



A Century of Rice Water Weevil (Coleoptera: Curculionidae): A History of Research and Management With an Emphasis on the United States

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ABSTRACT. The rice water weevil (*Lissorhoptrus oryzophilus* Kuschel) is a native curculionid pest of rice in the southern and eastern United States. It was first identified as *Lissorhoptrus simplex* Say in the first report of damage from southern Georgia in 1881. In 1951 Chilean systematist Guillermo Kuschel reclassified it as *L. oryzophilus* following a reevaluation of New World genera within Curculionidae. Management of the weevil has changed throughout the years, as environmental issues, regulatory actions, and pesticide resistance have required researchers, pest management practitioners, and growers to adapt. In the 2010s, management of the rice water weevil has expanded with the use of anthralic diamides and neonicotinoids as the latest conventional options, generally delivered as seed treatments in southern U.S. rice production, and the possible emergence of *Bacillus thuringiensis* as a viable alternative to chemical controls. Delayed flooding and planting are common cultural controls used in southern U.S. rice production while levee weed control and winter flooding are used in California production. The history of this insect pest including management, life history, and invasion biology in rice production regions of the temperate world will be discussed with an emphasis on the United States.

Key Words: *Lissorhoptrus oryzophilus*, *Oryza sativa*, parthenogenesis, invasion, control

Rice water weevil (*Lissorhoptrus oryzophilus* Kuschel) is the most deleterious invertebrate pest in rice (*Oryza sativa* L.) agriculture in the United States. It causes yield losses up to 25% in untreated situations (Reay-Jones et al. 2008). The adults inflict minor damage by consuming leaf tissue, leaving typical longitudinal scars along the leaf blade (Stout et al. 2002a, Shi et al. 2008). The percentage of plants with scarring on the two newest leaves has been used to gauge the intensity of the infestation in California, but this parameter is a poor predictor of damage by larvae and yield losses (Grigarick 1992). The majority of the damage is the result of root-feeding by soil-dwelling larvae (Zhang et al. 2004). The goal of this article is to summarize the current knowledge of rice water weevil since the first reported sighting of damage in 1881. Management strategies and future directions of research on the insect will be discussed.

Early History

The rice water weevil (*L. oryzophilus*) is native to the marshlands of the Mississippi basin, with populations as far north as Canada and east to New England (Isely and Schwardt 1934). However, rice water weevil was not a pest on rice when the crop was introduced into the United States in the late 1700s (Adair et al. 1966). It is unclear when rice water weevil began the transition to *O. sativa* as a source of food. The earliest record of damage by this insect was published in a report by the Commissioner of Agriculture for the year 1881–1882 by Riley and Howard (Newell 1913). At the time the rice water weevil was classified as *Lissorhoptrus simplex* Say, and the report describes damage caused near fields in Savannah, GA. The second recorded report of damage came from Dr. W.D. Pierce in Texas in 1904, and the third report of damage came from Louisiana in 1909. In a U.S. Department of Agriculture report from 1912, the author predicted that the problem was only going to get worse in Texas, Louisiana, and Arkansas, as rice wetland acreage increased and replaced the rice water weevil's original marshland habitat (Tucker 1912).

However, a problem in the 1910s was that some researchers were uncertain of the degree of damage and yield loss caused by rice water weevil, even though a U.S. Department of Agriculture report indicated that the “rice root maggot” was responsible for the damage (Tucker 1912, Webb 1914). Tucker emphasized that damage was not uniform across the southern U.S. rice production region. The lack of quanti-

tative evidence for rice water weevil negatively impacting rice added to the level of uncertainty regarding the extent of damage.

In the late 1920s, researchers at the Louisiana Experiment Station reported the rice water weevil as a minor pest for causing negligible damage (Ingram 1927). A report in 1930 again refuted the assertion that rice water weevil was the source of yield reductions in rice (Ingram and Douglas 1930). However, in 1934 rice water weevil was confirmed to be reducing rice yields in Arkansas by Isely and Schwardt (1934), which contradicted studies by Ingram and Douglas (1930). In the Arkansas study, the researchers confined rice water weevil adults to rice within small cages in the field and quantified the number of larvae and the yield. Isely and Schwardt tried to explain the differences between the Arkansas and Louisiana studies by speculating that Arkansas rice was more vulnerable to rice water weevil attack. They explained that the rice water weevil in Arkansas is living within its optimum climatic zone, but as rice is a tropical plant, it would be growing at suboptimal conditions. Therefore, rice water weevil pressure would be greater on rice in Arkansas than in Louisiana. However, this idea did not seem to hold true given that both states had already been afflicted with rice water weevil, with reported infestations of the weevil as far south as Crowley, LA, since the 1910s (Tucker 1912). It is not entirely clear why this discrepancy occurred, but it did not matter in the long run because as rice acreage increased, so did the presence of rice water weevil.

After rice water weevil was established as an economic problem, research transitioned to finding control measures for this pest. Draining fields was the first best option to control rice water weevil. Researchers had suggested the use of arsenical powders, but it was concluded that the risk of accidental poisoning downstream might be too great (Newell 1913). Draining was the preferred method for managing heavy rice water weevil infestations until the 1950s (Whitehead 1954). Management changed significantly in 1952 when researchers began experiments with modern insecticides (Whitehead 1954). In addition, the rice water weevil was reclassified under its present scientific name, *Lissorhoptrus oryzophilus* (Kuschel 1951). Rice water weevil remained exclusively a problem in southern U.S. rice until the late 1950s when the weevil was first found in California in 1958 (Lange and Grigarick 1959). From there the weevil began a steady spread around the temperate rice growing regions of the world,

invading Japan in 1976, Korea in 1980, China in 1988, and most recently Italy in 2004 (Kisimoto 1992, Jiang and Cheng 2003b, Lupi et al. 2010). This invasive ability is aided by a particular and peculiar aspect of this weevil's biology, the fact that a small percentage of the population in its native range reproduces by parthenogenesis (Jiang et al. 2008).

Description of Life Stages

Rice water weevil belongs to the family Curculionidae in the order Coleoptera. The weevil mainly feeds on aquatic and semiaquatic plants in the family Poaceae and Cyperaceae (Tindall and Stout 2003, Lupi et al. 2009). The rice water weevil is a semiaquatic beetle that is well-adapted to life in water. Adults diapause during the winter months on levees and vegetated banks (Nilakhe 1977, Palrang et al. 1994, Jiang et al. 2004). The original host of rice water weevil has been suspected to be wild rice *Zizania aquatica* L., which shares similar physical and habitat characteristics as *O. sativa* (Newell 1913), but this is speculative, as rice water weevil is well-adapted to feeding on a wide range of aquatic grasses.

