In particular, studies conducted by Stout et al. (2002), Zou et al. (2004), and Adams et al. (2016) have reported yield losses ranging from 0.3–4.1% per *L. oryzaophilus* larva. The *L. oryzaophilus* pressure in this study is consistent with commercial fields in the region (Hummel et al., 2014). The reductions in *L. oryzaophilus* densities in chlorantraniliprole-treated (protected) plots reported in this study are comparable to previous studies which demonstrated 72–96% reductions in *L. oryzaophilus* densities when rice was treated with chlorantraniliprole (Hamm et al., 2014; Hummel et al., 2014; Villegas et al., 2019). However, there were variations in *L. oryzaophilus* control by seed treatment across cultivars in this study. This suggests that efficacy of seed treatment may vary among cultivars and should be further examined.

The lack of influence of seeding rate on *L. oryzaophilus* densities in this study is consistent with a previous study that showed no evidence of oviposition preference by female *L. oryzaophilus* among rice plots planted at different seeding rates (Aghaee et al., 2015). Conversely, Stout *et al.* (2009) indicated that, although low seeding rates were sometimes associated with higher infestations of *L. oryzaophilus*, this association is inconsistent. This relationship warrants further investigation in studies that compare *L. oryzaophilus* densities on a per plant basis.

The similarity in infestation levels among cultivars in our results is consistent with previous studies by Saad et al. (2018) and Vyavhare et al. (2016) that reported little to no

differences in resistance to *L. oryzaophilus* among widely grown hybrid and inbred cultivars in Texas and Louisiana. These studies, together with results reported herein, add to a body of evidence over nearly four decades that *L. oryzaophilus* infestations are generally similar among commercial rice cultivars (Smith and Robinson, 1982; N'guessan and Quisenberry, 1992; Heinrichs and Quisenberry 1999; Stout et al., 2001). While most rice cultivars have limited potential to reduce *L. oryzaophilus* infestations, our results support that reduced yield losses can be achieved by planting cultivars tolerant to *L. oryzaophilus*.

Results from this study suggest that the integration of tolerant cultivars into the management program of *L. oryzaophilus* is a potentially valuable strategy, particularly when combined with other control tactics. The use of tolerant cultivars may be sufficient to reduce yield losses in the absence of insecticides where *L. oryzaophilus* pressure is low or in organic rice production systems. It is also a suitable alternative management approach in situations where insecticide use is not desirable, such as fields located in proximity to ponds used for crayfish production. Continued research into tolerance to *L. oryzaophilus* can enhance sustainability of future pest management in rice.

Chapter 3. Assessment of Tolerance and Resistance of Inbred Rice Cultivars to Combined Infestations of Rice Water Weevil and Stemborers

3.1. Introduction

Crop losses attributable to arthropod pests are estimated at 18–26% of annual crop production worldwide (Oerke, 2006; Culliney, 2014). These losses have occurred despite the extensive use of pesticides over the last several decades (Oerke and Dehne, 2004); thus, there is a need to develop alternative management approaches with less reliance on chemical inputs. In particular, plants possess defensive traits that can be employed in pest management. Stout (2013) developed a framework for differentiating plant defense strategies (resistance and tolerance) in a crop protection context. In this framework, the term ‘resistance’ broadly encompasses plant traits that reduce the extent of injury to a plant by arthropod herbivores, whereas ‘tolerance’ encompasses plant traits or physiological processes that reduce the amount of damage (in terms of plant fitness or yield loss) per unit injury. There is a need for studies that focus on both plant defense strategies in the context of pest management (Mitchell et al., 2016).

The rice water weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), is the most destructive and widely distributed early-season pest of rice (*Oryza sativa* L., Poaceae) in the USA (Way, 1990; Aghaee and Godfrey, 2014). Adult weevils typically cause minor injury to rice plants by feeding on leaf tissues, leaving characteristic narrow longitudinal scars parallel to the venation of the leaves (Stout et al., 2002). The majority of economic loss is caused by the soil-dwelling, root-feeding larval stage (Shang et al., 2004).

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Root pruning due to larval feeding can cause extensive injury to rice root systems, resulting in reductions in tiller numbers, grain weights, and grains per panicle (Zou et al., 2004a). Yield losses associated with unmanaged rice water weevil infestations can exceed 25% (Stout et al., 2000).

A complex of stem-boring lepidopteran pests (Crambidae) composed of the Mexican rice borer, *Eoreuma loftini* (Dyar), the sugarcane borer, *Diatraea saccharalis* (Fabricius), and the rice stalk borer, *Chilo plejadellus* Zincken, can infest USA rice from tillering to maturity (Harrell et al., 2019). Feeding by stemborer larvae in rice stems disrupts flows of nutrients, resulting in blanked panicles or ‘whiteheads’ (Chaudhary et al., 1984). Rice yields are negatively associated with numbers of whiteheads (Way et al., 2006a; Reay-Jones et al., 2007). Stemborers, particularly the invasive Mexican rice borer, are becoming increasingly problematic in the rice-producing regions of Louisiana, USA. The Mexican rice borer was first detected in southwest Louisiana in 2008 and has since become a consistent pest of rice (Hummel et al., 2010; Wilson et al., 2015a, 2017). Continued expansion of the Mexican rice borer in Louisiana rice is predicted to cause economic losses exceeding US \$40 million annually in the absence of effective management strategies (Reay-Jones et al., 2008).

Currently, insecticidal seed treatments are extensively used to control insect pests in rice in the southern USA (Wilson et al., 2019; Bateman et al., 2020). Seed treatments such as chlorantraniliprole, thiamethoxam, clothianidin, or cyantraniliprole are applied primarily to control the rice water weevil (Stout et al., 2011a; Hummel et al., 2014; Villegas et al., 2019; Wilson et al., 2021a). Chlorantraniliprole seed treatment also reduces injury by stemborers in rice (Sidhu et al., 2014; Wilson et al., 2015a; Villegas et al., 2019). Whereas insecticidal seed treatments have been effective, alternative control strategies need to be investigated. In

particular, the use of resistant or tolerant cultivars allows for more sustainable pest control and is compatible with other management tactics (Smith, 2005). Thousands of rice lines have been screened in the past for resistance to rice water weevil across the USA, but none of the lines evaluated to date possess high levels of resistance (Bowling, 1963; Smith and Robinson, 1982; N'Guessan & Quisenberry, 1992; N'Guessan et al., 1994a,b; Rice et al., 1994; Heinrichs & Quisenberry, 1999; Stout et al., 2001). More recently, Vyavhare et al. (2016) and Saad et al. (2018) reported very little variation in resistance to rice water weevil among rice cultivars that are widely grown in the southern USA. Conversely, susceptibility of Louisiana rice cultivars to stemborers, especially under field conditions, is not well studied due to the historically sporadic nature of infestations. However, with the increasing prevalence of the Mexican rice borer and subsequent impacts on Louisiana rice (Wilson et al., 2017), there is both an increased need and increased opportunity to investigate the susceptibility of rice lines and cultivars to stemborers. A study conducted by Way et al. (2006a) in Texas, USA, revealed varying levels of injury and yield losses among rice cultivars to stemborer infestations.

Due to the increasing prevalence of the Mexican rice borer, rice water weevils and stemborers are typically present in the same fields in Louisiana. No prior studies have investigated infestations by both pests or evaluated the combined impact of these insect pests on rice yields. The objectives of this study were to evaluate the influence of inbred rice cultivars commonly grown in Louisiana on infestation by both rice water weevils and stemborers under field conditions (resistance), and to assess whether yield losses associated with infestations by these pests differed among the rice cultivars (tolerance).

3.2. Materials and Methods

Field experiments were conducted from 2017 to 2019 at the Louisiana State University Agricultural Center, H. Rouse Caffey Rice Research Station in Crowley, LA, USA. Rice cultivars used in this study were selected from commonly grown inbred rice cultivars in Louisiana (Table 3.1) and represent ca. 50% of acreage planted in 2019 (Harrell, 2020). Seeds were drill-planted in plots measuring 5.5 m in length with seven rows spaced 18 cm apart at a seeding rate of 67 kg ha⁻¹ (Table 3.2). Pest infestation levels were manipulated by treating seeds with chlorantraniliprole (Dermacor X-100; Corteva Agriscience, Wilmington, DE, USA). Three rates of seed treatment were employed – 0 (nontreated), 7.9 (low rate), and 78.5 (label rate) g a.i. ha⁻¹ – in order to achieve high, moderate, and low infestation levels, respectively (Villegas et al., 2019). Seeds were treated following the methods of Lanka et al. (2014). Plots were laid out according to a split-plot randomized block design with four blocks. Each block contained a cultivar (whole-plot) × insecticide rate (split-plot) factorial arrangement. Fields were surface irrigated as needed to facilitate plant emergence and stand establishment. Permanent flood (5-10 cm) was applied 4-6 weeks after planting, depending on the year (Table 3.2). Field plots were maintained in accordance with water management, weed control, fertilization, and other production practices recommended for drill-seeded rice in Louisiana (Saichuk, 2014).

Numbers of rice water weevil immatures (larvae and pupae) were evaluated 3-4 weeks after permanent flood according to established procedures (N’Guessan and Quisenberry, 1992; Stout et al., 2001). Root-soil core samples, with each sample containing a minimum of one rice plant with intact roots, were taken from each plot using a metal corer (9.2 cm diameter, 7.6 cm deep). Core sampling was conducted twice in 2017 (four cores per plot, 768 samples total), twice in 2018 (three cores per plot, 576 samples total), and once in 2019 (three cores per plot, 288

samples total) (Table 3.2). Individual core samples were processed by washing the soil from the roots in 40-mesh screen sieve buckets that were then placed in basins of a saturated salt solution. Rice water weevil larvae were counted as they floated to the surface and pupae were counted by inspecting bottoms of sieve buckets. The numbers of larvae and pupae in the 3-4 core samples from each plot were averaged to obtain an estimate of densities of rice water weevil immatures in each plot.

Table 3.1. Rice cultivars used in this study.

Cultivar	Cultivar type	Grain type	Year released	Acreage (ha) ¹	Acreage (% of total)
Catahoula	Conventional inbred	Long	2008	7.3	0.004
Cheniere	Conventional inbred	Long	2003	20427.7	12
CL111	Herbicide tolerant inbred	Long	2010	20696.0	12
CL151	Herbicide tolerant inbred	Long	2008	5218.4	3
Cocodrie	Conventional inbred	Long	1997	182.5	0.11
Jazzman-2	Conventional inbred	Long	2011	119.4	0.07
Jupiter	Conventional inbred	Medium	2005	16026.4	10
Mermentau	Conventional inbred	Long	2012	15189.1	9

¹Acreage planted in 2019 in Louisiana, USA (Harrell, 2020). Total = 165750 ha.

Stemborer infestation in the field is commonly measured by examining whitehead densities (Reay-Jones et al., 2007). At 100% heading, whiteheads resulting from stemborer infestations were visually assessed in each plot (Table 3.2). The total number of whiteheads in each plot was recorded and converted to whiteheads per m². Whiteheads were collected and were brought back to the laboratory to retrieve and identify the stemborer species (Beuzelin et al., 2016).

Entire plots were harvested using a small-plot combine at grain maturity. Grain weights were adjusted to 12% moisture and converted to kg ha⁻¹. Yield losses (%) were calculated for each cultivar in each block, using the formula: % yield losses = [(yield_{protected} – yield_{infested})/yield_{protected}] × 100, where ‘protected yields’ were yields from plots treated with the label rate (78.5 g a.i. ha⁻¹) and ‘infested yields’ were yields from nontreated plots or plots treated with the low rate (7.9 g a.i. ha⁻¹) of chlorantraniliprole for a given block.

Table 3.2. Dates of agronomic practices and insect sampling in rice field experiments over 3 years.

Activity	2017	2018	2019
Planting	10 April	5 April	03 April
Permanent flood	19 May	15 May	31 May
First core sampling ¹	15 June	5 June	24 June
Second core sampling ¹	23 June	12 June	-
Whitehead count ²	25 July	20 July	24 July
Harvest	01 September	30 August	28 August

¹Root-soil core sampling for rice water weevils. ²Whiteheads (blanked panicles) are a measure of stemborer damage.

Initially, multivariate analysis was performed with weevil count, whitehead density, and yield as response variables and cultivar, seed treatment, and year as fixed variables using Proc GLM. To interpret the overall significant results at multivariate level, appropriate univariate tests were utilized. Rice water weevil data were analyzed using repeated-measures generalized linear mixed-models (Proc GLIMMIX) with cultivar, seed treatment, year, and their interactions as fixed effects, sampling time as a repeated measure, and block(year) as a random effect. The analysis of rice water weevil data was modelled using a Poisson distribution. Whitehead density and yield loss data were analyzed using generalized linear-mixed models (Proc GLIMMIX) with cultivar, seed treatment, year, and their interactions as fixed effects and block(year) as a random

effect. The analyses were modelled using the Gaussian distribution. Residuals were examined (Proc UNIVARIATE) to ensure normality and homogeneity of variances. Yield loss data were arcsine transformed prior to analysis but untransformed means are presented. For all analyses, Kenward-Roger adjustment was used to calculate error degrees of freedom and Tukey's honestly significant difference (HSD) post hoc analysis ($\alpha = 0.05$) was used for all mean separations.

Because pest infestation levels were deliberately manipulated in the study, the influence of cultivar, rice water weevil density, and whitehead density on rice yields were examined using ANCOVA (Proc GLM). Previous studies have reported that the rice cultivar 'Cocodrie' appeared to be somewhat tolerant to rice water weevil infestations (Stout et al., 2001; Zou et al., 2004b) and moderately tolerant to stemborers (Way et al., 2006a); thus, pairwise slope comparisons (yield \times rice water weevil density) were conducted between Cocodrie and other cultivars (Proc GLM). Linear relationships between rice water weevil densities and yields for each cultivar were analyzed using Proc REG to estimate yield loss on a 'per weevil' basis. All analyses were performed in SAS v.9.4 (SAS Institute, Cary, NC, USA).

3.3. Results

Multivariate analysis indicated overall effects of year ($F_{6,490} = 96.69$), cultivar ($F_{21,704.06} = 6.16$), and seed pesticide treatment ($F_{6,490} = 67.24$, all $P < 0.001$) on response variables. Univariate analyses of the effects of year, cultivar, and seed treatment on rice water weevil immatures, whiteheads, and yield loss were next conducted.

Numbers of immature rice water weevils (larvae and pupae) on roots of rice plants were influenced by main effects (year, cultivar, and seed treatment) and interactions (year*seed treatment and year*cultivar*seed treatment) (Table 3.3). Results are presented for all main effects (Fig. 3.1) and the highest order interaction (Fig. 3.2). The medium-grain rice cultivar

Jupiter supported 31-51% more weevils than Cocodrie, Mermentau, or Cheniere, whereas weevil numbers in plots of the other four cultivars were intermediate (Fig. 3.1A). Rice water weevil immatures were reduced by 86 and 44% in plots treated with label and low rates of chlorantraniliprole, respectively, compared to nontreated plots across all years and cultivars (Fig. 3.1B). Weevil numbers in 2019 were 82 and 162% higher than in 2017 and 2018, respectively (Fig. 3.1C).

In 2017, 45% of the stemborer larvae recovered from plants showing whitehead symptoms were Mexican rice borers and 55% were a combination of sugarcane borers and rice stalk borers. In 2018 and 2019, in contrast, 100% of the recovered larvae were Mexican rice borers. Whitehead densities were influenced by cultivar, seed treatment, and the year*seed treatment interaction (Table 3.3). High levels of stemborer injury were observed in rice cultivars CL151, Cocodrie, and Mermentau, whereas low levels of stemborer injury were observed in Cheniere and Jazzman-2 (Fig. 3.3A). Treatment of seeds with chlorantraniliprole at the label rate reduced whitehead densities by 63 and 59% compared to nontreated plots and plots treated with low rate of chlorantraniliprole, respectively (Fig. 3.3B). Whitehead densities were consistent across years. Seed treatment at the label rate provided a greater level of stemborer control in 2019 (80-85%) relative to 2017 (31-49%) (Fig. 3.3C).

Table 3.3. Results from generalized linear mixed models of the effects of year, cultivar, seed pesticide treatment, and their interactions on rice water weevil densities, whitehead densities (a measure of stemborer damage), and rice yield loss

Fixed effect	Weevil densities			Whitehead densities			Yield loss		
	d.f. ¹	F	P	d.f. ²	F	P	d.f. ³	F	P
Year	2	149.71	<0.001	2	0.61	0.55	2	7.94	<0.001
Cultivar	7	3.34	0.002	7	13.18	<0.001	7	0.64	0.72
Seed treatment	2	569.39	<0.001	2	30.00	<0.001	1	4.32	0.04
Year*cultivar	14	1.01	0.44	14	1.64	0.07	14	1.32	0.21
Year*seed treatment	4	12.29	<0.001	4	3.42	0.01	2	2.18	0.12
Cultivar*seed	14	1.55	0.09	14	1.62	0.08	7	0.49	0.84
treatment									
Year*cultivar*seed	28	1.87	0.004	28	1.31	0.15	14	0.69	0.78
treatment									

¹Denominator d.f. = 1557. ²Denominator d.f. = 184. ³Denominator d.f. = 141.

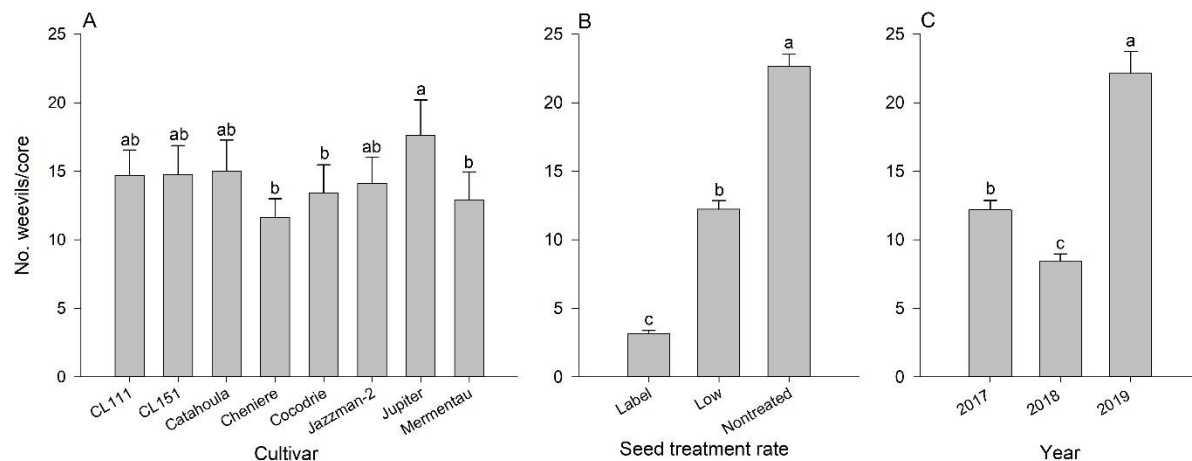


Figure 3.1 Mean (+ SE) number of rice water weevil immatures per root-soil core as affected by (A) rice cultivar, (B) seed pesticide treatment, and (C) year (n = 288). Seeds were treated with chlorantraniliprole at 78.5 (label), 7.9 (low), or 0 (nontreated) g a.i. ha⁻¹. Means within a panel capped with the same letter are not significantly different (Tukey's HSD: P>0.05).