Eggs and Oviposition. Adults oviposit directly into the plant tissue in the leaf sheath slightly below the water surface (Bowling 1972b). Before the 1960s, researchers had assumed that eggs were laid on the roots, possibly because the larvae fed on the roots (Webb 1914, Isely and Schwarzt 1930). In 1964, Grigarick and Beards (1965) corrected that assumption by observing that the eggs are oviposited directly into the sheath tissue. The peak oviposition period based on number of eggs found in the sheath was approximately two weeks after flooding (Everett and Trahan 1967). Weevils prefer ovipositing in the younger tissues of the plant, as seen in experiments with second (ratoon) rice crops (Thompson and Quisenberry 1995). Nitrogen fertilization can influence ovipositional preferences by increasing the desirability of the plant with increased nutrients (Jiang and Cheng 2003a). The eggs hatch 4–9 d after oviposition and the larvae mine the leaf tissue within the water (Raksarat and Tugwell 1975). They then drop down to the soil and burrow toward the roots (Grigarick and Beards 1965) (Fig. 1).

Larval and Pupal Stages. There are four larval instars that take 28–35 d to develop into pupae in the field and are over 1 cm long at maturity (Fig. 2); it takes 50 d at 20°C in a laboratory setting for eggs to complete development to an adult (Grigarick and Beards 1965, Cave and Smith 1983, Flint et al. 2013). In the southern United States, this interval is much shorter at 14–21 d for the completion of larval development, probably due to warmer seasonal temperatures (Cave et al. 1984). The larvae have special adaptations of their tracheal system, modified chitinized spiracles shaped as dorsal hooks, that pierce plant tissue enabling them to respire in the anoxic environment of the flooded rice paddy (Zhang et al. 2006). Larvae take advantage of the fact that rice roots are composed of aerenchyma cells, which are specialized cells that facilitate gas exchange with the atmosphere (Lupi et al. 2009, Kögel-Knabner et al. 2010). Oxygen from the atmosphere and leaf photosynthates are transported by diffusion through these spongy cells to the roots for cellular functions. Larvae use this oxygen supply by directly tapping into the aerenchyma or building special mud chambers that fill with oxygen upon piercing the roots (Zhang et al. 2004). But the larvae are not simply confined to a single plant in this submerged zone. It has been observed that larvae that have established on aquatic weeds will migrate to rice through the submerged soils (Rolston and Rouse 1964). Larvae build and attach their pupal chambers to the rice root to allow for gas exchange. The silk cocoon is surrounded by an oval pupal cell which excludes water and prevents air leakage into the surrounding rhizosphere. The pupal stage takes 5–14 d to complete; 21 d at 22°C in a laboratory setting (Wu and Wilson 1997, Saito et al. 2005, Flint et al. 2013).

Adult Stage. The adults are only 4 mm long upon emergence with a light brown coloration and sometimes have a dark spot running the length of the elytra (Fig. 3, Jiang et al. 2006, Flint et al. 2013). The adult has two adaptations that confer an ability to lead an aquatic



Fig. 1. Rice water weevil plant damage from greenhouse study. Top picture shows undamaged root systems. Bottom picture shows the diagnostic root pruning by rice water weevil larvae.

lifestyle. The mesothoracic legs contain hydrophobic hairs that enable adults to swim proficiently in water in the same manner as other aquatic coleopterans and hemipterans. Their plastron facilitates gas exchange while the adults are submerged (Hix et al. 2000).

After pupal emergence, the rice water weevil adults feed on the rice plant or the weeds on levees before moving offsite. This feeding event is to build up fat reserves in preparation of winter diapause (Muda et al. 1981). In California, most of Japan, and Korea, the adults will move to the levees or vegetated banks for hosts and shelter (Fig. 4) in August and September and then enter winter diapause in November (Lee and Uhm 1992, Espino 2012). In the southern United States and



Fig. 2. Rice water weevil pupa and two larvae shown side by side for size comparison. Viewed at 60 \times magnification.



Fig. 3. Rice water weevil adult feeding on *Bromus* spp. leaves in the laboratory at UC Davis and the resulting damage on the rice leaf blade showing diagnostic longitudinal feeding scars by rice water weevil adults.

China, adults will go through additional generations because of the longer growing season and multiple crop cycles (Ingram and Douglas 1930, Chen et al. 2005).

Research into the biology of rice water weevil diapause has found that mortality in diapausing weevils was almost 100% when temperatures were -20°C in moist soil as opposed to 30.5% mortality in dry soil at the same temperature. These results suggest that diapause in vegetated areas serves to protect the weevil during the wet winter months (Morimoto 2011). Physiological studies on weevil diapause revealed that it is very difficult to break diapause during the winter, despite raising temperature and increasing photoperiod, as only 10% of weevil adults subjected to spring-like conditions break diapause prematurely (Knabke 1973). The goal of these studies was to develop colonies of *L. oryzaophilus* for offseason studies, but because of the diapause it was unfeasible.

In the field, dormancy cessation begins when temperatures are above $15\text{--}21^{\circ}\text{C}$. This is typically the weevil's cue to conduct dispersal flights under low wind and warm crepuscular conditions (Grigarick et al. 1991). The date of spring emergence closely tracks that of spring-time temperatures (Morgan et al. 1984). The period of emergence and weevil flight lasts three months peaking around late April or early May (Webb 1914, Muda et al. 1981). The weevils feed on weeds to

build up their energy reserves for flight and reproduction (Palrang and Grigarick 1993). The host range of *L. oryzaophilus* in both the United States and Italy includes various weeds in rice paddies such as barnyard grass (*Echinochloa crus-galli* L.), Dallis grass (*Paspalum dilatatum* Poir), and yellow nutsedge (*Cyperus esculentus* L.; Knabke 1973, Tindall and Stout 2003, Lupi et al. 2009). In one case in Louisiana, rice water weevil was observed to prefer fall panicum (*Panicum dichotomiflorum* Michx) more than rice (Tindall et al. 2004b). Even being in the presence of these food sources can initiate regeneration of the flight muscles (Morgan et al. 1984).

The regeneration of flight muscles is also temperature dependent, with 18°C determined as the threshold for muscle regeneration (Morgan et al. 1982). Researchers in Louisiana using rice water weevils captured from light traps over the past 14 years found that a lower temperature threshold of 15.6°C was required for muscle regeneration to begin. Using a degree-day model based on the light trap data, these researchers were able to predict spring emergence with an error of less than seven days (Zou et al. 2004b).