Percent yield losses from combined infestations of rice water weevils and stemborers (relative to yields in plots treated with the label rate of chlorantraniliprole) were affected by year and seed treatment, but not by cultivar or any of the interactions (Table 3.3). Yield losses from plots under high pest infestation levels (nontreated plots) were 37% greater than losses under moderate infestation levels (low rate) (Fig. 3.4A). Lower yield losses were observed in 2018 compared to 2017 or 2019 (Fig. 3.4B). Yield losses among cultivars ranged from 10 to 18%, but differences were not significant (Fig. 3.4C).

Yields varied among cultivars after controlling for rice water weevil and whitehead densities (ANCOVA: $F_{7,250} = 2.33$, $P = 0.03$). Furthermore, yields were negatively associated with densities of both rice water weevil immatures and whiteheads; however, the association between whitehead densities and yields ($F_{1,256} = 2.99$, $P = 0.09$) was weaker than the association between rice water weevil densities and yields ($F_{1,256} = 9.36$, $P = 0.003$). Slope comparisons (yield \times rice water weevil density) between Cocodrie and other cultivars revealed that Cheniere was less tolerant to weevil infestations than Cocodrie (mean \pm SE = 92 ± 32 vs. 8 ± 19 kg yield loss per weevil per core; $F_{1,69} = 5.13$, $P = 0.03$) (Fig. 3.5). No differences in slopes were detected between Cocodrie and the remaining cultivars.

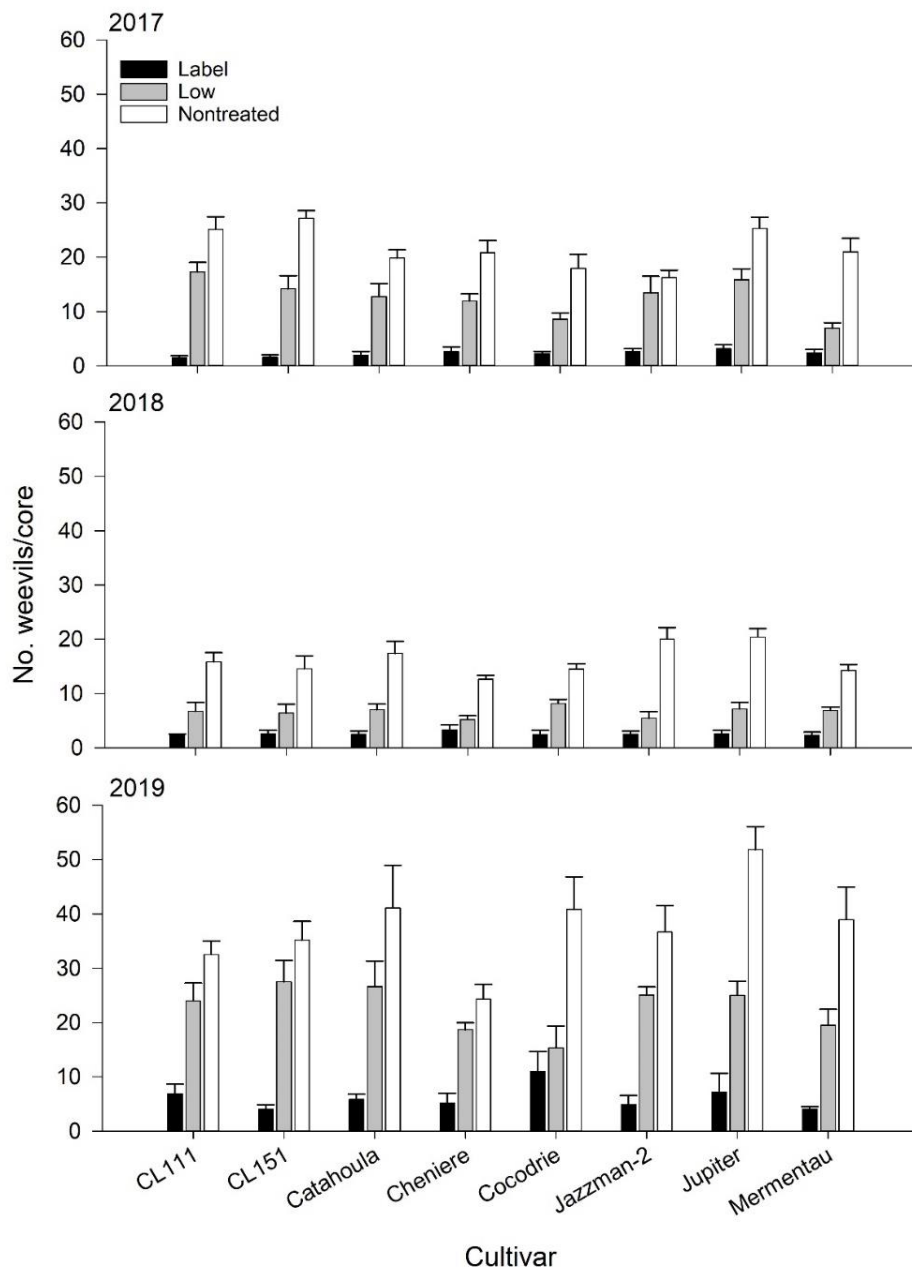


Figure 3.2. Mean (+ SE) number of rice water weevil immatures per root-soil core for eight rice cultivars and seed pesticide treatments in 2017, 2018, and 2019 (n = 288). Seeds were treated with chlorantraniliprole at 78.5 (label), 7.9 (low), or 0 (nontreated) g a.i. ha⁻¹.

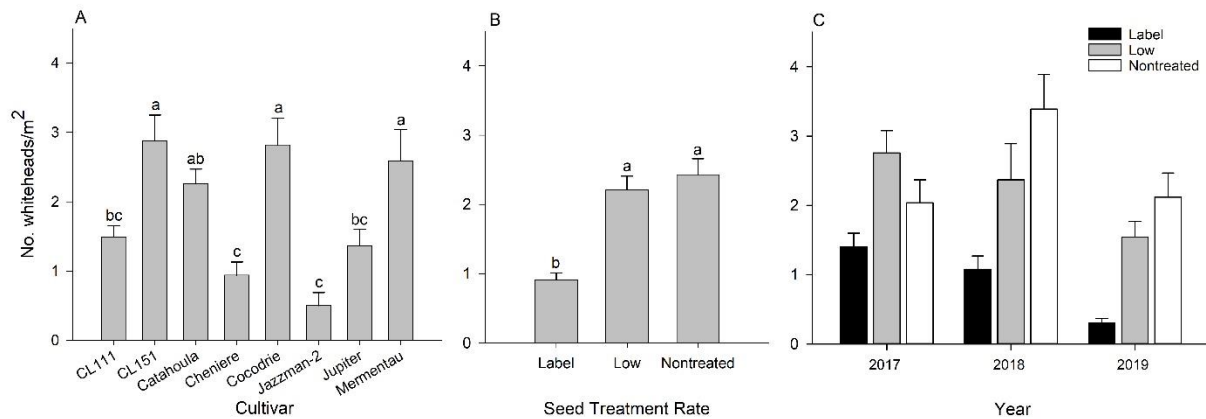


Figure 3.3. Mean (+ SE) whitehead (blanked panicle) densities as affected by (A) rice cultivar, (B) seed pesticide treatment, and (C) seed treatment \times year interaction ($n = 288$). Seeds were treated with chlorantraniliprole at 78.5 (label), 7.9 (low), or 0 (nontreated) g a.i. ha⁻¹. Means within a panel capped with the same letter are not significantly different (Tukey's HSD: $P > 0.05$).

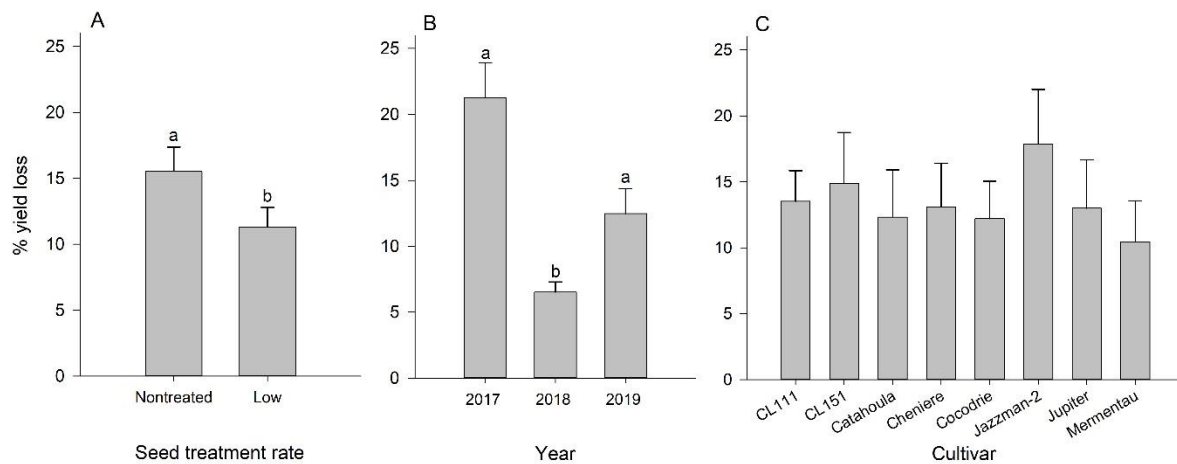


Figure 3.4. Mean (+ SE) yield losses (%), relative to plots treated with a label rate of chlorantraniliprole, as affected by (A) seed pesticide treatment, (B) year, and (C) rice cultivar ($n = 288$). Seeds were treated with chlorantraniliprole at 78.5 (label), 7.9 (low), or 0 (nontreated) g a.i. ha⁻¹. Means within a panel capped with the same letter are not significantly different (Tukey's HSD: $P > 0.05$).

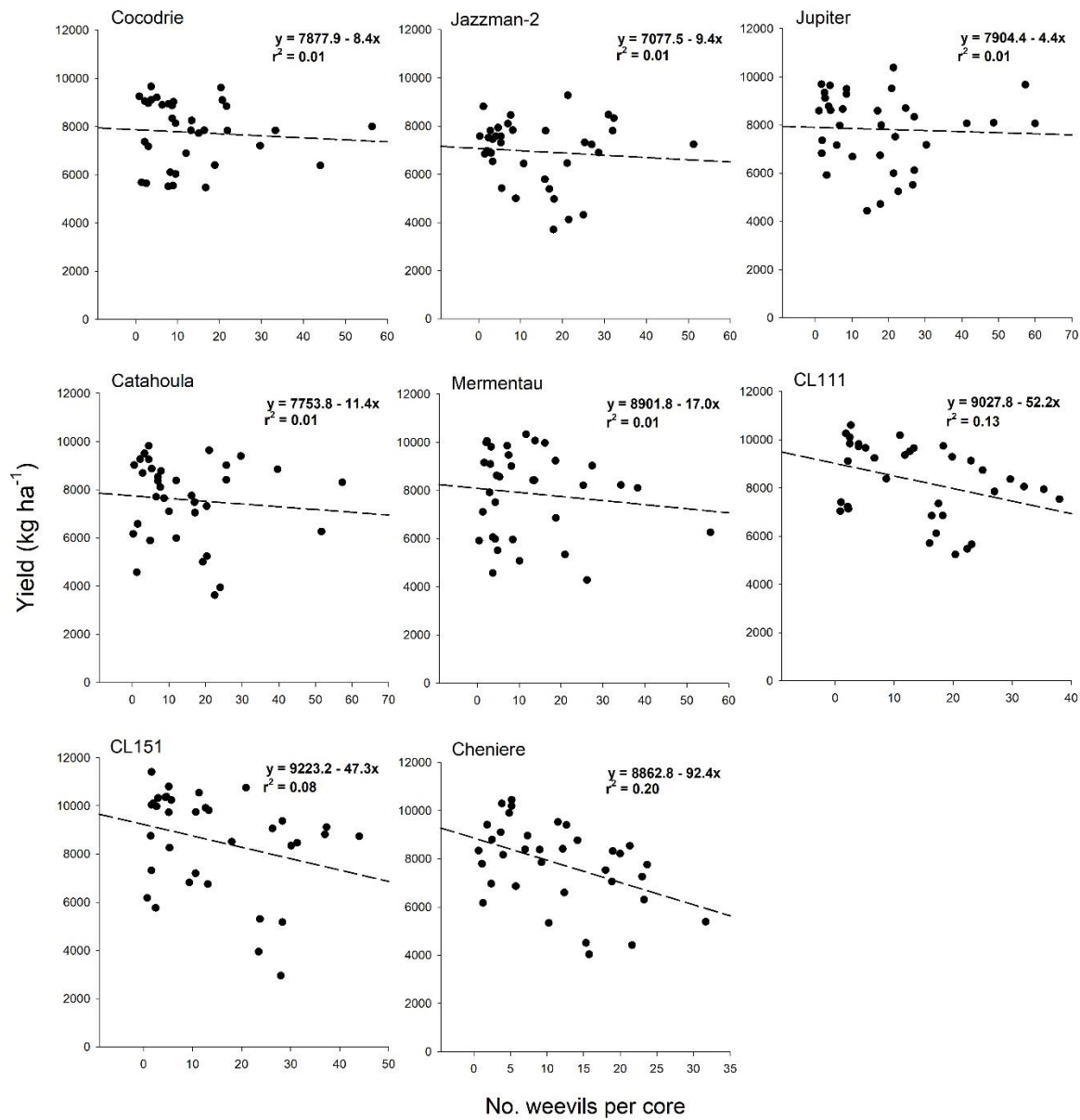


Figure 3.5. Linear relationships between yield (kg ha^{-1}) and number of immature rice water weevils per root-soil core for eight rice cultivars. Data from 2017–2019 are combined ($n = 36$).

3.4. Discussion

Results from this study demonstrate substantial reductions in rice yields from combined infestations of rice water weevils and stemborers. The >15% yield loss in non-pesticide-treated plots observed over the 3 years of this study demonstrates the significant economic impact from

the combined infestations of weevils and stemborers. The use of chlorantraniliprole seed treatment, which reduced both whitehead and rice water weevil densities, limits the degree to which losses from weevils and stemborers can be distinguished. Prior studies have reported yield losses of 2-33% due to rice water weevil infestations (Stout et al., 2000, 2001, 2011b), and Reay-Jones et al. (2007) reported a reduction of 2% in rice yields for each whitehead per m² caused by mixed infestations of sugarcane borer and Mexican rice borer in Texas. However, the impact of stemborers in Louisiana rice, particularly the invasive Mexican rice borer, is not well established. Given the importance of rice water weevil in Louisiana rice and the consistently high levels of infestation in this study, the majority of yield loss reported in this study was probably attributable to weevils. This is further supported by the weak association between whitehead densities and yields found in the ANCOVA. Nevertheless, the economic importance of stemborers relative to weevils could change if stemborer incidence continues to increase. Future studies should attempt to differentiate impact of these insect pests on rice yields.

Similar to earlier studies, this study showed little variation in resistance to weevils as measured by densities of immature weevils on rice roots 3-5 weeks after flooding (Stout et al., 2001; Vyavhare et al., 2016; Saad et al., 2018). The rice cultivar Jupiter, a popular medium-grain rice in Louisiana, was also found to be the most susceptible to rice water weevil in a previous study (Saad et al., 2018), and medium-grain cultivars in general appear to be more susceptible to infestation than long-grain cultivars (Stout et al., 2001). Tolerance in this study was determined by comparing yields in infested (nontreated or low rate of chlorantraniliprole) and protected (label rate of chlorantraniliprole) rice plants of the same cultivar. The differences in yield loss among inbred cultivars observed in this study were minimal, suggesting that, in general, these cultivars do not differ in levels of tolerance. However, when yield loss per weevil relationships

were considered, yield loss was 11-fold greater in Cheniere relative to Cocodrie. A study conducted by Villegas et al. (2021) reported differences in tolerance among hybrid and inbred rice cultivars to the rice water weevil, with hybrid cultivars, which were not included in this study, generally suffering lower yield losses than inbred cultivars. Similarly, N'Guessan et al. (1994a,b) reported that several experimental rice lines had moderate levels of tolerance to rice water weevil with yield losses that ranged from 5 to 12%, but these lines were not released as commercial cultivars because of undesirable agronomic characteristics. In the current study, the presence of stemborers at damaging levels in addition to rice water weevils may have obscured varietal differences in tolerance to the rice water weevil. Furthermore, rates of root consumption differ markedly among age classes of rice water weevil immatures (Wu and Wilson, 1997). Age classes of larvae infesting rice roots were not monitored in this study, and age classes of larvae on roots may have differed among cultivars and sampling dates. The addition of this information would provide a better understanding of the relationships between densities of weevil immatures and rice yields.

The severity of stemborer infestations was similar across years (1.3-2.2 whiteheads per m²). In contrast, weevil densities varied across years but were high in all 3 years of the study (8.5–22 immature weevils per core). Factors that affect weevil densities include nitrogen fertilization (Way et al., 2006b), planting date (Stout et al., 2011b), seeding rate (Stout et al., 2009), and timing of flood (Zou et al., 2004b). The lower weevil densities observed in 2018 may have been due to lower spring temperatures relative to 2017 or 2019 as reported in the Louisiana Agriclimatic Information System (<https://weather.lsuagcenter.com>). This, in part, may explain the low overall yield losses observed in 2018. Interestingly, weevil densities were highest in 2019 but yield losses were relatively low. Establishment of permanent flood in 2019 was ca. 2

weeks later than in 2017 or 2018, which delayed weevil infestations until rice plants were older. Tolerance of rice to weevils may have been influenced by plant age. In fact, Stout et al. (2002) reported that young rice plants appeared to be less tolerant than older plants to weevil injury and Zou et al. (2004b) showed that delaying flood led to increased tolerance to rice water weevil infestations. In addition, Wu and Wilson (1997) reported that the greater the number of degree days since planting to peak fourth-instar weevil density, the lower the resulting injury for a particular larval population size. Future studies should examine plant tolerance alongside cultural controls including flood timing.