By April, the weevil flight muscles have regenerated coinciding with peak flight periods, but by peak oviposition times most weevils have degenerated their flight muscles (Muda et al. 1981). Degeneration of flight muscles can be induced by the presence of moist or



Fig. 4. Levees with an abundance of weeds in early spring provide rice water weevil adults ample resources for regeneration of flight muscles and ovary development. A common sight around rice fields in the Northern Sacramento Valley in early March.

flooded soil and the availability of an appropriate food source. It was found that flight from unflooded and flooded habitats without rice was higher when compared with flooded habitats with rice. It was suggested that the presence of rice in a flooded habitat was important in arresting weevil flight (Palrang and Grigarick 1993). If they have flown, then the adult indirect flight muscles will degenerate within 5–7 d of landing (Haizlip 1979, Lorenz and Hardke 2013). Once fields are flooded, the adults swim out into the edges of the flooded paddy (Stout et al. 2002b, Flint et al. 2013). They will typically clump in areas adjacent to the levee and feed within several meters of the edge of the field (Sooksai and Tugwell 1978, Espino 2012). It was found that these adult populations peaked after flooding, which coincided with an increase in the number of leaf feeding scars (Muda et al. 1981).

Reproductive Biology. Rice water weevil populations in California, Asia, and Europe differ in their reproductive biology from those in the native range of the southern United States (Grigarick and Beards 1965, Jiang et al. 2008). The majority of adults in the southern United States reproduce sexually, with <10% of the native population being parthenogenetic (Jiang et al. 2007). The male and the female are told apart by their differences in the ventral parts of the abdomen. The female rice water weevil is larger with the first two ventral abdominal segments that are flat and convex at the midline, while the male is concave at these two segments. It was found that differences in the posttibial mucro were useful in sex determination: the female had a single, slender pointed spine with a premucro while the male had a bifurcated mucro (Everett and Newsom 1964).

However, the weevil populations in California and abroad are exclusively composed of parthenogenetic females, which is the form that has invaded much of the world's temperate rice production regions (Chen et al. 2005, Lupi et al. 2013). Parthenogenetic females reproduce by oogenesis without the aid of male genetic material. The mechanism of their reproductive differences has been a topic of interest to scientists in China who have examined gene expressions within the ovaries of rice water weevil. They found overexpression of genes involved with the formation of the mitotic spindle and signal transduction pathways such as beta-1 type tubulin, gephyrin, and nucleolar GTP binding protein. These protein products were expressed several fold higher than in the sexually reproducing weevils, indicating their possible role in parthenogenesis (Jiang et al. 2008). Researchers at Zhejiang University and Texas A&M University investigated the possibility of *Wolbachia* as a cause of parthenogenesis, but found that both sexual strategies of *L. oryzaophilus* required *Wolbachia* for oogenesis. Fecundity in all populations declined after treatment with

the antibiotic tetracycline (Chen et al. 2012). Further research into the weevil's reproductive biology found that temperature has an effect on oogenesis. Early season oocyte development is markedly affected by changes in temperature, but not affected later in the season. Ovariole length increased as temperature increased, which may explain the phenomenon of increasing voltinism in regions with higher seasonal temperatures (Shi et al. 2007).

Invasion and Spread. Pest invasions are typically fast and can spread within new territories in a short period of time. *L. oryzaophilus* fits this common model. When it reached Japan in 1976, the weevils expanded at a rate of 20–30 km per year and by 1986 had spread throughout the Japanese archipelago. Studies of their spread over Japan concluded that wind direction and speed aided their dispersal as opposed to anthropogenic forces (Asayama and Nakagome 1992). In China, *L. oryzaophilus*, or the American rice water weevil as it is called there, was first introduced from Korea in 1988. The dispersal rate of *L. oryzaophilus* was calculated at 36 km per year along the coast in southwest and northeast directions from foci in Zhejiang province. It was found that connectivity of early season rice fields was a major factor in the rate of dispersal as *L. oryzaophilus* moved through these rice corridors (Chen et al. 2005, Wang et al. 2011).

This knowledge of rice water weevil biology and ecology has led to the current methods of sampling and monitoring that have been in place for over 40 yr. It is a prerequisite for the development of monitoring and sampling methods that lead to effective management strategies for both conventional and alternative management methods.

Monitoring and Sampling

Effective pest management requires knowledge of the relative abundance of pests in the field and the ability to predict the severity of damage by pests. Researchers have developed sampling techniques to aid in the prediction of the severity of infestation of rice water weevil. Most of these techniques focus on the adults and the larvae, and in rare cases the egg stages.

Sampling rice water weevils at the egg stage is an option that is seldom used because it is not effective or practical in the field. Oviposition by rice water weevil is measured by counting the number of eggs within the rice sheath. This involves bleaching the plant tissue to reveal the eggs (Gifford and Trahan 1969b). This technique is useful for studying the effects of pesticides or other treatments on fecundity as was done with research on Dimilin (Chemtura, Middlebury, CT) in the 1980s (Smith et al. 1985) and most recently with thiamethoxam (Lanka et al. 2013a).



Fig. 5. Aquatic barrier trap used to sample rice water weevil adults and other aquatic.

That said, it is much more practical to sample the number of adult weevils in the field after flooding. The use of postflood applications of insecticides at the 3-leaf stage allowed for monitoring of weevil populations and adult feeding in the California water-seeded rice system. Aquatic barrier traps were developed as a way to assess rice water weevil adult populations taking advantage of adult swimming abilities to force them into small enclosures for counting after flooding but before rice emergence (Fig. 5, Hix et al. 2001). This technique was thought to be applicable as the insecticide management approach switched to pyrethroid insecticide treatments in the 2000s, but this method was never widely adopted (Hummel et al. 2012, Lorenz and Hardke 2013, Way and Espino 2014). So far the most appropriate method of monitoring for adults is to count the number of feeding scars on the leaf. This method offers an estimate of the level of infestation within the field, although it will not be necessarily indicative of the level of larval infestation, which is affected by injury tolerance, plant age, and temperature Cave et al. 1984). This gives the grower an opportunity to treat before larval eclosion and well before the larval reach peak densities 4–5 wk later (Morgan et al. 1989). Some agencies provide specific threshold for adult scouting techniques (Lorenz and Hardke 2013), but others may recommend treatment only if leaf scars and conditions for oviposition are present (Hummel et al. 2012, Flint et al. 2013).

There were some early attempts to measure field populations of weevils before flooding by sampling the levees. Sampling for weevils in levee vegetation takes considerable effort because of their patchy distribution and because they are ensconced at the base of bunch grasses. Sampling requires removing the bunch grass with the soil attached and submerging it in water to force the weevils to emerge to water surface (Choo and Rice 2007). This method may not truly reveal the extent of the rice water weevil adult populations in the spring and probably why is it never used (Gifford and Trahan 1969a).

The most commonly sampled life stage of rice water weevil for monitoring purposes is the larval stage. Larval populations are measured using cylindrical metal corers with a 10–12 cm depth and 10 cm diameter to sample the rice plant and the surrounding soil, although these dimensions may vary depending on the manufacturer. The sample is then washed through a sieve to count the number of instars and pupae (Stout et al. 2009, Way and Espino 2014). Core sampling is considered to be the most reliable method for quantifying larval populations, but only measures the population at a single moment and typically is a lower estimate of the true population (Espino et al. 2009). The method may be biased toward later stage instars, as the small and fragile first and second instars might be destroyed during the process (Wu and Wilson 1997).

All these methods help researchers determine the effects of treatments on the various life stages of rice water weevil. However, the coring method is not ideal for growers and pest management practitioners because it is time consuming especially given a large acreage. Leaf scarring is still an important indicator for pest presence and can provide information to inform a grower on possible management

actions. This is an area that is still in need of further research and development.

Rice Water Weevil Damage and Susceptibility

Rice water weevil can significantly reduce rice grain yields, with reductions averaging 10% and in some cases up to 25% yield loss. Adult damage does not reduce yields, but larval damage can inflict high yield loss through root pruning during the vegetative stage of rice (Zou et al. 2004b). This is the time when the plant is growing and has begun to put out tillers that will later develop panicles and rice grains. The mechanism for yield reduction is through the reduction of grains per panicle and loss of tillers, which in effect amplifies the overall effect of larval root pruning (Zou et al. 2004c). Early reports of control efforts found a yield recovery up to 614 lb/acre rice when the field was treated at the most optimum time (Gifford and Trahan 1975). Bowling found that immediately spraying one week after flooding gave the best yield recovery of over 500 lbs/acre compared with a 100 lbs/acre recovery two weeks after flooding (Bowling 1976).

It is still difficult to develop action thresholds based on adult densities because of poor correlation between adult density and yield. Tolerance, plant age, and flood regime are just some of the factors that confound these data because high adult densities do not necessarily translate into corresponding larval densities (Zou et al. 2004c). Rice plant age is an extremely important factor that has been known to affect tolerance of injury (Bang and Tugwell 1976). Experiments manipulating timing of infestation found that later stage tillering rice plants did not show a relationship between yield loss and larval density as it did with early and mid-stage vegetative rice plants (Stout et al. 2002a).

Later research confirmed that rice plants are vulnerable to damage from the early vegetative stage to the reproductive stage; however, no choice experiments by Stout showed that there are preferences by the rice water weevil. Tillering plants were more often chosen by females, and it was suggested that this was because of the availability of numerous oviposition sites on the individual plant (Stout et al. 2013). Even the presence of symbiotic fungi can affect weevil preference. Ecological studies on the effects of arbuscular mycorrhizal associations in the rice rhizosphere revealed an increased preference for oviposition by rice water weevil, but the mechanisms have not been resolved as to why this occurs (Cosme et al. 2011).

Even with these confounding factors, researchers have been able to derive threshold to guide growers on when it is most appropriate to treat. In California, the action threshold is 1 adult rice water weevil found per trap per day in the first seven days of flooding or 1 larva per plant per core (Flint et al. 2013). If 20% of the plants had scarring from rice water weevil adults on either of the two newest rice leaves, then treatment is recommended (Flint et al. 2013). In the Arkansas, it may be as high as 10–20 larvae per core. In drill seeded the rice thresholds are based on scars per group of 40 plants. The minimum threshold for treatment is 40 scars in the first group of 40 plants that are checked (Bernhardt 2012). In Louisiana, the larval action threshold is an

average of 5 larvae per core comprised from at least six samplings of the field (Hummel et al. 2012). Studies from Texas and Louisiana reported that an average of 1 larvae found per core for series of samples from the field contributes to an estimated loss of 1% in yield (Zou et al. 2004a, Lorenz and Hardke 2013).

Rice Water Weevil Management

Management depends on various chemical and cultural controls in both California and the southern United States and on the type of rice production system, water or drill-seeded rice (Bowling 1960, Hill et al. 1994). The drill-seeded system that is predominate in the southern United States allows for the rice plant to develop to the 4–5 leaf stage (or larger) before the permanent flood is applied. Drill-seeding delays plant exposure to rice water weevil until the permanent flood is applied, and this system generally has a higher yield in the southern United States because of better percentage germination and other cultural factors (Bernhardt 1998). California uses a water-seeded production system primarily as a means to aid in weed management. In this system, the pregerminated seeds are aerially deposited directly into the flooded field (Flint et al. 2013). There are other major differences between rice productions in these two regions that potentially impact management of rice water weevil. In the southern United States, rice production includes multicropping crayfish with rice and the growing of a second (ratoon) crop (Hummel et al. 2012). In California, there is a high level of environmental scrutiny in California given that the aquatic rice agroecosystems are linked to the Sacramento River waterway, providing drinking water to many urban areas, and ultimately to the San Francisco Bay estuary (Hill et al. 1994).

Despite these differences in rice production, in both types of systems, draining rice fields was the primary control method for rice water weevil but by the mid-1960s it was discontinued because it was unreliable and because of the availability of effective insecticides (Everett 1966). Research into other alternative methods for controlling rice water weevil has yielded mixed results. Research for integrated management has explored various cultural controls such as changes in fertilization and seeding rate, various biological controls with nematodes and microbial pesticides, and host plant resistance (Bowling 1963a, Rice 1996, Stout et al. 2001). Even so, insecticides remain to be the most important management option for growers. These findings are highlighted in the following sections.