Pheromone trapping data and field sampling shows that the invasive Mexican rice borer has become firmly established in the rice-producing region of southwest Louisiana since its initial detection in 2008 (Hummel et al., 2010; Wilson et al., 2017). Results from this study suggest that Mexican rice borer may have surpassed the sugarcane borer and the rice stalk borer in economic importance as indicated by high recoveries of Mexican rice borer larvae from whiteheads in 2018 and 2019. Mexican rice borer, like the sugarcane borer, attacks other crops such as sugarcane (*Saccharum* spp.), maize (*Zea mays* L.), and sorghum [*Sorghum bicolor* (L.) Moench] (Showler & Reagan, 2012; Showler et al., 2012). Mexican rice borer was also detected in Florida in 2012 and, although it has not been established in rice yet, range expansion toward the rice and sugarcane production area of Florida is expected (Hayden, 2012; Roldan et al., 2020).

In contrast to results with the rice water weevil, our results demonstrate substantial variation in susceptibility among rice cultivars to stemborers. Low levels of stemborer injury were observed in Cheniere and Jazzman-2, suggesting that these cultivars express traits that confer resistance to stemborers. Our results are consistent with the findings of Way et al.

(2006a), who reported low levels of stemborer injury (mixed infestations by Mexican rice borer and sugarcane borer) in Cheniere when evaluated under field conditions in Texas. In contrast, high sugarcane borer injury in Cheniere was observed in a field experiment conducted in northeast Louisiana (Sidhu et al., 2013). Moreover, Hamm et al. (2011) reported oviposition preference by sugarcane borer for Cheniere, especially at the tillering stage of development. This suggests that resistance to one stemborer species is not necessarily associated with resistance to another stemborer species. This has been observed in sugarcane, in which the cultivar HoCP 04-838 is highly susceptible to the Mexican rice borer but resistant to sugarcane borer (Zhou et al., 2010; Wilson et al., 2015b, 2021b). Several plant traits such as stem diameter, plant height, length and width of flag leaf, tight leaf sheaths, thick layers of sclerenchymatous or lignified plant tissues, narrow stem lumen, and physiological and biochemical factors influence stemborer resistance (Chaudhary et al., 1984). In Asia, the use of resistant rice cultivars is an important component of integrated pest management for stemborers (Zhu et al., 2007). In sugarcane and sorghum, deployment of resistant cultivars has successfully reduced yield losses caused by the Mexican rice borer and sugarcane borer (VanWeelden et al., 2015; Wilson et al., 2015b, 2018). Thus, plant resistance has the potential to be a critical tactic for managing stemborers in Louisiana rice.

Current management programs for stemborers and the rice water weevil rely on prophylactic applications of seed treatments, and there is a need for a more holistic approach to pest management in rice. Studies evaluating host plant resistance to insect pests in any crop should be conducted in a manner by which both resistance and tolerance are considered. The current study indicates that resistance may be a useful tactic against stemborers in the USA, whereas tolerance in inbred cultivars may have limited use against both pests. In contrast, hybrid

rice cultivars potentially possess a degree of tolerance to weevils (Villegas et al., 2021); thus, future studies are needed to investigate mechanisms of tolerance, which may provide valuable insights into why some cultivars, particularly hybrids, are more tolerant to weevils. The use of resistant cultivars in combination with other management tactics may reduce yield impacts, especially if stemborer incidence continues to increase in Louisiana rice.

Chapter 4. Integration of Host Plant Resistance and Cultural Tactics for Management of Root- and Stem-Feeding Insect Pests in Rice

4.1. Introduction

Rice, *Oryza sativa* L., is one of the most important crops globally and is consumed by more than half of the world's population (Mohanty, 2013). Rice in the southern U.S. is predominantly cultured by drill-seeding in dry soil followed by the establishment of permanent flood 4–6 weeks after planting. Of the approximately 180,000 ha of rice planted in Louisiana in the past two years, 70% was cultured in this manner (Harrell, 2020). In the U.S., the rice water weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), is the most destructive early-season pest of rice (Aghaee and Godfrey, 2014; Way, 1990). Adult weevils overwinter in leaf litter, bunch grasses, and stubble in and around rice fields and typically emerge from overwintering in early spring (Shang et al., 2004). When rice plants are available, adult weevils feed on the leaves of rice plants, leaving narrow longitudinal scars parallel to the venation of the leaves. Injury from adult feeding is generally not considered economically important except under unusually heavy infestations (Stout et al., 2013). The establishment of permanent flood in rice fields triggers female weevils to lay eggs in rice leaf sheaths beneath the water surface (Stout et al., 2002b). The majority of economic loss is caused by the soil-dwelling, root-feeding weevil larvae which cause extensive injury to rice root systems, resulting in reductions in tiller numbers, grain weights, and grains per panicle (Shang et al., 2004; Zou et al., 2004a). Yield losses can exceed 25% if rice water weevil infestations are left unmanaged (Stout et al., 2000).

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A complex of stem-boring lepidopteran pests (Lepidoptera: Crambidae) attacks U.S. rice from tillering to maturity with the predominant species in Louisiana being the Mexican rice borer, *Eoreuma loftini* (Dyar) (Beuzelin et al., 2016; Way, 2003). Larval feeding in rice stems disrupts flow of nutrients to the developing grains, resulting in blanked panicles or “whiteheads” (Chaudhary et al., 1984). Stemborer activity in the field is usually measured by evaluating whitehead density, which is negatively associated with rice yield (Reay-Jones et al., 2007a; Way et al., 2006a; Wilson et al., 2021a). Stemborers, particularly the invasive Mexican rice borer, are becoming increasingly problematic in southwestern Louisiana. The Mexican rice borer has become firmly established in the state’s rice production area as indicated by continued expansion over the past decade and high population density in many regions (Wilson et al., 2017, 2015). Economic losses in Louisiana rice are predicted to reach up to US \$40 million annually if infestations of the Mexican rice borer are not managed (Reay-Jones et al., 2008). Insecticidal seed treatments are currently the most widely used control tactic against insect pests of rice in the southern U.S. (Bateman et al., 2020; Wilson et al., 2019). Seed treatments are applied primarily to control the rice water weevil (Hummel et al., 2014; Stout et al., 2011a; Villegas et al., 2019; Wilson et al., 2021a, 2021b), but seed treatments containing chlorantraniliprole also reduce stemborer injury in rice (Sidhu et al., 2014; Villegas et al., 2019). Despite the effectiveness of insecticidal seed treatments against weevils and stemborers, alternative management strategies need to be investigated to reduce reliance on chemical control and mitigate resistance development. Recent studies reported that some rice cultivars grown in the southern U.S. were able to tolerate infestations by rice water weevil (Villegas et al., 2021a, 2021b). Tolerant crop cultivars are generally able to withstand pest injury and produce adequate yields such that tolerant genotypes suffer lower yield losses than susceptible genotypes when

subjected to similar levels of infestation or injury (Flinn et al., 2001; Smith, 2005). Previous studies also indicated that water management practices such as delaying application of permanent flood can reduce infestations and impacts of rice water weevil (Rice et al., 1999; Stout et al., 2001). When flooding is delayed until rice plants are older (after rice plants have begun tillering), the period of time in which rice plants are vulnerable to weevils is shortened, resulting in reductions in weevil infestations (Stout et al., 2013). The effect of delayed flood timing on stemborer injury in rice is unknown. Manipulation of planting date has also been investigated as a tactic for reducing weevil infestations. Rice planted earlier within the recommended range of planting dates is often subject to lower levels of weevil infestations (Stout et al., 2011b). This study was conducted to evaluate the influence of rice cultivars and flood timing on the infestations of rice water weevil and stem borers and the corresponding impacts on rice yields.

4.2. Materials and Methods

Four field experiments were conducted from 2019 to 2020 at the LSU AgCenter H. Rouse Caffey Rice Research Station in Crowley, Louisiana. In each year, two separate trials were established – one planted early and the other late relative to recommended planting dates (Table 4.1). For each trial, field plots were laid out according to a split-split-plot randomized block design with four blocks. Each block contained a flood timing (whole-plot) \times cultivar (sub-plot) \times insecticidal seed treatment (sub-sub plot) field plot arrangement. Rice cultivars used in this study are commonly grown in Louisiana which include two long-grain cultivars ('Cocodrie' and 'Mermentau'), a specialty long-grain cultivar ('Jazzman-2'), and a medium-grain cultivar ('Jupiter'). The rice cultivar 'Jupiter' has been reported susceptible to rice water weevil (Saad et al., 2018). Seeds were drill-planted at a seeding rate of 67 kg ha⁻¹ in plots measuring 5.5

m in length with seven rows spaced 18 cm apart. Before planting, each cultivar was either treated or not treated with chlorantraniliprole seed treatment (Dermacor[®] X-100, Corteva Agriscience, Wilmington, Delaware) at a rate of 78.5 g a.i. ha⁻¹ following the methods of Lanka et al. (2014). Dates of key production practices and data collection varied among trials (Table 4.1). After planting, fields were surface irrigated as needed to facilitate plant emergence and stand establishment. When the rice plants reached the five-leaf to early tillering developmental stage, permanent flood was applied to plots assigned to the normal flood timing treatment, whereas permanent flood was applied two weeks later to plots assigned to delayed flood timing. Field plots were maintained following the standard recommendations for weed control and fertilization for drill-planted rice in Louisiana (Saichuk, 2014).

Table 4.1. Field activities and corresponding dates.

Activity	2019				2020			
	Early-Planted		Late-Planted		Early-Planted		Late-Planted	
	Normal Flood	Delayed Flood	Normal Flood	Delayed Flood	Normal Flood	Delayed Flood	Normal Flood	Delayed Flood
Planting	Mar 22	Mar 22	May 17	May 17	Mar 16	Mar 16	May 22	May 22
Urea application	May 17	Jun 4	Jul 1	Jul 22	Apr 27	May 12	Jun 30	Jul 15
Permanent flood	May 19	Jun 5	Jul 3	Jul 24	Apr 29	May 13	Jul 1	Jul 16
Core sampling 1	Jun 11	Jun 28	Jul 24	Aug 15	May 21	Jun 3	Jul 22	Aug 4
Core sampling 2	Jun 28	Jul 5	Jul 30	Aug 22	May 27	Jun 12	Jul 29	Aug 11
Whitehead count	Jul 23	Jul 23	Aug 28	Aug 28	Jul 14	Jul 14	Sep 1	Sep 1
Harvest	Aug 22	Aug 22	Sep 23	Sep 23	Aug 12	Aug 12	Oct 6	Oct 6

Immature rice water weevil (larvae and pupae) densities were evaluated 3–6 weeks after permanent flood according to established procedures (N’guessan and Quisenberry, 1992; Stout et al., 2001). Root-soil core samples were taken from each plot using a metal corer (9.2 cm diameter \times 7.6 cm depth). Core sampling was conducted twice, and three core samples were taken in each plot per sampling time (768 samples total per year). Each core sample contained a minimum of one rice plant with intact roots, and each sample was processed by washing the soil from roots in a 40-mesh screen sieve bucket. The bucket was then placed in a basin with a salt-water solution. Rice water weevil larvae were counted as they floated to the surface of the solution and pupae were counted by inspecting bottoms of sieve buckets. Prior to analysis, the mean number of larvae and pupae across the three core samples from each plot was calculated.

Stemborer injury was evaluated when rice plants reached 100% heading. Number of whiteheads resulting from stemborer infestations were visually assessed and recorded in each plot. Whiteheads were collected and were brought back to the laboratory to retrieve and identify the stemborer species. Prior to analysis, the total number of whiteheads in each plot was converted to whiteheads per m².

When rice plants reached grain maturity, entire plots were harvested using a small-plot combine (Wintersteiger Delta Plot Combine, Wintersteiger Inc., Salt Lake City, UT). Rough grain weights were adjusted to 12% moisture and converted to kg ha⁻¹. Percentage yield loss was calculated for each cultivar using the formula: % yield loss = [(yield_{treated} – yield_{nontreated})/yield_{treated}] \times 100.

The experimental design utilized in this study allowed the effects of cultivar, flood timing, and seed treatment to be analyzed statistically but did not allow statistical comparisons among planting dates because of insufficient replications. To avoid over-parameterization of the

statistical model, data were analyzed separately by year and planting date. All analyses were performed in SAS version 9.4 (SAS Inst., Cary, NC). Rice water weevil and whitehead data were analyzed using generalized linear mixed-models (PROC GLIMMIX) with flood timing, cultivar, seed treatment, and their interactions as fixed effects and core date as a repeated-measure (weevil data only). Random effects were block, block \times flood, block \times flood \times cultivar, and block \times flood \times cultivar \times treatment (weevil only). Yield loss data were analyzed using the same model with cultivar, flood timing, and their interactions as fixed effects and block and block \times flood as random effects. The analyses were modeled using a Gaussian distribution. Data residuals were examined (PROC UNIVARIATE) to ensure normality and homogeneity of variances. Weevil and whitehead data were log and square root transformed, respectively, prior to analyses but untransformed means and standard errors are presented. Kenward-Roger adjustment was used to calculate error degrees of freedom. Tukey's HSD post hoc analysis ($\alpha = 0.05$) was used for all mean separations.

4.3. Results

Flood timing, cultivar, and insecticidal seed treatment influenced rice water weevil densities in all planting dates and years except cultivar and flood timing in the 2019 early-planted trial (Table 4.2). In the 2019 field experiments, insecticidal seed treatment reduced weevil densities by 83–84% across planting dates, cultivars, and flood timings (Fig. 4.1A). Weevil densities were greater in plots planted with 'Jupiter' than plots planted with 'Cocodrie' or 'Mermentau' in the late-planted trial only (Fig. 4.1B). Weevil densities were reduced by approximately 72% in plots subjected to delayed flood compared to normal flood timing across insecticide treatments and cultivars in the late-planted trial (Fig. 4.1C). Immature weevils captured in the second core sampling were greater than the first core sampling in the late-planted

trial but no effects of core date were observed in the early-planted trial (Table 4.2; data not shown). In the 2020 field experiments, insecticidal seed treatment reduced weevil densities by 70–84% across planting dates, cultivars, and flood timings (Fig. 4.1D). The rice cultivar ‘Jupiter’ had greater weevil densities compared to other cultivars in both the early- and late-planted trials (Fig. 4.1E). Delayed flood reduced weevil densities by 20% across insecticide treatments and cultivars in the late-planted trial but increased weevil densities by 16% in the early-planted trial (Fig. 4.1F). Weevil counts on the second core sampling were higher compared to the first core sampling in the early-planted trial only (Table 4.2; data not shown).

Table 4.2. Results of repeated measures general linear mixed models (repeated-GLIMMIX) for rice water weevil densities in 2019 and 2020 field trials at Crowley, Louisiana.

Fixed Effect	df	2019				2020			
		Early-Planted		Late-Planted		Early-Planted		Late-Planted	
		F	P	F	P	F	P	F	P
Cultivar	3	2.15	0.106	12.88	<0.001	21.48	<0.001	22.69	<0.001
Insecticide Trt	1	311.79	<0.001	656.82	<0.001	392.97	<0.001	180.53	<0.001
Flood	1	0.32	0.574	312.37	<0.001	4.28	0.044	4.99	0.030
Cultivar × Insecticide Trt	3	0.66	0.583	1.60	0.203	2.36	0.083	0.95	0.426
Cultivar × Flood	3	0.68	0.569	0.75	0.527	1.32	0.280	2.31	0.088
Insecticide Trt × Flood	1	1.17	0.286	123.49	<0.001	0.05	0.827	0.19	0.667
Cultivar × Insecticide Trt × Flood	3	1.20	0.318	2.68	0.058	0.65	0.585	3.04	0.038
Core date	1	1.89	0.175	4.64	0.036	25.19	<0.001	0.20	0.658
Core × Cultivar	3	0.51	0.679	2.26	0.093	0.46	0.714	0.87	0.463
Core × Insecticide Trt	1	0.02	0.894	0.03	0.874	0.88	0.352	1.22	0.274
Core × Flood	1	3.46	0.069	120.98	<0.001	1.08	0.304	24.56	<0.001
Core × Cultivar × Insecticide Trt	3	0.18	0.912	1.14	0.343	0.78	0.510	0.32	0.812
Core × Cultivar × Flood	3	0.97	0.416	1.39	0.257	0.61	0.610	0.44	0.727
Core × Insecticide Trt × Flood	1	13.99	<0.001	4.58	0.037	0.22	0.643	1.18	0.282
Core × Cultivar × Insecticide Trt × Flood	3	0.45	0.717	0.33	0.802	3.44	0.024	1.04	0.384
Error	48								

No interactions were detected among cultivar, insecticide treatment, and flood timing in the 2019 and 2020 early-planted trials (Table 4.2; Figs. 4.2A, C). There were significant insecticide treatment × flood interaction and marginally significant cultivar × insecticide treatment × flood interaction observed in the 2019 late-planted trial (Table 4.2). Weevil densities

were greater in nontreated plots subjected to normal flood timing (Fig. 4.2B). In the 2020 late-planted trial, cultivar \times insecticide treatment \times flood interaction was detected with the greatest weevil density observed on nontreated plots planted with ‘Jupiter’ and subjected to normal flood timing (Fig. 4.2D). Additional two- and three-way interactions involving core date were detected in some trials (Table 4.2; data not shown).

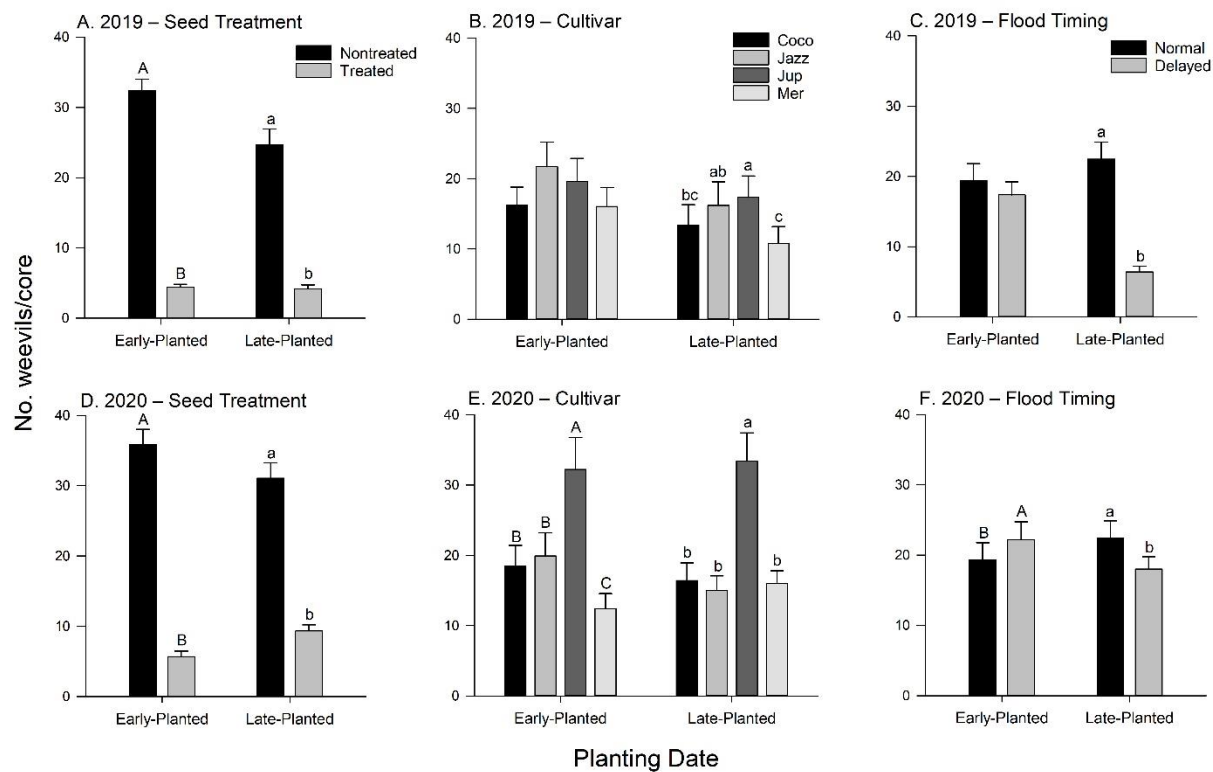


Figure 4.1. Mean (+ SEM) number of immature rice water weevils per root-soil core as affected by (A, D) insecticidal seed treatment, (B, E) rice cultivar, and (C, F) flood timing main effects, Crowley, Louisiana, 2019–2020. Analyses were conducted separately by year and planting date. Bars accompanied by the same letter do not differ significantly (Tukey’s HSD: $\alpha > 0.05$).