Insecticides. Whitehead conducted the first experiments with insecticides against rice water weevil from 1952 to 1953 where he tested organochlorines and found he could achieve 80% control with aldrin and heptachlor. Research with synthetic insecticides experimented with different delivery methods of aldrin, heptachlor, and dieldrin such as emulsifiable powders mixed with fertilizer, and seed treatments (Bowling 1957, 1959, 1961; Mathis and Schoof 1959). Seed treatments with aldrin were recognized as the best method for control (Bowling 1965, Gifford et al. 1972). However, as is the trend with pesticide use, resistance began to build up and was detected in a few populations in Texas in 1968, which spurred research into alternatives to aldrin and dieldrin (Graves et al. 1967, Bowling 1968, Donoso-Lopez and Grigarick 1969, Gifford and Trahan 1971). The LD₅₀ for aldrin had increased almost 500% from 0.19 micrograms per weevil in 1966 to 5.50 micrograms per weevil in 1972 (Bowling 1972a). Granular carbofuran became an effective alternative to aldrin beginning in 1969 as a pre-flood treatment (Bowling 1976). Other options such as chitin synthesis inhibitors (benzoylureas) and pyrethroids were first tested in the early 1980s. Fenvalerate was noted as having similar control as carbofuran, with the added bonus of having higher toxicities at low temperatures (Rahim et al. 1981). Trimifluron and diflubenzuron were also tested and found to have ovicidal activity and increased mortality in first-instar larvae (Smith et al. 1985, Smith and Grigarick 1989). However, it wasn't until the 1990s that pyrethroids and benzoylureas were given serious consideration as a viable replacement to carbofuran (Way and Wallace 1996). In addition, fipronil was

widely researched and found to provide outstanding rice water weevil larval control (Rice et al. 1996, Godfrey and Palrang 1996, Godfrey and Cuneo 1998, Sandberg et al. 1998, Weiland et al. 1998). Registration of carbofuran was cancelled in 2000 because of concerns over resistance and environmental health (Way and Wallace 1992, Bedient et al. 2005). By 2000, lambda-cyhalothrin had completely replaced carbofuran as the leading pesticide in California and the southern United States (California Department of Pesticide Regulation [CDPR] 2000, Stout et al. 2000). This switch not only involved a change in active ingredient but also in application timing and approach in California, i.e., from pre-flood application to a post-flood application. Fipronil was available for use and widely used for a few years during the mid-2000s in southern rice (since removed from the market) and was never approved for use in California because of environmental impacts and nontarget effects that harmed crayfish production (Mize et al. 2008).

Chemical control is still the main management option for growers against rice water weevil (Flint et al. 2013, Stout et al. 2009). In California, there are four registered compounds that are commonly used against rice water weevil: the pyrethroids lambda-cyhalothrin (Warrior [Syngenta, Greensboro, NC]), zeta-cypermethrin (Mustang [FMC Corporation, Philadelphia, PA]), gamma-cyhalothrin (Declare [Cheminova, Inc., Research Triangle Park, NC]), and the insect growth regulator diflubenzuron (Dimilin [Chemtura, Middlebury, CT]), which is an insect growth regulator and chitin synthesis inhibitor (Godfrey et al. 2007, CDPR 2011). Clothianidin (Belay [Valent USA Corp., Walnut Creek, CA]) was registered in 2013 and is gaining acceptance in the marketplace. Of the botanical insecticides only azadirachtin, which is a compound from the neem tree (*Azadirachta indica*), is approved for use in California. It functions as an antifeedant and can deter oviposition (Schmutterer 1990), but it is not in current use (CDPR 2014a). These same active ingredients and classes are registered for use in the southern U.S. rice production areas with a few differences.

Currently, neonicotinoids have been registered for use in some form across all the rice producing states. Thiomethoxam, under the trade name Cruiser Maxx or Cruiser 5FS (Syngenta), is approved as seed treatment in drill-seeded rice in Louisiana, Texas, Missouri, Mississippi, Arkansas, and for dry-seeded rice in California. Seed treatments have not been proven to be effective in the California water-seeded system, thus pre-flood and post-flood applications are used. Clothianidin, under the trade name Belay (Valent USA Corp.) is a sprayable formulation and Nipsit as a seed treatment are approved in all the rice producing states (Lanka et al. 2012a, Lorenz and Hardke 2013, CDPR 2013, 2014b, Way and Espino 2014). For southern U.S. rice growers that follow a rice–crayfish rotation, there is a recommendation to use neonicotinoids, as pyrethroids are acutely toxic to crayfish (Barbee and Stout 2009). The neonicotinoids function by affecting nicotinic acetylcholine receptors to impair nerve function in insects exclusively (Lanka et al. 2014). In addition, southern states have the option of using Dermacor-X-100 (DuPont, Wilmington, DE) seed treatment whose active ingredient is chlorantraniliprole, which belongs to a new class of chemistry called the anthralic diamides. Anthralic diamides such as chlorantraniliprole function by disrupting the ryanodine receptors that control the flow of calcium from the sarcoplasmic reticulum and thereby impair muscle function (Lanka et al. 2012b). Chlorantraniliprole has the advantage of having less acute toxicity to crayfish than pyrethroids, making it less likely to interfere with rice–crayfish production systems (Barbee et al. 2010). The primary focus of research with these compounds is on improving the effectiveness of their use (Barbee et al. 2010, Lanka et al. 2013b). Seed treatment options are made attractive to growers and researchers because of the additional pressures by grape colapsis (*Colaspis brunnea*), rice stink bug (*Oebalus pugnax*), rice stalk borer (*Chilo plejadellus*), and the Mexican stem borer (*Eoreuma loftini*; Taillon et al. 2014, Thrash et al. 2014).

Despite their effectiveness, it should be noted that maintaining a high reliance on synthetic insecticides continues a tradition where an insecticide is used until the pest becomes resistant. The threat of resistance to insecticides is particularly ominous when considering the use of seed treatments, which are proactive and dose the environment before any threat of pest pressure. This raises the danger of rice water weevil developing resistance quickly as it did against aldrin (Bowling 1968). Fortunately, we have yet to see resistance to the current insecticides classes of pyrethroids or neonicotinoids in rice water weevils.

Cultural Control. Before the use of insecticides, cultural controls were the only options available to growers. Draining fields, levee weed control, and delayed planting are cultural methods used to mitigate rice water weevil pest pressure on rice that have been used at some point in the history (Hesler et al. 1992, Reay-Jones et al. 2008, Stout et al. 2009). Today there are additional options available to growers such as winter flooding, delayed flooding, manipulation of flood depth, and nutrient augmentation. Each will be discussed in the following sections.

Draining. Draining rice fields was the first recommended treatment for dealing with rice water weevil because it was assumed that soil dryness contributed to mortality (Isely and Schwardt 1930). In the southern United States, it was found that early drainage was comparable to applying carbofuran in controlling rice water weevil adults after a 1–3 d drain (Morgan and Tugwell 1984). However, the tactic was unreliable because of secondary infestations and negative net returns in all the drained plots (Thompson et al. 1994b). It was also noted that it interfered with weed management (Quisenberry et al. 1992, Stout et al. 2009). However, due to the presence of other pressures from other pests, rice production guidelines from the southern rice belt still list temporary draining or flushing of paddies as an option for control (Hummel et al. 2012, Lorenz and Hardke 2013, Way and Espino 2014).