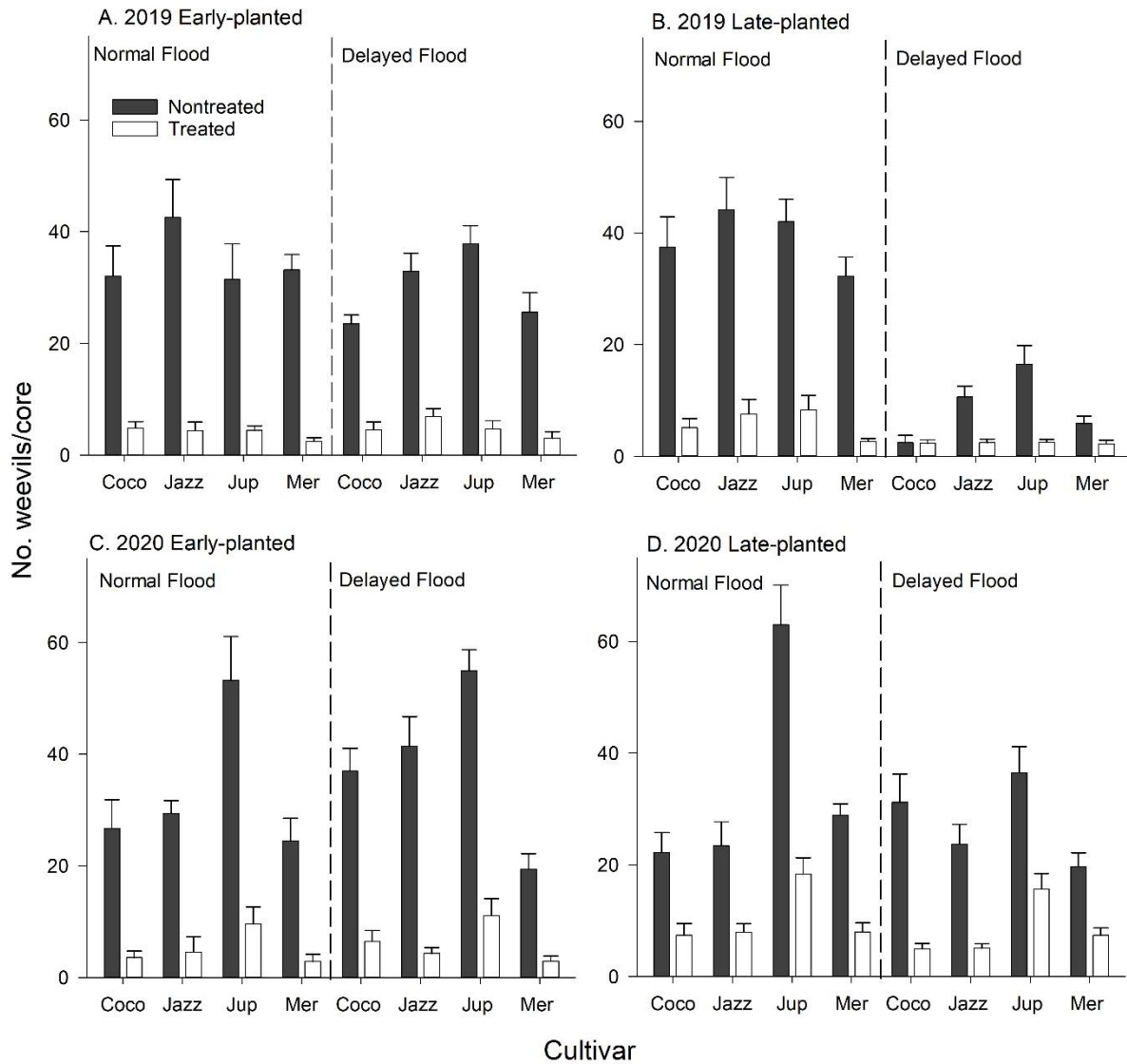


Figure 4.2. Mean (+ SEM) number of immature rice water weevils per root-soil core sample as affected cultivar \times seed treatment \times flood timing interactions, (A, B) 2019 early- and late-planted trials and (C, D) 2020 early- and late-planted trials, Crowley, Louisiana, 2019–2020. Analyses were conducted separately by year and planting date.

All stemborer larvae recovered from rice plants showing whitehead symptoms were determined to be Mexican rice borer. Insecticidal seed treatment influenced whitehead density in all trials (Table 4.3). Whitehead density was influenced by flood timing in the 2019 trials, but not in the 2020 trials. Cultivar influenced whitehead density in all trials except the 2019 early-

planted trial (Table 4.3). In the 2019 field experiments, insecticidal seed treatment reduced whitehead density by 91–93% across planting dates, flood timings, and cultivars (Fig. 4.3A). Whitehead densities were less in plots planted with ‘Jazzman-2’ relative to other cultivars in the late-planted trial, but no differences were observed among cultivars in the early-planted trial (Fig. 4.3B). Reductions of 79% and 93% in whitehead densities in early- and late-planted trials, respectively, were observed in plots subjected to delayed flood compared to normal flood timing across treatments and cultivars (Fig. 4.3C). In the 2020 field experiments, seed treatment reduced whitehead density by 87–94% across planting dates, cultivars, and flood timings (Fig. 4.3D). The rice cultivar ‘Jazzman-2’ had reduced whiteheads relative to other cultivars in both early- and late-planted trials (Fig. 4.3E). Flood timing did not affect whitehead density in either the early- or late-planted trials (Fig. 4.3F).

There were significant cultivar \times insecticide treatment and flood \times insecticide treatment interactions for whiteheads in the 2019 early-planted trial (Table 4.3). Whitehead densities differed between treated and nontreated plots for all cultivars except ‘Jazzman-2’ (Fig. 4.4A). Nontreated plots subjected to normal flood timing had greater whitehead densities than nontreated plots subjected to delayed flood, but the same effect of flood timing was not observed for insecticide-treated plots (Fig. 4.4A). Moreover, there was a significant cultivar \times insecticide treatment \times flood interaction in the 2019 late-planted trial with the greatest whitehead densities observed on nontreated ‘Cocodrie’, ‘Mermentau’, and ‘Jupiter’ subjected to normal flood timing (Fig. 4.4B). In the 2020 late-planted trial, a significant cultivar \times insecticide treatment \times flood interaction was detected with greater whitehead densities on nontreated ‘Jupiter’ and ‘Mermentau’ subjected to normal flood timing and nontreated ‘Cocodrie’ subjected to delayed

flood timing (Fig. 4.4D). There were no interactions among cultivar, insecticide treatment, and flood timing in the 2020 early-planted trial (Fig. 4.4C).

Table 4.3. Results of general linear mixed models (GLIMMIX) for stemborer injury (whitehead densities) in 2019 and 2020 field trials at Crowley, Louisiana.

Fixed Effect	df	2019				2020			
		Early-Planted		Late-Planted		Early-Planted		Late-Planted	
		F	P	F	P	F	P	F	P
Cultivar	3,6	3.71	0.081	18.34	0.002	5.76	0.034	7.05	0.022
Insecticide Trt	1,40	101.69	<0.001	551.04	<0.001	252.02	<0.001	341.10	<0.001
Flood	1,2	19.71	0.047	138.01	0.007	0.04	0.855	0.15	0.736
Cultivar × Insecticide Trt	3,40	10.43	<0.001	2.80	0.052	0.78	0.510	1.69	0.185
Cultivar × Flood	3,6	0.28	0.840	9.09	0.012	2.92	0.122	4.34	0.060
Insecticide Trt × Flood	1,40	23.69	<0.001	8.97	0.005	0.19	0.667	3.67	0.063
Cultivar × Insecticide Trt × Flood	3,40	0.94	0.431	3.24	0.032	2.00	0.130	5.70	0.002

Yield losses due to combined infestations of rice water weevil and Mexican rice borer ranged from 14–49% and were influenced by cultivar in all planting dates and years except in the 2020 early-planted trial. Flood timing influenced yield loss in the 2020 late-planted trial only. Flood timing × cultivar interactions were not detected in any trial (Table 4.4). In the 2019 field experiments, yield losses among cultivars across flood timings were 24–49% in the early-planted trial and 14–35% in the late-planted trial. In the early-planted trial, ‘Cocodrie’ had greater yield loss compared to other cultivars (Fig. 4.5A), whereas in the late-planted trial, yield loss was greater in ‘Jupiter’ compared to ‘Mermentau’ (Fig. 4.5C). Although yield losses were reduced by 22% and 42% on plots subjected to delayed flood compared to normal flood timing in the early- and late-planted trials, respectively, the differences were only marginally significant in the late-planted trial (Fig. 4.5B, D). In the 2020 field experiments, yield losses among cultivars were 22–28% in the early-planted trial and 22–34% in the late-planted trial. Yield loss was greater in ‘Jupiter’ compared to ‘Mermentau’ in the late-planted trial only (Fig. 4.5G). Application of

delayed flood significantly reduced yield loss by 38% compared to normal flood timing in the late-planted trial (Fig. 4.5H). Despite the 36% reduction in yield loss in the delayed flooded plots relative to normal flooded plots in the early-planted trial, this reduction is not statistically significant (Fig. 4.5F).

Table 4.4. Results of general linear mixed models (GLIMMIX) for yield loss in 2019 and 2020 field trials at Crowley, Louisiana.

Fixed Effect	2019					2020			
	df	Early-Planted		Late-Planted		Early-Planted		Late-Planted	
		F	P	F	P	F	P	F	P
Cultivar	3,18	3.02	0.057	3.67	0.033	0.07	0.975	4.31	0.017
Flood	1,6	1.39	0.284	4.68	0.074	0.97	0.363	12.0	0.013
Cultivar \times Flood	3,18	0.78	0.522	0.25	0.863	3.00	0.060	1.49	0.251

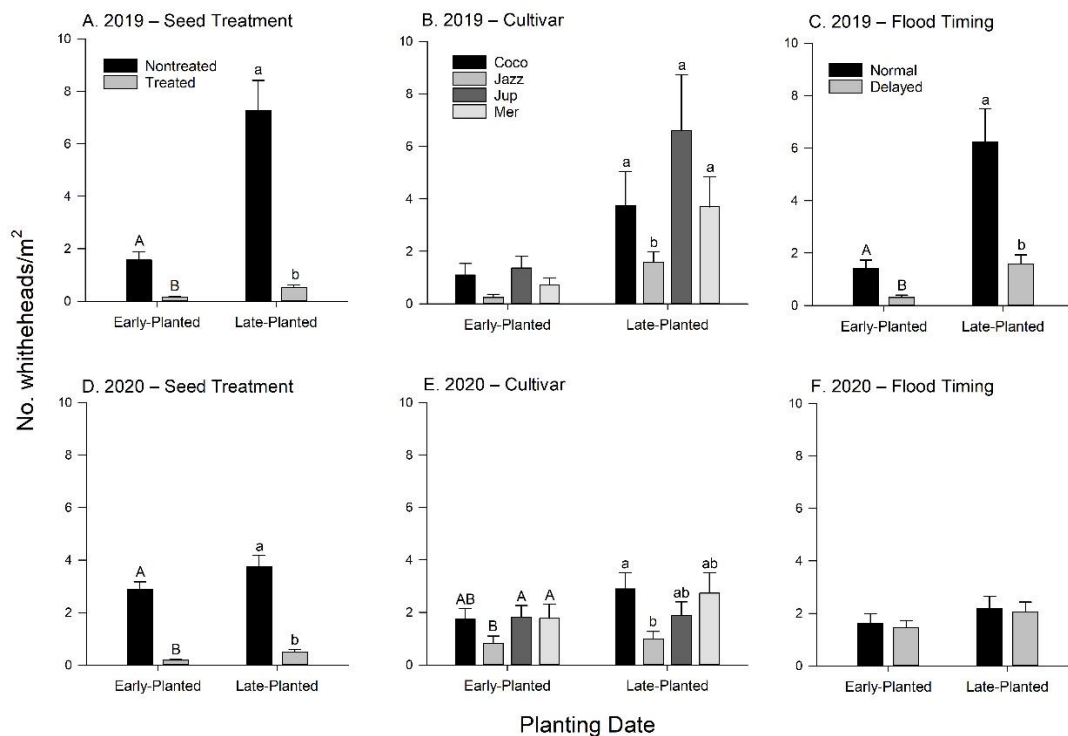


Figure 4.3. Mean (+SEM) whitehead (blanked panicles) densities as affected by (A, D) insecticidal seed treatment, (B, E) rice cultivar, and (C, F) flood timing main effects, Crowley, Louisiana, 2019–2020. Analyses were conducted separately by year and planting date. Bars accompanied by the same letter do not differ significantly (Tukey's HSD: $\alpha > 0.05$).

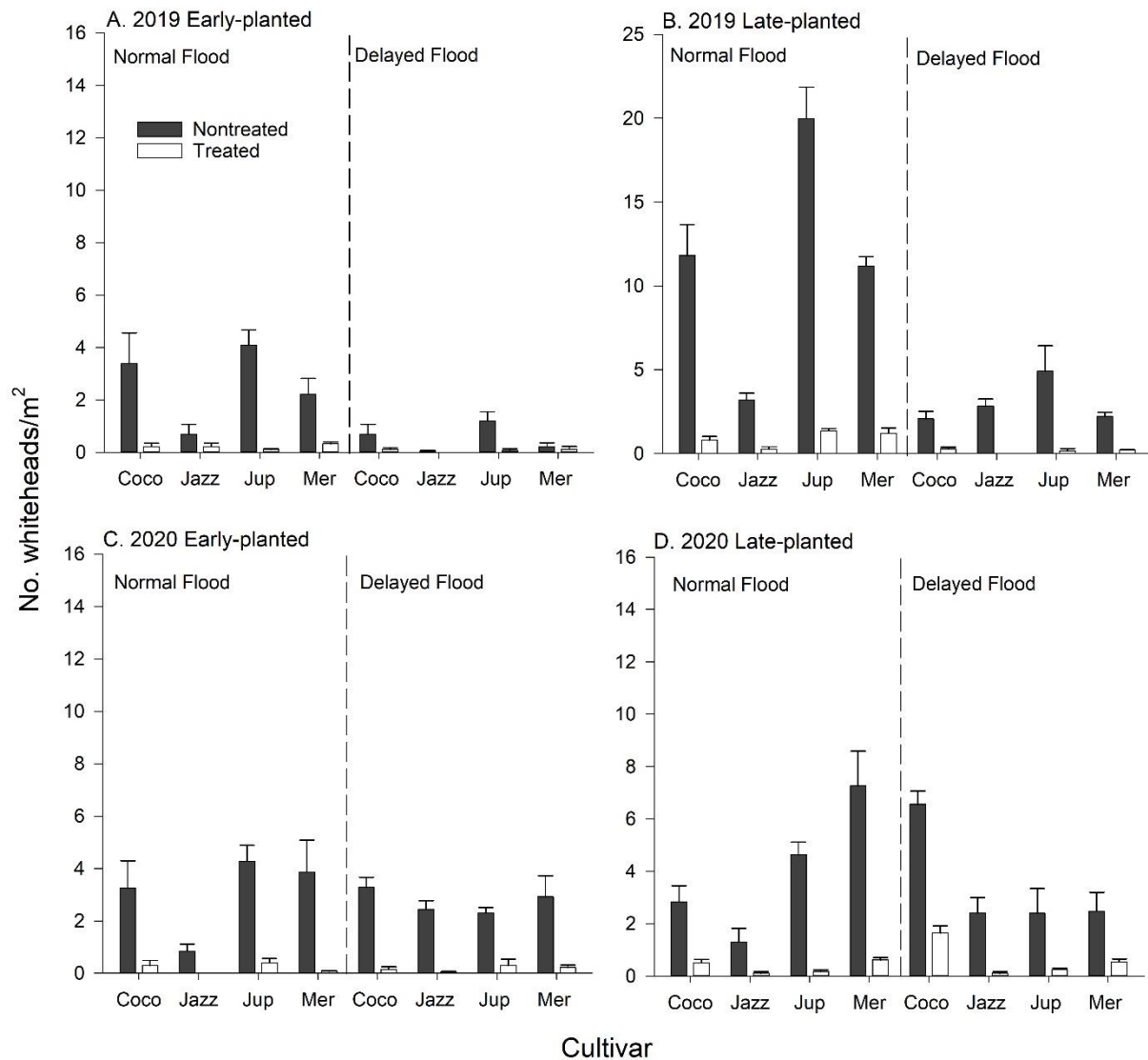


Figure 4.4. Mean (+SEM) whitehead (blanked panicles) densities as affected by cultivar \times seed treatment \times flood timing interactions, (A, B) 2019 early- and late-planted trials and (C, D) 2020 early- and late-planted trials. Crowley, Louisiana, 2019–2020. Analyses were conducted separately by year and planting date.

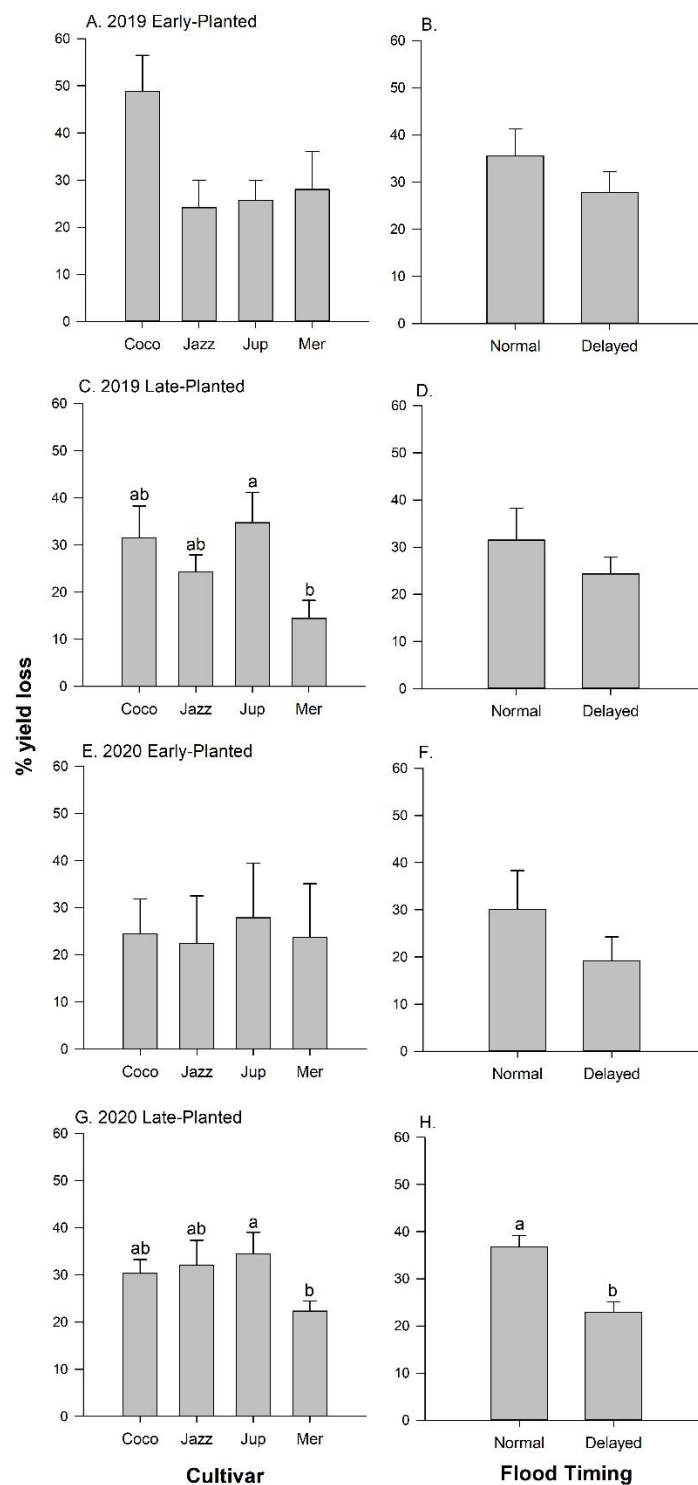


Figure 4.5. Mean (+SEM) yield loss as affected by (A, C, E, G) rice cultivar and (B, D, F, H) flood timing main effects, Crowley, Louisiana, 2019–2020. Analyses were conducted separately by year and planting date. Bars accompanied by the same letter do not differ significantly (Tukey's HSD $\alpha > 0.05$).

4.4. Discussion

This study examines alternative tactics to insecticidal seed treatments for managing infestations of rice water weevils and stemborers. The results from the experiments presented here demonstrate that rice cultivars vary in their susceptibility to infestations by rice water weevil and Mexican rice borer, and delaying flood application by only two weeks can reduce infestations and impact of these insect pests. Although delayed flood, rice cultivar, and insecticides have all been shown to affect rice water weevil impact individually, this is the first study to examine the interactions among these tactics. Further, this is the first study to examine the effect of flood timing on stemborer infestations and yield loss. No substantial antagonism was found among the tactics evaluated in this study. The significant interactions observed in this study arose from the persistent effect of the chlorantraniliprole seed treatment on weevil larvae and stemborer injury rather than the incompatibility of tactics.

Water management practices have a strong influence on the interaction between rice plants and the rice water weevil (Hesler et al., 1992; Lanka et al., 2015; Rice et al., 1999; Tindall et al., 2013). In particular, the presence of flood triggers the oviposition of adult rice water weevils in rice plants (Stout et al., 2002b). In this study, we found that delaying the application of permanent flood by two weeks reduced weevil densities in late-planted trials in both years. These results are consistent with a previous study that reported reductions in rice water weevil densities under a delayed flood system (2–4 weeks later than normal flood timing) (Rice et al., 1999). The field experiments conducted by Rice et al. (1999) were all established late in the planting season. We did not observe any differences in weevil densities between flood timings in the 2019 early-planted trial, whereas, in the 2020 early-planted trial, weevil densities were greater in the delayed flooded plots. Results observed from our early-planted trials were similar

to results of studies conducted by Zou et al. (2004c) and (Adams et al., 2015) that reported higher weevil densities on delayed flooded plots compared to normal flooded plots, while Stout et al. (2001) observed generally low weevil densities in delayed flooded relative to normal flooded plots but the differences were not statistically significant. The three studies mentioned conducted their field experiments earlier in the planting season relative to trials of (Rice et al., 1999) and the late-planted trials reported herein.

The differences in the effects of delayed flood application on rice water weevil densities across planting dates may be explained, in part, by the biology and behavior of the rice water weevil and the susceptibility of rice plant age to weevils. Prior studies reported the emergence of rice water weevil from overwintering begins in late March with peak emergence occurring during April and May (Shang et al., 2004; Zou et al., 2004b). Rice water weevil may go through several generations if rice plants are continuously available in the fields. Although weevils can infest rice plants from the early vegetative to reproductive developmental stages, weevils express a clear preference for plants in the early-tillering stage of development (Stout et al., 2013). Plant phenology was not recorded in this study, but it can be assumed that the differences between flood timings would be greater in late-planted rice when growth is occurring more rapidly. Rice growth and development is affected by the amount of growing degree days (GDD), which is the daily accumulation of heat units during the crop's development, thus later-planted rice which receives more growing degree days in the early stages of development matures rapidly relative to early-planted rice (Cerioli et al., 2021). In this study, the application of delayed flood in late-planted rice allowed plants to receive more growing degree days before weevils start infesting the fields. When core sampling was conducted on delayed-flooded plots in the late-planted trials, most of the rice plants were at the boot to panicle emergence developmental stages. This

indicates that the rice plants may have been at the late-tillering stage when permanent flood was established, a plant developmental stage less preferred by weevils (Stout et al., 2013).

Alternatively, the reduction on weevil densities in delayed-flooded plots may have been due to the decrease in adult weevil populations in the rice fields. Shang et al. (2004) reported that rice water weevils return to overwintering sites starting late June until October. In contrast to the late-planted trials, we observed an increase in weevil densities on delayed-flooded plots in the 2020 early-planted trial. The result from this trial may be due to the presence of high adult weevil populations in the field because the permanent flood in the early-planted trials was applied during the peak emergence of the rice water weevil. In contrast, weevil populations may be declining by July when the delayed-flooded application occurred in the late-planted trials as adults move to overwintering habitats. Regardless of whether it resulted from differences in plant phenology or weevil dynamics, the greatest difference between flood timings was observed in the 2019 late-planted trial, which had our latest flooding date. This suggests the effect is maximized the later into the growing season.

The historically sporadic nature of stemborer infestations in Louisiana has made it challenging to study this pest complex under field conditions. However, due to the increasing prevalence of Mexican rice borer populations, this insect pest can be reliably studied. To our knowledge, this is the first study to document the effects of flood timing on stemborer infestations in general and Mexican rice borer in particular. Our results showed significant reductions in stemborer injury in delayed flooded plots in both early- and late-planted trials in 2019 but no differences in flood timings were observed in the 2020 trials. The effect of water management on stemborer infestation in rice is not well studied. Nonetheless, two studies have reported reductions in stemborer and leaf folders infestations in rice under an alternate wetting

and drying (AWD) water management regime (Chapagain et al., 2011; Hasan et al., 2016). Since flood timing only affected stemborer injury in the first year of this study, further investigation should be conducted.

Results from this study also showed substantial variation in susceptibility among rice cultivars to the Mexican rice borer. Low levels of whitehead densities (stemborer injury) were observed in ‘Jazzman-2’ in this study, which is consistent with a recent study that reported this cultivar as moderately resistant to stemborers (Villegas et al., 2021a). Similarly, some variation in susceptibility to rice water weevil was observed among cultivars in this study. The high rice water weevil infestations in rice cultivar ‘Jupiter’ reported herein is consistent with previous studies, and the cultivar is now used as a susceptible standard in cultivar resistance evaluations (Saad et al., 2018; Stout et al., 2001; Villegas et al., 2021a; Wilson et al., 2021a). Densities of immature weevils remained somewhat similar across years and planting dates, whereas stemborer injury was observed to be higher in late-planted trials. This finding is consistent with increased infestations and yield loss from stemborers in late- compared to early-planted rice reported by Wilson et al. (2021a). The impact of planting dates, especially on stemborer infestations, needs to be further evaluated in replicated studies with several planting dates and multiple years.

Yield losses due to combined infestations of rice water weevil and Mexican rice borer in this study were generally lower in delayed flooded plots compared to normal flooded plots, but the differences were only significant in the 2020 late-planted trial. Previous studies reported a similar trend in which yield losses due to rice water weevils were reduced in delayed flooded plots (Stout et al., 2001; Zou et al., 2004c). Delaying flood application delays rice water weevil infestations until rice plants are older, which may enhance rice tolerance to this pest. Prior

studies have documented that older rice plants can better tolerate injury by rice water weevil larval feeding compared to younger rice plants, and thus are less susceptible to yield losses due to weevil injury (Stout et al., 2002a; Wu and Wilson, 1997). One of the possible reasons is that older plants have highly developed root systems, and are able to quickly recover from weevil injury. Villegas et al. (2021b) proposed that rice plants that are more tolerant to weevil injury have vigorous root systems (particularly in the case of hybrid cultivars). Moreover, N'guessan et al. (1994a, 1994b) reported that rice plants that have increased root regrowth after heavy weevil infestations are also less susceptible to yield losses. Rice cultivars also vary in their level of tolerance to insect pests. In this study, we found that the rice cultivar 'Mermentau' had the lowest yield loss in the late-planted trials despite having intermedidate stemborer injury and weevil infestations relative to other cultivars. This result is consistent with prior studies that documented some rice cultivars expressing varying levels of tolerance to rice water weevil injury (N'guessan et al., 1994a, 1994b; Stout et al., 2001; Villegas et al., 2021a, 2021b). Unfortunately, we were not able to distinguish yield losses from weevils and Mexican rice borer because the seed treatment we used in the study was effective in controlling both pests. Several studies have reported yield losses of 0.3–4.1% per weevil larvae per core (Adams et al., 2016; Stout et al., 2002a; Villegas et al., 2021a, 2021b; Wilson et al., 2021a; Zou et al., 2004a). A recent study also reported a loss of 1.7% in yields per whitehead per m² due to Mexican rice borer feeding (Wilson et al., 2021a).

The control of rice water weevil and stemborers can be best achieved by using insecticides but our results also indicate that these insect pests can be partly managed through the cultural practice of delaying flooding and the use of tolerant/resistant rice cultivars. Delaying permanent flood application until rice plants are older can be an effective strategy to reduce

weevil larvae infesting rice when fields are planted later in the season. Delayed flood application can potentially reduce stemborer injury, but further experiments should be conducted to elucidate the factors that may contribute to this effect. This study, in addition to previous studies (Rice et al., 1999; Stout et al., 2001; Zou et al., 2004c), has shown reductions in yield losses in delayed flooded fields, thus providing a strong rationale for the cultural practice of delayed flooding. Water management may impact weed and disease control, thus effects of delayed flooding on other pest management should be explored. Results from this study also indicate that plant resistance to Mexican rice borer may be a useful strategy as this pest continues to establish its population in Louisiana rice. Furthermore, this study has shown that some rice cultivars may be able to tolerate infestations by both pests. Overall, delaying flood and host plant resistance are suitable alternative management approaches especially in situations where insecticide use is not desirable (i.e., proximity to crawfish production and organic rice production systems).

Chapter 5. Effects of Chronic Root Herbivory by the Rice Water Weevil on Endogenous Phytohormones and Nutrient Concentrations in Rice Plants

5.1. Introduction

Root herbivory can be extremely damaging to plants, often leading to considerable yield losses in crop production (Blackshaw and Kerry, 2008; McKenzie et al., 2016). Belowground herbivory can alter plant performance in various ways. For instance, feeding by insects on plant roots can affect the synthesis of phytohormones, production of chemical defense metabolites, water and nutrient absorption, and carbohydrate storage (Blossey and Hunt-Joshi, 2003; Hara et al., 2000; Larcher, 1995). Plants have developed multiple strategies to mitigate the impact of herbivores by expressing traits that reduce the amount of injury caused by herbivores (resistance traits) or by expressing traits that reduce the yield or fitness losses resulting from injury by herbivores (tolerance traits) (Stout, 2020; Strauss and Agrawal, 1999). Plant defense traits can directly or indirectly affect the biology of phytophagous insect pests. Direct defenses include mechanical barriers (e.g., tissue toughness, pubescence, glandular, and non-glandular trichomes) and allelochemicals in plant tissues (e.g., cyanogenic glycosides, glucosinolates, alkaloids, and terpenoids) which directly affect herbivores, whereas indirect defenses include volatile organic compounds from damaged plants that help attract natural enemies of herbivores (Smith and Clement, 2012). Furthermore, plants possess physiological traits that allow them to tolerate injury by herbivores. The mechanisms typically associated with plant tolerance include increases in photosynthetic rates after injury, high growth rates, utilization of stored reserves, and changes in patterns of resource allocation after injury (e.g., diverting resources away from the site of attack) (Peterson et al., 2017; Qu et al., 2016). Although much of our understanding of plant-insect interactions is derived from studies of aboveground herbivory, a growing body of research has demonstrated that belowground herbivory can have a greater impact on plant fitness (Barber

et al., 2011; Strong et al., 1995). Since root herbivory is much harder to quantify and manipulate than leaf herbivory, we are only beginning to understand its effects on plant performance.

Rice plants are attacked by various insect pests throughout the growing season. The rice water weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), is the most destructive early-season pest of rice in the USA (Aghaee and Godfrey, 2014; Way, 1990). Root pruning by the soil-dwelling, root-feeding weevil larva results in extensive injury to rice root systems, thereby affecting tiller production, grain weights, and grains per panicle (Zou et al., 2004a). Yield losses due to weevil infestations can exceed 25% if fields are left unmanaged (Stout et al., 2000; Villegas et al., 2021b). The impact of rice water weevil feeding on yields differs among rice cultivars. A recent study reported that hybrid cultivars were able to better tolerate weevil infestations than inbred cultivars (Villegas et al., 2021). However, the mechanisms associated with hybrid tolerance to weevils were not investigated in that study. Additionally, rice plants can defend themselves against root herbivores. Lu et al. (2015) reported that root herbivory by rice water weevils induces jasmonic acid production (plant defense hormone) in the roots, which negatively affected the performance of the weevils. Root injury by weevil larvae also altered the oviposition of adult weevils in the injured rice plants (Kraus and Stout, 2019a). Plant hormone production aboveground due to weevil larval feeding belowground has not been quantified.

Our understanding of the effects of chronic root herbivory by the rice water weevil on rice remains limited. Because rice water weevils are multivoltine, different cohorts of weevils may infest rice plants over an extended period during the growing season. Thus, it is important to evaluate plant performance across several time points. It has been hypothesized that root pruning by weevils may interfere with nutrient uptake (Zou et al., 2004), but this has not been thoroughly

examined. This study investigates the effects of chronic feeding by rice water weevils on rice plant growth, nutrient uptake, and production of plant hormones in shoots between two cultivars (a weevil tolerant hybrid cultivar and a less tolerant inbred cultivar, Villegas et al. 2021) under field conditions.

5.2. Materials and Methods

5.2.1. Plot Establishment

Field experiments were conducted at the LSU AgCenter H. Rouse Caffey Rice Research Station in Crowley, Louisiana in 2020. Two separate trials were established – one planted early (April 2) and the other late (May 22) relative to recommended planting dates in Louisiana. For each trial, field plots were laid out following a randomized block design with six blocks. Each block contained a cultivar (hybrid and inbred) \times insecticidal seed treatment (treated and nontreated) factorial arrangement. Seeds of the hybrid cultivar ‘RT7521’ (RiceTec Inc., Alvin, TX) and inbred ‘CL151’ (LSU AgCenter, Baton Rouge, LA) were drill-planted at a seeding rate of 28 kg ha⁻¹ and 67 kg ha⁻¹, respectively, in plots measuring 5.5 m in length with seven rows spaced 18 cm apart. Prior to planting, seeds of each cultivar were either treated or not with a standard rate (78.5 g a.i. ha⁻¹) of insecticidal seed treatment, chlorantraniliprole (Dermacor X-100, Corteva Agriscience, Wilmington, DE), following the methods of Lanka et al. (2014). Treated and nontreated plots of the same cultivar were placed side-by-side to reduce variation in weevil infestations and yields. After planting, fields were surface irrigated as necessary to facilitate plant emergence and growth. Permanent flood was established at 4–5 weeks after planting when the rice plants reached the early-tillering developmental stage. Field plots were maintained following the standard recommendations for fertilization and weed control for drill-seeded rice in Louisiana (Saichuk, 2014).

5.2.2. Rice Water Weevil Density and Plant Biomass

Immature rice water weevil (larvae and pupae) densities were evaluated according to established procedures (N'guessan and Quisenberry, 1992; Stout et al., 2001). Root-soil samples were taken from each plot using metal a corer (9.2 cm diameter \times 7.6 cm depth). Core sampling was conducted five times (14, 22, 30, 36, and 42 days after permanent flood in the early-planted trial and 19, 26, 33, 40, and 48 days after permanent flood in the late-planted trial), and two core samples were taken from each plot per sampling point. Each core sample contained a minimum of one rice plant with intact roots, and each sample was processed by washing the soil and larvae from roots under moderate water pressure in a 40-mesh screen sieve bucket. The bucket was then placed in a basin containing salt-water solution and weevil larvae were counted as they floated to the surface. Pupae were counted by inspecting the bottoms of sieve buckets. To determine plant biomass, roots and shoots were separated from each sample and dried in an oven (60°C for a week). Dry weights of roots and shoots were recorded using a digital weighing scale (Easy Weigh, Tool Testing Lab Inc., Tipp City, OH).

5.2.3. Plant Nutrient Analysis

Concentrations of nutrients in plant shoots were evaluated in both early- and late-planted trials. Dried plant materials (shoots only) from core samples described previously were sent to LSU AgCenter's Soil Testing and Plant Analysis Laboratory (Louisiana State University, Baton Rouge, LA). The concentrations of N and C were determined by dry combustion using a LECO TruSpec CN analyzer (LECO Corp., St. Joseph, MI). The concentrations of other nutrients (K, P, S, Ca, Mg, Na, Fe, Mn, Al, Zn, B, Cu, and Mo) were determined by inductively coupled plasma (ICP) analysis.