In California, draining was found to be an effective option to deter adult feeding and to stop oviposition. It did not affect the survival of the eggs or larvae. The longer the duration of the drainage the greater the effects on the rice water weevil adults, but not against the early life stages of the weevil. It reaffirmed previous observations that drainage could interfere with weed control in addition to mosquito biological control that required the addition of fish (*Gambusia*) to the rice field (Hesler et al. 1992). It also provided protection from crayfish that are occasional rice seedling pests (Hesler and Grigarick 1992). There has been an increasing trend of growers draining fields to expose the soil and emergent weeds for full exposure to contact foliar herbicides (Greer et al. 2012). In addition, draining several days after seeding in California is often used to facilitate stand establishment. In this case, drainage may be an option for rice water weevil control if maintained long enough to deter rice water weevil oviposition and allow for the rice plant to mature. However, it remains to be seen if this combined tactic for weed management is effective.

Research with field draining has led to the current consensus that water is the biological cue that attract female weevils to oviposit in rice paddies based on studies where the timing of flood was manipulated. Even though draining itself is not effective in mitigating damage by weevil larvae, it has led to several tactics that exploit this biological cue for oviposition (Isely and Schwardt 1934, Hesler et al. 1992, Quisenberry et al. 1992).

Flood Depth. An extension of the work with draining is the direct manipulation of flood depth. Research to examine flood depth as a cultural control against *L. oryophilus* found fewer larvae at 5 cm depth compared with 10 cm flood depth (Stout et al. 2002b). The latest research on this topic expanded the scope of the study to Arkansas and Missouri and found that the number of larvae per core increases as flood depth increases. However, shallow flooding by itself is not a sufficient replacement for chemical control and it was recommended

that it should be part of an integrated approach for *L. oryophilus* control (Tindall et al. 2013).

Delayed Flood Timing. Another variation of using water management as a cultural control method for rice water weevil is the manipulation of the timing of flooding. The rationale for this method is to delay the onset of oviposition by rice water weevils, allowing the plants in a drill-seeded system to gain additional growth, without wasting water resources as is done with draining (Rice et al. 1999). In fact several studies from Louisiana have shown that early flooding is strongly correlated with heavy yield losses. In one study, early flooded plots had a 22% reduction in yield as compared with late flooded plots that experienced a 10.8% reduction in yield from weevil damage (Stout et al. 2002b). Further studies found that the reason for this apparent tolerance was that the mature rice plant was tolerant to rice water weevil damage compared with younger rice plants. It was recommended that delayed flooding combined with insecticide use could achieve better control together than individually (Zou et al. 2004c). The tactic of delayed flooding fits well with the drill-seeded system that is predominant in the south, but is not applicable to the continuously flooded water-seeded rice system used in California where the rice plant has greater temporal exposure to rice water weevil infestation (Stout et al. 2013). In Louisiana, the related method of delayed flooding was demonstrated to reduce weevil damage because older rice plants are better at tolerating larval feeding damage (Stout et al. 2002b).

Winter Flooding. Rice growers in California have traditionally burned fields after harvest to aid in disposal of the rice straw. However, burning also produced many pollutants, negatively impacting the air quality in the Sacramento Valley. State legislation was passed to significantly reduce the practice of rice burning between 1990 and 2000 and to address these air quality concerns (Elphick and Oring 1998). Since 2000, ≈10% of the acreage has been burned annually, allowed under the law as a means to mitigate plant diseases (California Rice Commission 2014). Growers widely adopted the use of winter flooding, from November to March, as a cultural method to aid in straw decomposition (Fig. 6). This method has several other benefits including waterfowl habitat and possible implications on pest management (Elphick and Oring 2003). California researchers examined the effects of winter flooding and four direct straw manipulation techniques (burning, baling, incorporation, and rolling) on several aspects of rice production with each treatment replicated four times in ≈2.5 acre plots. Populations of rice water weevil larvae were reduced by winter flooding by 41.5–74.2%, with reductions occurring six of the seven years of the study (L.D.G., unpublished data). During one year, excessive winter precipitation (19.9 inches from 1 January to 1 April) resulted in all plots being flooded and the resulting larval populations the following spring were equivalent across the two “treatments.” The four direct straw manipulation treatments had no effects on larval populations (Godfrey and Cuneo 2002). The mechanism through which winter flooding effects rice water weevil populations has not been experimentally determined.

Planting Date. Manipulation of planting date has been examined as a method for reducing the impact of rice water weevil. The rationale for this method is to reduce the rice plants exposure to rice water weevil during the period it is most vulnerable to the pest (Stout et al. 2011). In China, delayed transplanting by 3–4 wk was effective in reducing damage to yields (Chen et al. 2005). In Louisiana, planting date was found to have a greater effect on yield than carbofuran treatments and earlier planting was recommended because late season rice was more susceptible to damage (Thompson et al. 1994a). In southeastern Texas, delayed planting returned mixed results because when growers planted on optimum planting dates, higher yields were associated with higher populations of rice water weevil. But unlike in Louisiana, late season rice was more tolerant to rice water weevil damage (Espino et al. 2009). These differences in planting date



Fig. 6. A harvested field that is being flooded for the winter in the Northern Sacramento Valley. A common practice by growers when water availability is not an issue.

response between different production areas may be related to variation between rice varieties and the environmental conditions. This type of cultural control is impacted by the plant development as well as the pest population dynamics. In southern U.S. rice production, early planting has become an important tactic for avoidance of heavy infestations because weevil emergence from overwintering sites is not yet complete. By planting early, the grower is faced with a lighter weevil infestation that can be more easily managed with insecticides and therefore minimize yield losses compared with planting later in the season (Rice et al. 1999, Stout et al. 2011).

Weed Management. Weed removal from adjacent areas of the field is a tactic that can be used to control rice water weevil (Grigarick 1992). Weeds are an important food source for weevils before rice planting and help induce flight muscle regeneration and ovariole development. Weed removal during the rice harvest can deprive weevils of local areas used for diapause. Early season weed removal reduces the favorability of the area for weevils that are in flight (Palrang et al. 1994). Researchers in China found that weed removal was most effective after weevils had entered the early stage of oviposition development. Data from studies on delayed planting had shown that weevils that had not fully restored their metabolic functions from diapause are less susceptible to mortality from starvation (Jiang and Cheng 2003b). Jiang and Cheng found that early ovipositional stage weevils suffered more mortality from starvation than preovipositional weevils that had not begun ovariole development. Removal of levee vegetation could possibly serve as a mechanism of control if done at the right time by allowing the weevils to feed on the weeds to restore metabolic function. This would be then followed by weed removal to starve the weevils (Jiang and Cheng 2003b).