5.2.4. Plant Hormone Quantification

Rice shoots were collected at 10, 20, and 30 days after permanent flood in the early-planted trial for the quantification of plant hormones. For each time point, two plant samples (combination of leaves and stems) were taken from each plot and immediately flash-frozen in liquid nitrogen. Each sample was homogenized using a porcelain mortar and pestle. The homogenized samples were then sent to Creative Proteomics (Shirley, NY) for quantitative measurement of abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), jasmonic acid-isoleucine (JA-Ile), 12-oxo-phytodienoic acid (OPDA), and indoleacetic acid (IAA). Plant hormones were quantified using AB SCIEX API 4000 tandem mass spectrometry connected to a Waters Acquity UPLC.

5.2.5. Yield

At grain maturity, entire plots were harvested using a small-plot combine (Wintersteiger Delta Plot Combine, Wintersteiger Inc., Salt Lake City, UT). Grain weights were adjusted to 12% moisture. Percentage yield loss was calculated for each cultivar using the formula: % yield loss = $[(\text{yield}_{\text{treated}} - \text{yield}_{\text{nontreated}}) / \text{yield}_{\text{treated}}] \times 100$.

5.2.6. Statistical Analyses

Data were analyzed separately by planting date. All analyses were performed in SAS version 9.4 (SAS Inst., Cary, NC). Rice water weevil density, biomass (roots and shoots), nutrient concentration, and plant hormone data were analyzed using generalized linear mixed-models (PROC GLIMMIX) with cultivar, insecticidal seed treatment, and their interactions as fixed effects, sampling time as a repeated-measure, and block as a random effect. Yield loss data were analyzed using the same model with cultivar as a fixed effect and block as a random effect. The analyses of weevil data were modeled using a Poisson distribution while the analyses of the

rest of the data were modeled using a Gaussian distribution. Kenward-Roger adjustment was used to calculate error degrees of freedom and Tukey's HSD post hoc analysis ($\alpha = 0.05$) was used for all mean separations.

5.3. Results

5.3.1. Rice Water Weevil Density and Plant Biomass

Numbers of immature weevils (larvae and pupae) were influenced by the main effects of cultivar, insecticidal seed treatment, and time and the cultivar \times seed treatment interaction in both the early- and late-planted trials (Table 5.1). The hybrid cultivar supported 9 and 19% more weevils than the inbred cultivar in early- and late-planted trials, respectively (Figs. 5.1A, D). Seed treatment reduced densities of rice water weevil immatures by 71 and 72% in early- and late-planted trials, respectively (Figs. 5.1B, E). Numbers of immature weevils varied across sampling times with peak densities occurring approximately four weeks after the permanent flood was established in both early- and late-planted trials (Figs. 5.1C, F). Furthermore, in both trials, weevil densities in treated plots were higher in plots planted with the hybrid compared to plots planted with the inbred cultivar (Figs. 5.2A, B).

Table 5.1. Results of repeated measures general linear mixed models (repeated-GLIMMIX) for rice water weevil densities in the early- and late-planted trials at Crowley, LA, 2020.

Fixed Effect	df	Early-Planted		Late-Planted	
		F	P	F	P
Cultivar	1	10.53	0.001	16.46	<0.001
Seed Trt	1	213.76	<0.001	150.57	<0.001
Time	4	24.51	<0.001	22.86	<0.001
Cultivar \times Seed Trt	1	17.62	<0.001	16.41	<0.001
Cultivar \times Time	4	0.41	0.803	0.86	0.489
Seed Trt \times Time	4	1.61	0.173	1.35	0.254
Cultivar \times Seed Trt \times Time	4	0.88	0.478	0.98	0.418
Error	220				

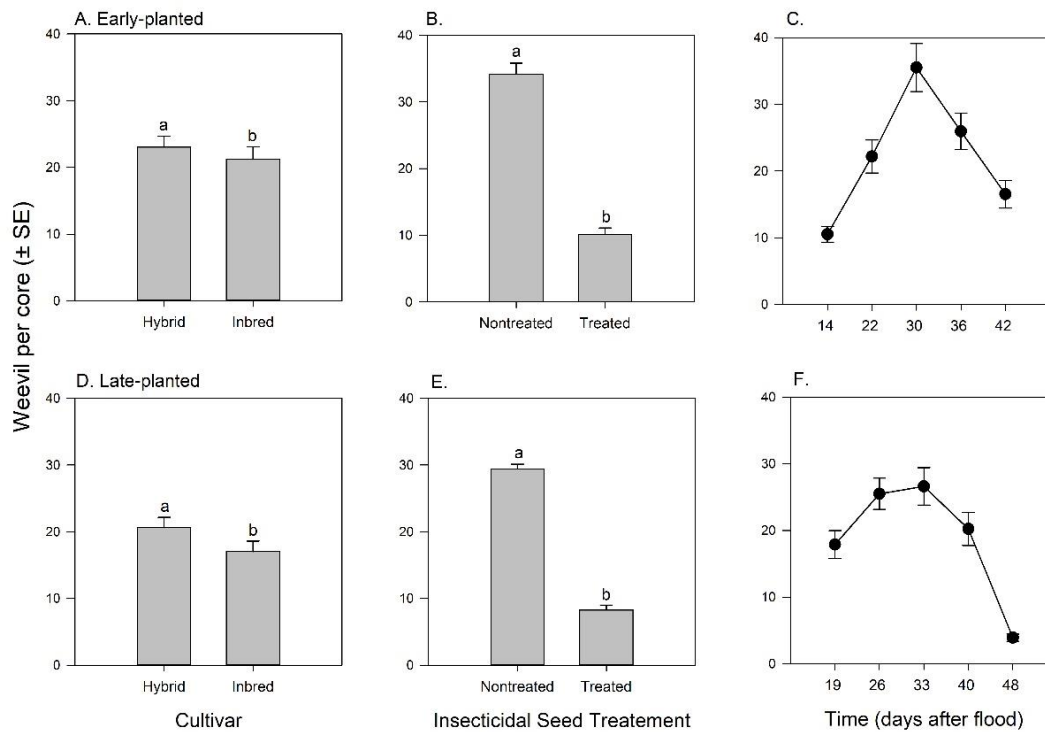


Figure 5.1. Mean (\pm SE) numbers of rice water weevil immatures per root-soil core sample as affected by (A, D) rice cultivar, (B, E) insecticidal seed treatment, and (C, E) days after flooding in early- and late-planted trials, Crowley, LA, 2020. Means were separated using Tukey's HSD ($\alpha = 0.05$).

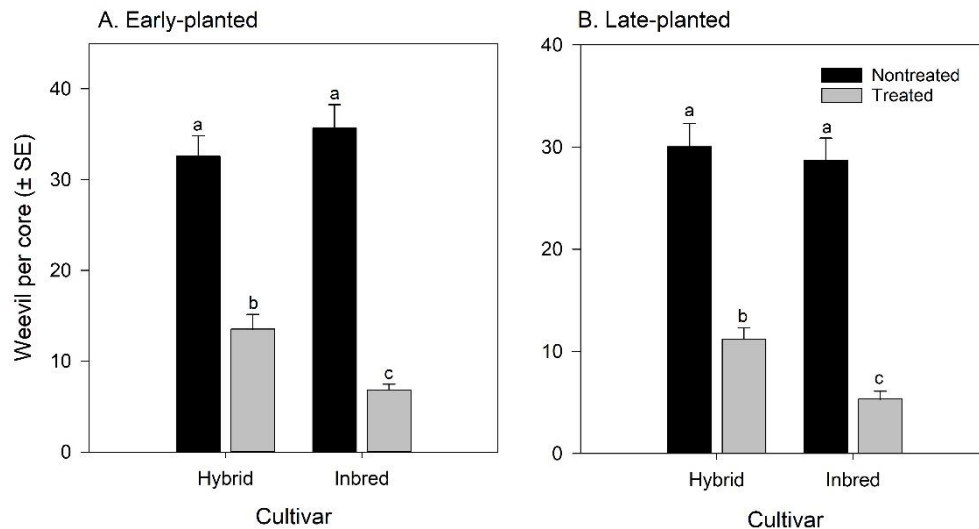


Figure. 5.2. Mean (\pm SE) numbers of rice water weevil immatures per root-soil core sample as affected by the cultivar \times seed treatment interaction in (A) early- and (B) late-planted trials, Crowley, LA, 2020. Mean within a panel capped with the same letter are not significantly different (Tukey's HSD: $P > 0.05$).

Shoot biomass was influenced by cultivar (except in the late-planted trial), insecticidal seed treatment, and time, whereas root biomass was influenced by cultivar, time, and cultivar \times time interaction (Table 5.2). Root dry weights were generally higher in the hybrid compared to the inbred cultivar across sampling times in both early- and late-planted trials. In particular, root dry weights at 36 and 40 days after flood were 44 and 51% higher in the hybrid than the inbred cultivar in the early- and late-planted trials, respectively (Figs. 5.3A, C). Shoot dry weights were higher in hybrid compared to inbred cultivar in the early-planted trial only (Fig. 5.3 B). High weevil infestations in nontreated plots reduced shoot biomass by 16 and 29% compared to treated plots (reduced weevil infestations) in the early- and late-planted trials, respectively (Figs. 5.3B, D). Both root and shoot dry weights increased proportionately with time (days after flood establishment) due to continuous plant growth.

Table 5.2. Results of repeated measures general linear mixed models (repeated-GLIMMIX) for plant biomass (roots and shoots) in the early- and late-planted trials at Crowley, LA, 2020.

Fixed Effect	df	Early-Planted				Late-Planted			
		Roots		Shoots		Roots		Shoots	
		F	P	F	P	F	P	F	P
Cultivar	1	15.04	<0.001	12.76	<0.001	44.51	<0.001	0.41	0.521
Seed Trt	1	1.68	0.197	6.84	0.009	0.53	0.467	14.84	<0.001
Time	3	33.47	<0.001	41.65	<0.001	20.44	<0.001	34.38	<0.001
Cultivar \times Seed Trt	3	0.00	0.977	1.01	0.316	0.76	0.384	0.84	0.361
Cultivar \times Time	3	4.71	0.004	2.46	0.065	7.06	<0.001	1.77	0.154
Seed Trt \times Time	1	0.12	0.946	2.23	0.086	0.29	0.835	0.47	0.704
Cultivar \times Seed Trt \times Time	3	0.71	0.550	0.08	0.971	0.55	0.647	0.87	0.460
Error	175								

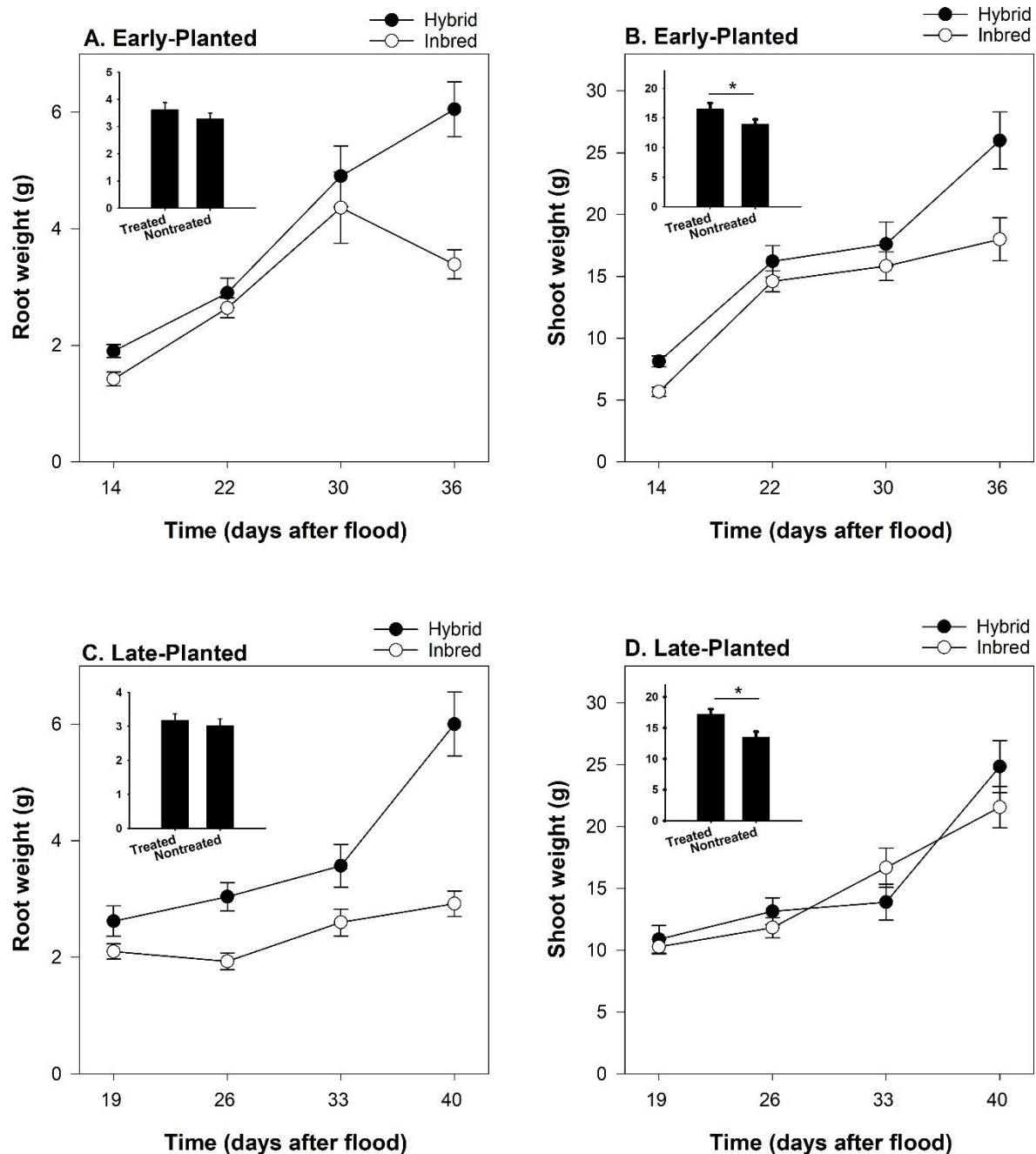


Figure 5.3. Mean (\pm SE) root and shoot dry weights as affected by the cultivar \times time interaction in the (A, B) early- and (C, D) late-planted trials, Crowley, LA, 2020. Bar graphs embedded within each panel show root and shoot dry weights between treated and nontreated plots. Bar graphs accompanied by an asterisk have significantly different means (Tukey's HSD: $P < 0.05$).

5.3.2. Concentrations of Nutrients in Rice Plants

The concentrations of nutrients in rice shoots were variably influenced by cultivar, insecticidal seed treatments, time, and their interactions in both early- and late-planted trials (Tables 5.3, 5.4, 5.5, 5.6). In the early-planted trial, concentrations of macronutrients N, K, and S and micronutrients Na and Zn were significantly higher in the hybrid compared to the inbred cultivar (Tables 5.7, 5.8). Weevil feeding negatively affected both macro and micronutrients in rice plants. The concentrations of macronutrients N, K, P, S, and Mg, and micronutrients Mn, Zn, and Cu were reduced in nontreated (weevil infested plants) compared to treated plants (Tables 5.7, 5.8). The majority of plant nutrients decreased across sampling time except for the concentrations of P, Na, Mn, and Mo which increased across sampling time (Tables 5.7, 5.8). Chronic feeding of weevil larvae reduced concentrations of nutrients across time as indicated by significant insecticidal seed treatment \times time interaction (Tables 5.3, 5.4). In particular, the concentrations of macronutrients P, S, Ca, and Mg and micronutrients Mn, Zn, B, and Cu were lesser in nontreated plants compared to treated plants across time (Fig.5.4). In the late-planted trial, the concentrations of Fe and Mn were higher in the inbred cultivar while the concentrations of K, S, and Mo were higher in the hybrid cultivar (Table 5.10). The concentrations of macronutrients K, P, Ca, and Mg and Mn, Zn, and Cu were reduced in nontreated (weevil infested) compared to treated plants, whereas the concentrations of C, Fe, and Al were higher in nontreated plants compared to treated plants (Tables 5.9, 5.10). The concentrations of plant nutrients decreased across sampling time (Tables 5.9, 5.10). Chronic feeding of weevil larvae in the late-planted trial only affected Zn concentrations in rice shoots (insecticidal seed treatment \times time interaction) (Table 5.6). The concentrations of Zn were lower in nontreated plots compared to treated plots across time (data not shown).

Table 5.3. Results of repeated measures general linear mixed models (repeated-GLIMMIX) for the concentrations of macronutrients in rice plants in the early-planted trial, Crowley, LA, 2020.

Fixed Effect		C	N	K	P	S	Ca	Mg
	df	F	F	F	F	F	F	F
Cultivar	1	0.01	6.55**	9.72**	3.70	20.22**	1.95	0.01
Seed Trt	1	0.05	9.61**	4.55*	19.62**	5.31*	0.07	21.77**
Time	3	6.68**	68.21**	12.74**	20.93**	71.91**	14.35**	6.68**
Cultivar × Seed Trt	1	0.78	0.74	0.92	2.87	1.68	1.47	0.37
Cultivar × Time	3	0.54	4.09**	1.11	1.98	1.52	0.40	1.67
Seed Trt × Time	3	0.82	0.43	2.31	7.61**	4.19*	3.54*	7.97**
Cultivar × Seed Trt × Time	3	0.05	0.35	0.77	1.18	1.11	0.50	0.87
Error	80							

* $P \leq 0.05$; ** $P \leq 0.01$

Table 5.4. Results of repeated measures general linear mixed models (repeated-GLIMMIX) for the concentrations of micronutrients in rice plants in the early-planted trial, Crowley, LA, 2020.

Fixed Effect		Na	Fe	Mn	Al	Zn	B	Cu	Mo
	df	F	F	F	F	F	F	F	F
Cultivar	1	10.86**	0.05	0.99	0.68	159.24**	1.92	3.0	1.81
Seed Trt	1	0.84	2.57	49.96**	1.27	59.51**	2.14	5.8*	0.07
Time	3	22.26**	8.9**	27.18**	40.7**	16.29**	19.18**	122.87**	31.37**
Cultivar × Seed Trt	1	0.11	0.13	6.14*	0.43	5.9*	0.15	0.57	2.67
Cultivar × Time	3	2.07	0.09	3.02*	2.28	5.79**	0.36	1.0	2.16
Seed Trt × Time	3	0.87	1.08	10.37**	0.82	10.47**	2.91*	2.63*	1.64
Cultivar × Seed Trt × Time	3	1.07	1.29	0.97	0.54	1.08	0.33	0.28	0.43
Error	80								

* $P \leq 0.05$; ** $P \leq 0.01$

Table 5.5. Results of repeated measures general linear mixed models (repeated-GLIMMIX) for the concentrations of macronutrients in rice plants in the late-planted trial, Crowley, LA, 2020.

Fixed Effect		C	N	K	P	S	Ca	Mg
	df	F	F	F	F	F	F	F
Cultivar	1	1.19	3.16	13.35*	0.29	10.69**	0.49	3.54
Seed Trt	1	35.72**	2.92	4.81**	32.60**	0.02	4.07*	50.91**
Time	3	10.62**	23.72**	51.11**	1.13	76.21*	12.57**	7.27**
Cultivar × Seed Trt	1	0.91	2.37	1.32	2.73	2.62	6.72*	2.33
Cultivar × Time	3	1.08	0.91	1.13	0.74	1.66	1.51	0.22
Seed Trt × Time	3	0.83	0.45	1.07	1.91	0.93	0.17	0.60
Cultivar × Seed Trt × Time	3	1.27	0.20	1.29	0.96	0.52	0.07	1.13
Error	80							

* $P \leq 0.05$; ** $P \leq 0.01$

Table 5.6. Results of repeated measures general linear mixed models (repeated-GLIMMIX) for the concentrations of micronutrients in rice plants in the late-planted trial, Crowley, LA, 2020.

Fixed Effect		Na	Fe	Mn	Al	Zn	B	Cu	Mo
	df	F	F	F	F	F	F	F	F
Cultivar	1	3.46	1.04	34.09**	4.36*	40.97**	0.1	2.55	8.51**
Seed Trt	1	3.34	5.13*	62.14**	10.39**	19.7**	1.02	25.48**	0.65
Time	3	17.51**	7.25**	19.52**	12.49**	161.48**	38.49**	63.14**	1.01
Cultivar × Seed Trt	1	1.58	0.34	7.58**	0.71	2.28	0.03	2.53	6.17
Cultivar × Time	3	0.28	0.64	1.34	2.3	0.03	0.27	0.57	4.24**
Seed Trt × Time	3	0.12	0.79	0.46	0.13	5.47**	0.65	2.16	0.54
Cultivar × Seed Trt × Time	3	0.64	0.49	1.44	0.22	1.21	0.03	0.18	0.35
Error	80								

* $P \leq 0.05$; ** $P \leq 0.0$

Table 5.7. Mean (\pm SE) concentrations (% dry weight) of plant macronutrients (C, N, K, P, S, Ca, and Mg) as affected by the cultivar, insecticidal seed treatment, and time main effects in the early-planted trial, Crowley, LA, 2020. Standard error for each nutrient is shown across the main effects. Means accompanied with the same letter are not significantly different (Tukey's HSD: $P > 0.05$).

Main Effect	C	N	K	P	S	Ca	Mg
Cultivar	± 0.312 SE	± 0.059 SE	± 0.043 SE	± 0.004 SE	± 0.003 SE	± 0.004 SE	± 0.004 SE
Hybrid	40.622	2.234a	2.140a	0.184	0.220a	0.193	0.196
Inbred	40.670	2.106b	1.948b	0.173	0.201b	0.201	0.196
Seed Trt	± 0.312 SE	± 0.057 SE	± 0.043 SE	± 0.004 SE	± 0.003 SE	± 0.004 SE	± 0.004 SE
Nontreated	40.693	2.803a	1.978b	0.166b	0.205b	0.197	0.184b
Treated	40.598	2.054b	2.110a	0.191a	0.215a	0.198	0.208a
Time (d)	± 0.441 SE	± 0.085 SE	± 0.061 SE	± 0.006 SE	± 0.004 SE	± 0.006 SE	± 0.005 SE
14	40.007a	2.594a	2.110a	0.140b	0.241a	0.218a	0.202a
22	39.432c	2.328b	2.228a	0.197a	0.236a	0.193b	0.205a
30	40.044bc	2.142b	2.113a	0.192a	0.200b	0.209a	0.201a
36	41.101a	1.648c	1.725b	0.183a	0.164c	0.169c	0.176b

Table 5.8. Mean (\pm SE) concentrations (mg/kg) of plant micronutrients (Na, Fe, Mn, Al, Zn, B, Cu, and Mo) as affected by the cultivar, insecticidal seed treatment, and time main effects in the early-planted trial, Crowley, LA, 2020. Standard error for each nutrient is shown across the main effects. Means accompanied with the same letter are not significantly different (Tukey's HSD: $P > 0.05$).

Main Effect	Na	Fe	Mn	Al	Zn	B	Cu	Mo
Cultivar	± 166.0 SE	± 26.7 SE	± 9.4 SE	± 14.9 SE	± 0.8 SE	± 0.1 SE	± 0.1 SE	± 0.1 SE
Hybrid	6483.1a	516.2	441.2	326.3	56.4a	9.7	4.6	1.9
Inbred	5709.7b	524.6	427.9	308.9	42.9b	9.4	4.3	1.8
Seed Trt	± 166.0 SE	± 26.7 SE	± 9.4 SE	± 14.9 SE	± 0.7 SE	± 0.1 SE	± 0.1 SE	± 0.1 SE
Nontreated	5989.0	550.6	387.4b	3329.4	45.5b	9.7	4.2b	1.9
Treated	6203.7	490.7	481.8a	3057.0	53.9a	9.4	4.7a	1.9
Time (d)	± 234.7 SE	± 37.7 SE	± 13.4 SE	± 21.0 SE	± 1.1 SE	± 0.2 SE	± 0.2 SE	± 0.1 SE
14	4490.6b	640.1a	344.4c	506.6a	49.2b	10.0a	6.8a	1.1c
22	6452.8a	404.3b	479.6a	210.8c	55.5a	9.4b	4.5b	2.2ab
30	7031.3a	589.8a	498.1a	317.7b	48.8b	10.4a	3.6c	2.3a
36	6410.9a	447.4b	416.2b	235.1c	45.1c	8.5c	2.8d	2.0b

Table 5.9. Mean (\pm SE) concentrations (% dry weight) of plant macronutrients (C, N, K, P, S, Ca, and Mg) as affected by the cultivar, insecticidal seed treatment, and time main effects in the late-planted trial, Crowley, LA, 2020. Standard error for each nutrient is shown across the main effects. Means accompanied with the same letter are not significantly different (Tukey's HSD: $P > 0.05$).

Main Effect	C	N	K	P	S	Ca	Mg
Cultivar	± 0.096 SE	± 0.060 SE	± 0.036 SE	± 0.004 SE	± 0.004 SE	± 0.004 SE	± 0.004 SE
Hybrid	40.216	2.299	2.187a	0.211	0.189a	0.172	0.177
Inbred	40.068	2.106	2.000b	0.214	0.173b	0.167	0.167
Seed Trt	± 0.096 SE	± 0.060 SE	± 0.036 SE	± 0.004 SE	± 0.004 SE	± 0.004 SE	± 0.004 SE
Nontreated	40.547a	2.232	2.037b	0.197b	0.181	0.163b	0.04b
Treated	39.737b	2.109	2.149a	0.228a	0.180	0.176a	0.153a
Time (d)	± 0.136 SE	± 0.085 SE	± 0.051 SE	± 0.005 SE	± 0.005 SE	± 0.006 SE	± 0.005 SE
19	40.159a	2.693a	2.501a	0.211	0.236a	0.190a	0.182a
26	39.512b	2.327b	2.239b	0.217	0.183b	0.174a	0.181a
33	40.436a	2.142b	1.989c	0.218	0.174b	0.175a	0.174a
40	40.460a	1.648c	1.644d	0.205	0.130c	0.139b	0.151b

Table 5.10. Mean (\pm SE) concentrations (mg/kg) of plant micronutrients (Na, Fe, Mn, Al, Zn, B, Cu, and Mo) as affected by the cultivar, insecticidal seed treatment, and time main effects in the early-planted trial, Crowley, LA, 2020. Standard error for each nutrient is shown across the main effects. Means accompanied with the same letter are not significantly different (Tukey's HSD: $P > 0.05$).

Main Effect	Na	Fe	Mn	Al	Zn	B	Cu	Mo
Cultivar	± 179.0 SE	± 27.1 SE	± 11.3 SE	± 12.5 SE	± 0.8 SE	± 1.0 SE	± 0.1 SE	± 0.1 SE
Hybrid	5078.9	411.6	412.0b	240.9a	52.2b	12.5	4.6	2.1a
Inbred	4608.2	372.6	505.7a	204.1b	59.6a	12.9	4.9	1.7b
Seed Trt	± 179.0 SE	± 27.1 SE	± 11.3 SE	± 12.5 SE	± 0.8 SE	± 1.0 SE	± 0.1 SE	± 0.1 SE
Nontreated	5075.1	435.5a	395.6b	250.9a	53.3b	12.0	4.3b	1.9
Treated	4612.0	348.8b	522.1a	194.1b	58.5a	14.0	5.2a	2.0
Time (d)	± 253.2 SE	± 38.3 SE	± 16.0 SE	± 17.6 SE	± 1.2 SE	± 1.4 SE	± 0.2 SE	± 0.1 SE
19	6046.2a	416.7a	483.6a	284.4a	74.8a	9.9b	6.6a	1.8
26	5035.3b	484.3a	510.7a	246.6ab	59.1b	25.6a	4.6b	2.0
33	4821.6b	423.1a	487.0a	221.5b	49.6c	7.6b	4.6b	2.0
40	3471.9c	244.5b	354.1b	137.5c	40.2d	7.7b	3.3c	1.8

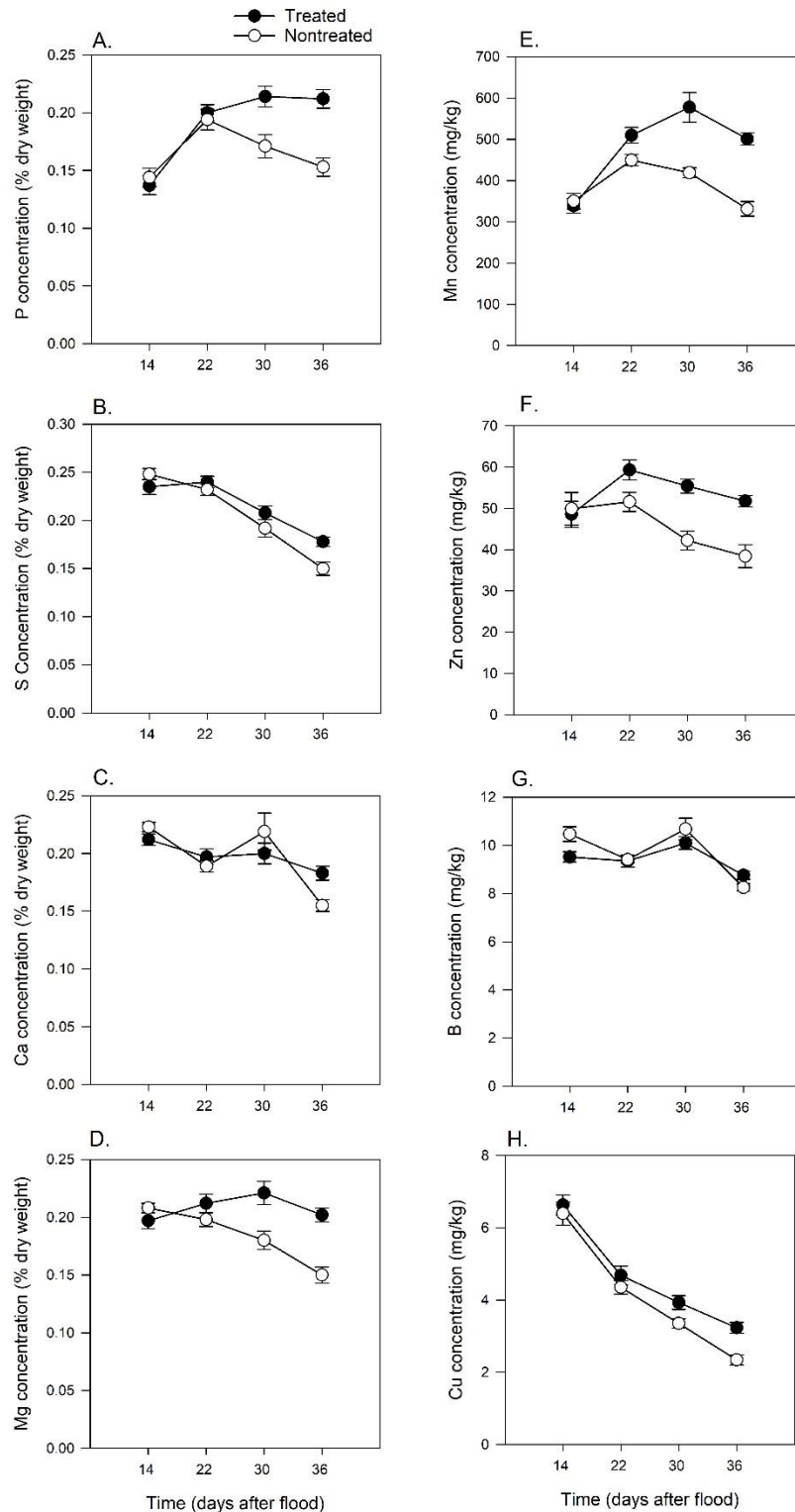


Figure 5.4. Mean (\pm SE) concentrations of plant macronutrients (% dry weight) P, S, Ca, and Mg (A, B, C, and D) and micronutrients (mg/kg) Mn, Zn, B, and, Cu (E, F, G, and H) as affected by the insecticidal seed treatment \times time interaction in the early-planted trial, Crowley, LA, 2020.

5.3.3. Plant Hormones

Production of JA and OPDA in rice shoots was influenced by cultivar (Table 5.11). The concentrations of JA and OPDA were 23 and 20% higher, respectively, in the hybrid cultivar compared to the inbred cultivar across sampling time (Figs. 5.5A, C). Weevil feeding increased the production of OPDA. The concentration of OPDA was 11% higher in nontreated plants (weevil infested) compared to treated plants (Fig. 5.5C). An increase in the production of JA, JA-Ile, OPDA, and JA was observed at 10 d after flood and the concentrations of these plant hormones subsequently decreased at 20 and 30 d after flood (Figs. 5.5A, B, C, D).

5.3.4. Yield Response

Yield losses due to rice water weevil infestations ranged from 8–35% across planting dates and cultivars. Percent yield losses were affected by cultivar in the late-planted trial ($F_{1,5} = 8.22$; $P = 0.03$) but not in the early-planted trial ($F_{1,5} = 0.37$; $P = 0.57$). Inbred cultivar exhibited 27% greater yield loss than hybrid cultivar in the late-planted trial (Fig. 5.6B).

Table 5.11. Results of repeated measures general linear mixed models (repeated-GLIMMIX) for plant hormones in rice shoots in the early-planted trial, Crowley, LA, 2020.

Fixed Effect	df	Phytohormone					
		JA F	JA-Ile F	OPDA F	SA F	IAA F	ABA F
Cultivar	1	4.75*	0.00	13.06**	0.14	0.05	0.56
Seed Trt	1	2.22	2.59	3.93*	0.02	0.96	0.56
Time	2	74.64**	50.11**	44.93**	27.19**	0.65	0.02
Cultivar × Seed Trt	1	2.95	0.00	0.12	0.64	5.80*	2.73
Cultivar × Time	2	0.37	3.41*	1.25	3.73*	1.62	0.97
Seed Trt × Time	2	0.54	0.16	0.36	0.03	0.05	1.78
Cultivar × Seed Trt × Time	2	2.37	0.00	0.72	0.15	0.26	0.29
Error	36						

* $P \leq 0.05$; ** $P \leq 0.01$

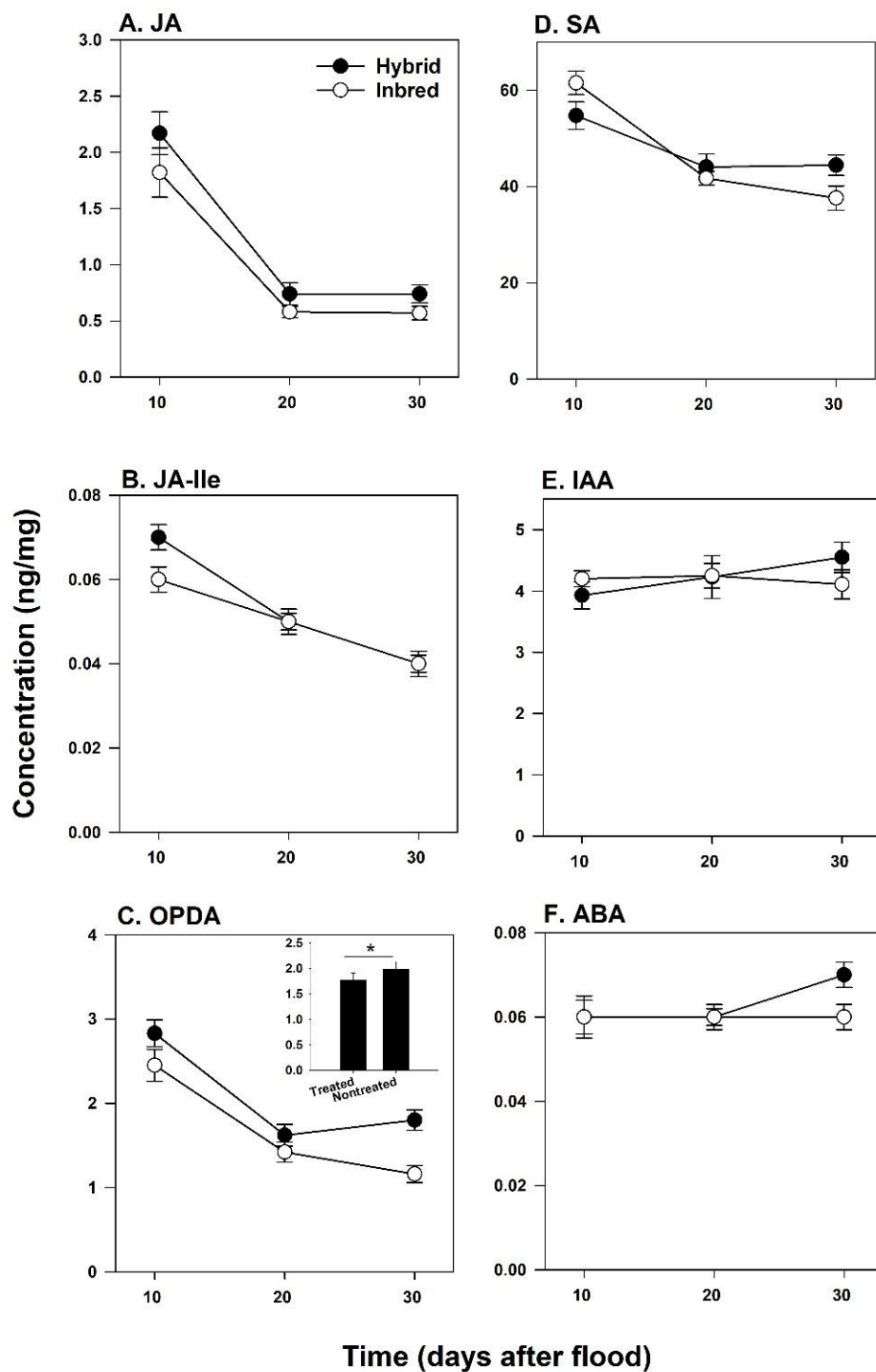


Figure 5.5. Mean (\pm SE) concentrations (ng/mg) of (A) JA, (B) JA-Ile, (C) OPDA, (D) SA, (E) IAA, and (F) ABA in rice shoots as affected by cultivar and in the early-planted trial, Crowley, LA, 2020. Bar graph embedded within panel C shows OPDA concentrations between treated and nontreated plots. Bar graph accompanied by an asterisk have significantly different means (Tukey's HSD: $P < 0.05$).