Nutrient Augmentation. Several studies have examined fertilization as a means of enabling the rice plant to recover from weevil induced root damage. It was thought that root pruning reduced the uptake and availability of nutrients to the plant, but nitrogen fertilization studies in Texas and Louisiana in the presence of rice water weevil demonstrated that this is not the case. Nitrogen fertilization did not increase tolerance of rice plants to rice water weevil injury (Zou et al. 2004a, Way et al. 2006, Reay-Jones et al. 2008). However, the effect of rice water weevil damage on the uptake of other essential nutrients has not been investigated. Preliminary studies on the uptake of silicon into the rice in the presence of rice water weevil has shown that the pest does not affect the uptake of that micronutrient and the addition of silicon does not add further protection to the plant (M.-A.A. and L.D.G., unpublished data).

Host Plant Resistance. Research in plant resistance to rice water weevil began in the early 1960s with variety trials to identify the plants that had the least damage, but larval populations did not differ between the experimental lines and varieties that were tested. In some cases there was insufficient yield or that a final recommendation could not be reached due to complications in analysis (Bowling 1963b). Bowling later developed an early screening method designed with a focus on adult preference for oviposition and the survival of early instars (Bowling 1972c). Work continued in both California and Louisiana throughout the 1970s and 1980s but of the thousands of experimental lines and varieties tested, one variety in California and only four of exotic origins were found to show any resistance to rice water weevil (Gifford et al. 1975; Grigarick et al. 1986). Beginning in the late 1970s, a large cooperative effort had begun among researchers on finding new cultivars resistant to rice water weevil, looking at every variety grown in the United States since 1900 and in international seed banks. Eleven experimental lines and varieties were found to show consistent reactions that suggested resistance and two varieties exhibited some tolerance (Smith and Robinson 1982). After initial screenings in California during the 1970s, another series of studies revealed a variety that was tolerant to rice water weevil damage and had fairly desirable agronomic traits (Grigarick and Way 1982). However, the conclusions from these early studies were that crosses with varieties with more desirable agronomic traits were needed.

By the mid-1980s, research on host plant resistance had focused on identifying the type of host plant resistance in the resistant lines and their comparative performance in insecticide treated and untreated plots, recovery periods, and yields (Grigarick et al. 1986). The variety M-9 and experimental line 2404 demonstrated tolerance as opposed to antibiosis (Grigarick et al. 1988). The research on California tolerant experimental lines eventually ended with the attempted development of the PI5062130 line which had low levels of tolerance, but the program was eventually ended in 2003 following few gains in agronomic traits.

In the south, research into host plant resistance followed a similar trend. Researchers at Louisiana Agricultural Experiment Station conducted a series of trials in 1990 to detect the following types of host plant resistance, antixenosis, antibiosis, and tolerance, in over 66 lines and varieties (N'Guessan and Quisenberry 1994). Their work revealed two experimental lines that were tolerant to rice water weevil damage and could recover from damage. Trials in 1992 showed two varieties with antixenotic properties as evidenced by low populations of weevil

larvae. However, all these varieties had very low yields compared with the susceptible varieties and it was suggested that their germplasm could be used for the development of high yielding resistant varieties as had been demonstrated in the 1970s (Gifford and Trahan 1976). Additional tests on the tolerant experimental lines 953527 and 952836 revealed that they lacked appropriate agronomic traits; they were either too prone to lodging or the grains were too small (N'Guessan et al. 1994a,b,c). Since then research into host plant resistance seems to have halted, as the prospect of direct genetic modification has introduced the possibility of transgenic rice, such as herbicide-resistant rice that was introduced into Louisiana in the early 2000s (Tindall et al. 2004a) and Bt rice in Korea (Lee et al. 2013). Ultimately the goal of this research is to integrate it with other tactics to create an effective management plan that reduces rice water weevil damage below action thresholds (Stout and Davis 2009).

Transgenic Rice. Glufosinate-resistant rice produced under the name Clearfield is a not a true genetically modified organism; it was produced through mutagenesis and traditional breeding techniques to confer tolerance to imidiazolinone herbicides. Libertylink is another glufosinate-resistant technology that was produced through recombinant DNA technology, but it was never commercialized for business reasons (Lemaux 2007). Researchers at Louisiana State University examined the effect that these lines would have on rice water weevil populations and found no differences in larval populations between the untransformed and transformed lines. However, the differences in management require the glufosinate-resistant rice fields to be drained, which may positively impact management of rice water weevil (Tindall et al. 2004a).

In the case of the insect-resistant transgenic rice, research from Korea reports on newly developed Bt rice transformed with the Cry3A gene. This Bt endotoxin had been shown previously to cause mortality in beetle pests through diet bioassays (Krieg et al. 1989). Experimental data over six years showed a significant drop in the number of weevil larvae found on the transgenic plant (Lee et al. 2013). The status of such a management approach for rice water weevil in the United States remains to be seen.

Biological Control. There is a very sparse record in the literature concerning biological control agents and methods for rice water weevil. There have been reports of long-horned grasshoppers and katydids feeding on adult weevils in Arkansas, but the extent of its use in management is unknown (Lorenz and Hardke 2013). The first recorded entomopathogenic organism in rice water weevil was a mermithid nematode emerging from a rice water weevil collected in the vicinity of Stuttgart, AR, in the 1970s (Bunyarat et al. 1977). It was found to be exclusively infesting female weevils in field surveys from 1973 to 1976. The nematode reduced fecundity and led to peaks of mortality in June and August. This led researcher to consider *Steinernema carpocapsae* as a possible biological agent against rice water weevil in Japan. It was found to cause mortality under laboratory settings but failed to work in the field (Nagata 1987). In Cuba, there was success using *Steinernema* spp. against the rice water weevil with up to 80% control in field trials (Carbonell 1983). In California, research with both *Steinernema carpocapsae* and *Heterorhabditis* spp. found that nematodes provided control of rice water weevil larvae when applied to drained soil that was reflooded 8 d later (Grigarick and Orazé 1990). However, the widespread application or adoption of nematodes against rice water weevil in Asia or North America has not been possible for economic reasons (Choo and Rice 2007).

In the 1980s, ecological studies were done on the spider fauna in a rice paddy agroecosystem and their possible roles as top down control of rice water weevil (Orazé et al. 1988). *Pardosa ramulosa* (McCook) was found to fit the role of a biological control agent. It had one generation per year and its populations peaked on the levees before field flooding, similar to the rice water weevil life cycle (Orazé et al. 1989). However the spider was found to be a better at controlling populations of the aster leafhopper (*Macrosteles fascifrons* Stål) than

rice water weevil. In addition, densities 22 spiders per square meter resulted in spider cannibalism events (Orazé and Grigarick 1989).