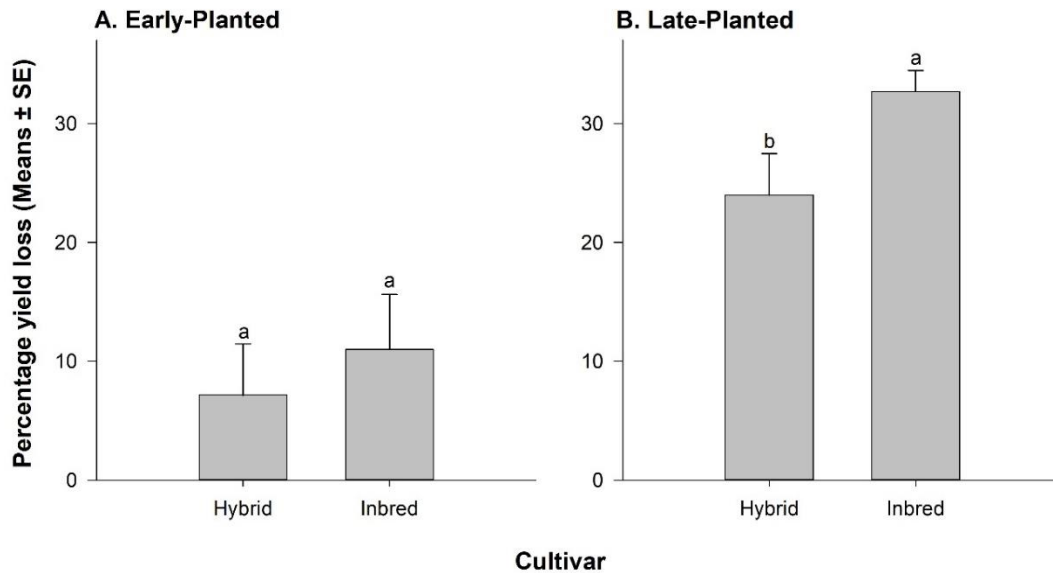


Figure 5.6. Mean (\pm SE) yield loss as affected by cultivar in the (A) early-planted and (B) late-planted trials, Crowley, LA, 2020. Mean within a panel capped with the same letter are not significantly different (Tukey's HSD: $P > 0.05$).

5.4. Discussion

This study investigated the effects of chronic root feeding by weevil larvae on plant growth, nutrient uptake, and production of plant hormones in a hybrid and an inbred rice cultivar. The results from the experiments presented here demonstrate that chronic root herbivory reduced plant growth, yields, and nutrient uptake. Our results also corroborate the findings of Villegas et al. (2021, Chapter 2) which reported that hybrid cultivars were generally more tolerant to rice water weevil infestations than inbred cultivars.

The hybrid cultivar used in this study supported higher numbers of immature weevils compared to the inbred cultivar. Weevil densities observed in both cultivars were 4-fold higher than the larval thresholds of five per core which indicate relatively high weevil pressure in the experimental site, consistent with weevil pressure observed in commercial fields in the region (Hummel et al., 2014). Chlorantraniliprole seed treatment reduced weevil infestations at a level similar to previous reports (Hamm et al., 2014; Hummel et al., 2014; Villegas et al., 2019).

Infestations of weevil larvae on roots were observed approximately two weeks after permanent flood was established, but infestations may have started earlier as previously reported by Zou et al. (2004). Weevil densities increased by 2.5-folds in the two weeks following the first sampling point, which suggests persistent infestations of rice water weevil in the field. The injury caused by weevil larvae is a chronic process as shown by the interaction between sampling time and root and shoot biomass. Reductions in shoot biomass due to weevil infestations were observed in both early- and late-planted trials in this study. Previous studies have documented significant reductions in shoot biomass due to weevil larval feeding in rice plants (Kraus and Stout, 2019a; Zou et al., 2004a). In contrast, no differences in root biomass were observed between weevil-infested and weevil-protected plants. The lack of differences in root biomass between weevil treatments may indicate that either cultivar compensated for root injury by weevil larvae over the course of the experiments. In this study, root biomass accumulation, particularly in the hybrid cultivar, increased substantially at later sampling times. Obtaining entire intact root systems from rice plants grown under field conditions is challenging, thus may have also affected the results of root biomass presented here. Nonetheless, several studies have presented root biomass loss in rice plants due to direct feeding by weevil larvae (Kraus and Stout, 2019a; N'guessan et al., 1994a, 1994b; Zou et al., 2004a). The rest of the results presented in this study suggests that root pruning by weevil larvae did occur.

Our understanding of the mechanisms by which root pruning by weevil larvae leads to poor plant performance is still limited. There are two nutrient uptake pathways plants typically utilize: plant roots absorb nutrients directly from the soil and plants take up soil and atmospheric nutrients indirectly through symbiotic relationships in the rhizosphere (Smith and Read, 1997). Insect herbivory negatively influences both pathways of nutrient uptake but the negative effect of

herbivory on the direct nutrient uptake pathway from the soil is greater than the indirect pathway via the symbionts (Katayama et al., 2014). The reductions in shoot biomass and yields in weevil infested plots reported herein may be explained, in part, by the reductions in nutrient uptake by rice plants. Both macro and micronutrients essential for rice growth and development were, in some instances, severely reduced in weevil-infested rice plants. In particular, concentrations of N, P, K, S, Ca, Mg, Mn, Zn, and Cu were negatively affected by weevil infestations. Four macronutrients (N, P, K, and S) and one micronutrient (Zn) are critical for high-yielding rice in Louisiana (Harrell and Saichuk, 2014). These nutrients play important roles in physiological processes in plants including photosynthesis, root and shoot development, plant vigor, response to biotic and abiotic stresses, etc. (Shrestha et al., 2020). Deficiency on N, P, or K in rice plants results in reduced tillering, plant stunting, delayed maturity, and yield reductions (Harrell and Saichuk, 2014), which are similar symptoms associated with weevil infestations in rice (Zou et al., 2004a). Like what was observed in this study, root herbivory in other crops affected nutrient uptake as well. For instance, infestation by the white grub, *Ligyrus subtropicus*, on sugarcane reduced concentrations of N, P, and K in the leaves, resulting in low sugar yield (Coale and Cherry, 1989). Root pruning by western corn rootworm, *Diabrotica virgefera virgefera*, on maize plants resulted in decreased concentrations of K, Mg, and Ca in shoots, shoot dry weights, and yields (Godfrey et al., 1993; Kahler et al., 1985). Additionally, chronic feeding of weevil larvae in roots exacerbated the reductions in nutrient uptake particularly of P, Zn, Mn, and Mg. In contrast, we observed that concentrations of C were higher in nontreated plants (weevil-infested) compared to treated plants in the late-planted trial. This observation agrees with other studies which reported that plants accumulate storage carbohydrates on shoots when attacked by root herbivores (Borowicz et al., 2005; Dunn and Frommelt, 1995). This study is one of the few

studies directly linking nutrient uptake and biomass loss in rice–rice water weevil interaction. Although a study conducted by Way et al. (2006) indicated that increasing rates of N fertilization of rice in the presence of rice water weevil infestation did not compensate for weevil damage, future studies should investigate the potential of other nutrients to mitigate weevil damage. For instance, experiments examining whether increasing the rates of P and K fertilization will reduce damage by rice water weevil infestations should be conducted.

Alternatively, the activation of defense systems by rice plants due to weevil injury may have interfered with plant growth and development. The deployment of defense mechanisms is imperative for plant survival, however, defense activation generally comes at the expense of plant growth – commonly known as a growth-defense tradeoff (Huot et al., 2014). The assumption behind the ‘growth-defense tradeoff’ phenomenon is that plants possess a limited pool of resources that can be invested either in growth or in defense (Herms and Mattson, 1992). Plant hormones (small organic molecules) are required by plants to regulate processes such as growth, development, reproduction, and defense responses. In particular, defense hormones such as salicylic acid (SA) and jasmonic acid (JA) play important roles in the regulation of plant immune responses both locally and systematically to coordinate plant defenses in different parts of the plants against different types of arthropod herbivores and pathogens (Erb et al., 2012b; Wasternack, 2013). Results from the study conducted by Lu et al. (2015) revealed that root herbivory by rice water weevil in rice plants induced jasmonate signaling in the roots and that jasmonates improved plant resistance against root-feeding insects. Moreover, their results showed that root injury by weevil larvae increased JA by 30% in the rice roots but this herbivore-induced JA burst in the roots was significantly lower when compared to JA levels in leaves induced by rice striped stem borer, *Chilo suppressalis*, feeding in rice shoots (Erb et al.,

2012a, 2012b). In this study, we found that levels of 12-oxo-phytodienoic acid (OPDA, precursor of JA biosynthesis) in shoots were greater in weevil-infested rice plants. However, we did not observe any differences in levels of JA, JA-Ile, SA, IAA, and ABA in weevil-infested and weevil protected plots. Similar to what was observed in this study, Erb et al. (2009) reported that neither JA nor SA were found to be induced in the shoots of maize plants by the western corn rootworm. Perhaps the production of these phytohormones is concentrated in the roots where the injury is occurring. Future studies should examine spatial and temporal dynamics of hormone concentrations in both roots and shoots as affected by root feeding by weevil larvae. Although not shown in this study, defense hormones do in fact influence rice growth and development. Studies conducted by Kraus and Stout (2019b) and Bhavanam and Stout (2021) documented that the application of jasmonates to rice seeds enhanced plant resistance to rice water weevil but was accompanied by reductions in plant growth. Chronic feeding by weevils in the field may actively induce plant defense at an extended period thus affecting plant growth and development.

Yield losses due to weevil infestations in this study ranged from 8–35% across planting dates and cultivars. Results presented here were consistent with previous studies which reported yield losses of 2–33% caused by weevil infestations (Stout et al., 2011a; Villegas et al., 2021b, 2021a; Wilson et al., 2021a). In the late-planted trial, yield loss was lower in the hybrid compared to the inbred cultivar. Villegas et al. (2021a) have reported that hybrid cultivars were generally more tolerant to weevil injury than inbred cultivars. Plant traits typically associated with tolerance are biomass accumulation, root-regrowth (compensation), nutrient allocation, and yield potential (Horgan and Crisol, 2013; Strauss and Agrawal, 1999). In this study, root and shoot biomass in hybrid were higher compared to inbred cultivar. Additionally, root biomass

accumulation in the hybrid cultivar increased at a rate greater than the inbred cultivar, especially at later sampling times. This inherent trait of the hybrid cultivar may have contributed to higher nutrient uptake compared to the inbred cultivar. Thus, the hybrid cultivar in the study was least affected by weevil infestations than the inbred cultivar.

Overall, results from this study suggest that chronic root herbivory by rice water weevil affects nutrient uptake by rice plants, thereby reducing plant growth. Plant hormones elicited by chronic weevil feeding also play an important role in plant development and should be investigated further in a more controlled environment. The hybrid cultivar in this study was more tolerant to weevil infestations than inbred cultivar perhaps due to higher root and shoot biomass accumulation and yield potential. Rice water weevil feeding in rice is chronic, thus future studies should aim to provide an in-depth understanding of the effects of chronic feeding on rice physiology and rice-pest interaction.

Chapter 6. Summary and Conclusion

By 2030, the world population is expected to reach 8.5 billion with the most growth in the developing parts of the world. The challenge is to produce enough food for the growing population with limited resources. Rice is one of the most important crops worldwide and a staple for half of the world's population. The U.S. is a major rice producer globally and Louisiana is the third-largest rice producer in the country. Rice plants are subjected to various pressures by insect pests and diseases throughout their growth and development. The rice water weevil, *Lissorhoptrus oryzophilus* Kuschel, is consistently the most destructive early-season pest of rice in the U.S. This insect pest poses a global threat to rice production having invaded rice-producing regions of Asia and Europe. In addition, lepidopteran stemborers, particularly the invasive Mexican rice borer, *Eoreuma loftini* (Dyar), are increasing in economic importance as pests of rice in Louisiana. Sustainability in pest management programs is often achieved by the integrated and balanced use of available control tactics. Ideally, the management of rice water weevil and stemborers should incorporate combinations of control strategies; however, current management programs rely heavily on chemical control. Alternative approaches to chemical control are needed. Of the available alternative tactics, host-plant resistance may have the most potential to contribute to a more sustainable pest management program. In particular, tolerance is a type of plant defense that allows crop plants to maintain yield in spite of injury by herbivores, such that a more susceptible rice genotype generally suffers a greater yield loss than tolerant genotype when exposed to similar levels of injury. Plant tolerance has not been adequately investigated as a management tactic against the rice water weevil and stemborers.

Field experiments were established in Louisiana, Texas, and Mississippi to test whether hybrid rice cultivars possess greater tolerance to rice water weevil injury than inbred rice

cultivars. Tolerance was determined by comparing yields from plots of the same cultivar that were protected and not protected from rice water weevil infestations. Results from this study demonstrated that yield losses from hybrid cultivars were lower than yield losses from inbred cultivars under similar weevil densities. Yield reduction associated with every immature rice water weevil was approximately 71 kg in inbred rice cultivars and 8 kg in hybrid rice cultivars. This supports the hypothesis that hybrid cultivars are generally more tolerant to weevils.

Another experiment was conducted to evaluate the influence of commonly grown inbred rice cultivars in Louisiana on infestation by both weevils and stemborers (resistance) and to assess whether yield losses associated with these insect pests differed among the rice cultivars (tolerance). Results from this study demonstrated that the medium-grain rice cultivar ‘Jupiter’ supported the highest numbers of immature weevils relative to other cultivars, while weevil densities on other cultivars were intermediate. Stemborer larvae recovered from plants showing whitehead symptoms were initially a combination of Mexican rice borers, sugarcane borers, and rice stalk borers (2017). However, in the next two years (2018 and 2019) 100% of the recovered larvae were Mexican rice borers. This indicates that the Mexican rice borer may have surpassed the sugarcane borer and rice stalk borer in economic importance in Louisiana rice. Low levels of stemborer injury were observed in ‘Cheniere’ and ‘Jazzman-2’, which suggests that these cultivars express some level of resistance to stemborers, whereas high stemborer injury was observed in ‘Cocodrie’, ‘CL151’, and ‘Mermentau’. Combined infestations of rice water weevil and stemborers negatively affected rice yields, however, the differences in overall yield losses among inbred cultivars were minimal.

The influence of rice cultivars and flood timing on the infestations of rice water weevil and stemborers and the corresponding impact on rice yields were also examined. Early- and late-

planted trials were established, and permanent flood was applied at normal timing (approximately at the five-leaf stage of rice plants) or delayed by two weeks. Similar to previous results (Chapter 3), the rice cultivar ‘Jupiter’ consistently supported the highest numbers of immature rice water weevils, whereas low levels of stemborer injury were observed in ‘Jazzman-2’. Rice water weevil densities were lower in plots subjected to delayed flood compared to normal flood timing in late-planted trials only. Stemborer injury was also reduced in delayed-flooded plots. Yield losses due to weevil and stemborer infestations were generally lower in plots subjected to delayed flood compared to normal flood timing.

Lastly, experiments were conducted to investigate the effects of chronic feeding by rice water weevil on plant growth, nutrient uptake, and production of plant hormones in a hybrid and an inbred rice cultivar. Results from this study demonstrated that chronic root herbivory by rice water weevil negatively affected plant nutrient uptake of macro and micronutrients essential for growth and development. The reductions in nutrient uptake in weevil-infested plants may be the primary cause for subsequent reductions in plant growth and yields. The hybrid cultivar in this study, as previously reported (Chapter 2), was more tolerant to weevil infestations than the inbred cultivar. This may be due to higher root and shoot biomass accumulation and yield potential in the hybrid compared to the inbred cultivars.

Current management programs for rice water weevil and stemborers rely heavily on chemical control. There is a need for a more holistic approach to pest management in rice. Results from these studies suggest that the integration of tolerant cultivars into insect pest management programs is a potentially valuable strategy, particularly when combined with other control tactics (e.g. delayed flood timing). The use of tolerance cultivars may be sufficient to reduce yield losses in the absence of insecticide where weevil pressure is low or in organic rice.

Plant tolerance is also a suitable alternative approach in situations where insecticide use is not desirable. Additionally, plant resistance may serve as a valuable component of an integrated pest management program for stemborers, especially if stemborer incidence continues to increase in Louisiana rice. Future studies should investigate in-depth the plant traits associated with tolerance to facilitate the development of tolerant rice cultivars.

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Tolerance to rice water weevil, *Lissorhoptus oryzophilus* Kuschel (Coleoptera: Curculionidae), infestations among hybrid and inbred rice cultivars in the Southern U.S.

Author: James M. Villegas, Blake E. Wilson, Michael O. Way, Jeffrey Gore, Michael J. Stout

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Vita

James was born in Bacolod City, known as the “City of Smiles”, in the Philippines. He received his B.S. in Life Sciences with specialization in molecular biology and biotechnology at the Ateneo de Manila University in 2012. His undergraduate thesis was on the molecular characterization and phylogenetic analyses of RNA segments 5 and 6 of rice ragged stunt virus transmitted by brown planthopper in Southeast Asia. He joined the Entomology group at the International Rice Research Institute in 2013 and was involved in developing ecological engineering approaches to restore and conserve ecosystem services for pest management in rice. He got his M.S. in Entomology with a minor in applied statistics at the Louisiana State University in 2017. His master’s thesis was focused on the independent and interactive effects of nitrogen fertilization and soil silicon amendment on the rice insect pest complex. He was hired as a research associate by Dr. Blake Wilson in 2018 to work on IPM in rice and sugarcane. He is currently a Ph.D. candidate at LSU and will graduate in Fall 2021. He intends to continue working in row crops IPM.