Current research at Louisiana State University has looked at the possibility of building up higher guild predators to feed on rice water weevil through the addition of manure to rice fields before flooding. The idea behind this research is that the manure is used to attract detritivores that would further attract predators that could reduce the population of rice water weevil adults in the field (Mercer and Stout 2014). The success of this approach is uncertain at this time.

Microbial Control. Of all the alternatives available and reported herein, the most promising may be opportunities with the entomopathogenic fungi *Beauveria bassiana* (Vuillemin) and the soil bacterium *Bacillus thuringiensis* (Berliner). The entomopathogenic fungus, *B. bassiana*, releases spores that drill through the cuticle of the insect exoskeleton and produce mycelia inside the body of the insect that kill it in the process. The mycelia grow into fruiting bodies that are released from the body of the insect to continue the life cycle (Flexner et al. 1986, Copping and Menn 2000). The mode of action for *B. thuringiensis* is the release of a crystalline spore that contains an endotoxin that disrupts the lining of the larval midgut peritrophic membrane. The spores are ingested as the insect feeds on plant tissue in its larval stage (Garczynski and Siegel 2007).

Beauveria bassiana. Research into the use of *Beauveria bassiana* against rice water weevil began in the early 1990s in California, Louisiana, and Japan. Studies conducted in California with *B. bassiana* found that it controlled 91% of adults within 14 d of treatment but found very little efficacy against the larvae (Godfrey et al. 1993). In Louisiana, native *B. bassiana* fungal spores were isolated from infested rice water weevils and similar results were found (Urtz and Rice 1997). Researchers found that environmental persistence of the conidia dropped by 90% in the field within 48 h of treatment, but the addition of UV protectants improved persistence (Rice 1996). However, the team also found that microorganisms that live on the rice plants inhibited *B. bassiana* growth. In Japanese field studies, both *B. bassiana* and *Metarhizium anisopliae* (Metschnikoff) were found to infect rice water weevil at a high level, but it took 3–9 d to kill the weevil. This was enough time for the infested weevils to oviposit and to nullify the effect of mortality on the adults (Yoshizawa 1992). Recent research with entomopathogenic fungi includes *Metarhizium anisopliae* testing in China, but it was found to have very low control on rice water weevil (Chen et al. 2000).

Bacillus thuringiensis. In the 1990s, there were tests of various *B. thuringiensis* spp. *tenebrionis* products for effectiveness against rice pest (Rice 1998). One such product was Novodor that proved very successful and on par with chemical pesticides in its efficacy against rice water weevil (L.D.G., unpublished data). However, the company that manufactured Novodor was bought and merged into another company. Tests of the product after the merger did not show the same efficacy, and it was believed that the bacteria strain and formulation had been lost. Recently Phyllo Bioproducts LLC, a biopesticide company based in the San Francisco area, has been working with a product based on *Bacillus thuringiensis* spp. *galleriae* for use against turfgrass grub pests. The products are derived from the Cry toxin of the bacteria *B. thuringiensis* spp. *galleriae*, which has been previously shown to be effective against Scarabeid grubs (Asano et al. 2003). The greenhouse and field trials showed some effectiveness against rice water weevil, and tests in 2012 and 2013 showed a similar performance to lambda-cyhalothrin (M.-A.A., unpublished data). This area of research has much potential in the future.

Future Directions

In the southern United States, the current focus of rice water weevil management is on finding new synthetic pesticides that can be applied as effectively as possible. In China, the focus of management is on implementing landscape-level changes in agricultural cropping sys-

tems and quarantine actions to prevent the spread of rice water weevil farther into mainland China (Wang et al. 2011).

However, research into alternative strategies requires further knowledge of the biology of the insect (Zou et al. 2004b). There are still many questions that remain unresolved regarding the biology of the rice water weevil. In California, rice water weevil experiences periodic boom and bust cycles that have not been sufficiently explained. Knowledge of below ground herbivory and plant defenses remains a relatively unexplored area of research particularly in regard to rice water weevil (Van Dam 2009).

Interactions between foliar and root herbivory is also a relatively unexplored area, which is of particular importance in rice production areas with both types of feeding pressures. A study in Louisiana did find that rice acted as a medium of competition between rice water weevil and fall armyworm, but the impact on management is uncertain (Tindall and Stout 2001). A similar study that expanded on the foliar and root herbivore interaction found that armyworm-injured plants had greater resistance to rice water weevil as evidenced by the lower number of eggs on treated plants. It was found that applying jasmonic acid to rice plants caused a similar decrease in the number of eggs found on the plant and the number of larvae in the first set of sampling. However, the commercial use of jasmonic acid as an elicitor to reduce damage by rice water weevil is hampered by high costs and lack of reliability (Hamm et al. 2010).

Another area of interest is the microbiota within the digestive tract of the rice water weevil. Recent work on the bacteria within the midgut of the rice water weevil showed very low diversity. The applicability of this research is to finding suitable bacteria that can be transformed to cause mortality to overwintering weevil or reduce their fecundity (Lu et al. 2013).

Another important unknown is the mechanism for decreased tillering response to root pruning (Zou et al. 2004a). It had been initially assumed to be caused by poor nutrient uptake but that does not seem to be the case as seen in nitrogen fertilization studies in the United States (Way et al. 2006, Reay-Jones et al. 2008). One could speculate that it has to do with strigolactone, a class of plant hormones that has been found to inhibit tillering in rice (Arite et al. 2009). The Jasmonic acid pathway that regulates wound response (Bari and Jones 2009) could be upregulating strigolactones in response to weevil attack, but this is speculation at this point. The physiological plant response to rice water weevil wounding is an area that needs study.

Conclusions

The rice water weevil was exclusively a problem of New World rice production until the 1970s. The increasing volume of trade between nations heightened the likelihood of an invasion as demonstrated in the literature on invasion biology (Simberloff 2013). The rice water weevil parthenogenetic phenotype that has become invasive is of minor importance in its native range. The ability to reproduce without males and its increased fecundity gives parthenogenetic rice water weevil a great advantage to expand its range across Eurasia given the increase in trade and travel. Cultural controls that were developed in the 1910s are largely not favorable because of the cost of water and interference with the individual pest management program of growers, but delayed flooding and delayed planting are viable options. The development of anthranilic diamides and neonicotinoids offer new conventional options for growers to replace pyrethroids. *B. thuringiensis* endotoxin offers growers a more environmentally friendly option, but more research must be done to find the most effective formulation and delivery system. There are still more questions that need to be answered regarding the differences between the sexual and parthenogenetic reproducing weevils, which could help reveal possible methods for providing more effective control of this pernicious pest.

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